Songbird species diversity and its relationship to vegetation composition and structure in Black Rock Forest, Cornwall, NY

Sarah Jean Gilly

Department of Environmental Science

Barnard College, Columbia University

sjg2142@barnard.edu

Mentor: Terryanne Maenza-Gmelch, Ph.D.

Barnard College Dept. of Environmental Science

tm263@columbia.edu

Adviser: Natalie Boelman

Lamont Doherty Earth Observatory

nboelman@ldeo.columbia.edu

December 11th, 2012

TABLE OF CONTENTS

Abstract 3

Introduction 4

Methods 6

Results 11

Discussion 14

Conclusion 16

Acknowledgements 17

References 18

FIGURES AND TABLES

Figure 1 7

Table 1 8

Figure 2 10

Figure 3 11

Figure 4 12

Figure 5 13

Figure 6 14

ABSTRACT

Forest birds keep forests healthy by performing important ecosystem services such as insect control and seed dispersal. Threats to forests such as habitat loss due to fragmentation, invasive species and fire suppression, among others, are having negative impacts on birds. Black Rock Forest (BRF), in Cornwall, NY, is a forest rich in flora and fauna that acts as an important connector of other green spaces. In an attempt to identify biodiversity hotspots we characterized the songbird populations of BRF in six habitats within the forest, which we categorized as either structurally homogeneous or structurally heterogeneous. By creating a habitat-based and long-term database of bird populations and vegetation structures, we hoped to be able to determine the relationships between our habitat metrics and songbird community size and richness. At each of our study sites we conducted a vegetation survey with horizontal and vertical components and collected 100 minutes of bird point- counts throughout May, June, and July of 2011 and 2012 in order to assess whether pant species richness or vertical canopy complexity was more important in encouraging bird species richness. In general, we found that heterogeneous habitats were more frequented by birds and had higher bird species richness values compared to homogeneous habitats. Throughout the study we also took note of several birds, including the Acadian flycatcher (*Empidonax virescens)* and chestnut-sided warbler (*Dendroica pensylvanica)* that are known to be dependent on specific habitats that could be at risk of changing at BRF. Our results suggest that forest management should work to preserve the heterogeneous nature of these habitats in an effort to preserve Black Rock Forest's rich songbird diversity and the ecosystem services they provide.

INTRODUCTION

The important mutualism between forest birds and forests has been well documented. Maintaining bird biodiversity contributes to ecosystem biodiversity, which is important due to the vast array of ecosystems services a healthy forest can provide – limiting the spread of infectious diseases (Keesing *et al*. 2010); decomposition, pollination and seed dispersal (Sekercioglu *et al.* 2004); and general forest health. Marquis & Whelan (1994) highlighted the role that insectivorous birds play in facilitating tree growth by gleaning leaf-chewing insects. However, despite these benefits, there has been a measured decline in many bird species globally (Keesing *et al.* 2010) and in New York State (Smith & Marks 2008). One of the greatest threats to songbird communities is habitat loss due to forest fragmentation (Flather & Sauer 1996, Donovan & Flather 2002). Anthropogenic development associated with this fragmentation also increases the risk of nest predation (Borgmann & Rodewald 2004) and cowbird parasitism (Robinson & Wilcove 1994). Avian communities are known to be sensitive to development and the negative affects are only likely to increase as development increases (Pidgeon *et al.*2007).

Other causes of songbird population declines are the result of forest modifications via plant diseases such as hemlock woolly adelgid (Orwig *et al.* 2002), biological invasions (Borgmann & Rodewald 2004), deer browsing (deCalesta 1994), fire suppression (Saab & Powell 2005), and storm damage and natural succession (Holmes & Sherry 2001). Given that climate change will likely intensify these disturbance regimes we must prepare ourselves to buffer against these changes in the coming years in order to preserve songbird species and their habitats.

The first step in preservation is to determine where birds are in the forest and how they are related to their local habitats. This can be done with bird census counts and various vegetation surveys. In doing so it is also important to note the location of any specialist species, especially those who may be at risk of severe population declines. For example, Acadian flycatchers rely heavily on the structure provided by the eastern hemlock (*Tsuga Canadensis*) (Tingley *et al.* 2002), which is currently being attacked by the hemlock woolly adelgid (Orwig *et al.* 2002). By taking note of species like this one can observe the changes in presence and abundance over time. However, since many species do not rely on a certain plant species in this way it is beneficial to have a general understanding of bird populations and the habitats they occupy.

Whether or not habitat heterogeneity and vertical canopy complexity or plant species richness is more important in encouraging associated animal species richness has been debated in the literature. There have been studies done as far back as the 1960s that looked into these relationships. MacArthur & MacArthur (1961) found foliage height profiles to be a good predictor of bird species richness. Similarly, Freemark & Merriam (1986), Goetz *et al.* (2007), and Verschuyl *et al.* (2008) determined that habitat heterogeneity and structural complexity were the strongest predictors of bird species richness. Additionally, Murdoch *et al.* (1972) found plant diversity to be the more important factor in determining the relationship between plants and insects while, on the other hand, Dennis *et al.* (1998) and Brose (2003) found that vegetation structure was more important in determining associated insect diversity. Although it can be difficult to determine which vegetation metric truly is the most strongly correlated with animal species richness, most bird species, especially migratory songbirds, are significantly correlated with at least one landscape variable (Lichstein *et al.* 2002).

Considering this debate and the point made by McGowan and Corwin (2008) that no published studies from New York have simultaneously and continuously tracked changes in both songbird communities and vegetation communities over substantially long periods of time, we have begun to establish permanent forest-wide and habitat-based bird survey points at Black Rock Forest (BRF) in order to develop this long-term database of bird populations in relation to habitat change. The objective of the current study is to determine to what extent plant species composition and/or vertical canopy complexity drive songbird community size and richness. We hypothesized that vertical canopy complexity is more important to songbird community size and richness than plant species richness due to our prediction that a variety of structural layers could host a greater number of bird species with different nesting and foraging preferences.

METHODS

Study Site

Black Rock Forest (BRF) in Cornwall, NY makes up nearly 4,000 acres of mixed deciduous forest in the Hudson Highlands. The forest is dominated primarily by red oak (*Quercus rubra*), which, along with chestnut oak (*Q. prinus*), makes up 66% of the forest's basal area. The next most common species is red maple (*Acer rubrum*), which accounts for only 8% of the basal area but has the highest overall stem count (Turnbull *et al*. 2002). The wide variety of habitats found in this mixed deciduous area make BRF an ideal candidate for a study of bird communities and their potential reliance on certain vegetation structures.



Fig. 1: Map of Black Rock Forest (google.com/maps) with stars representing the six habitats used in the study.

The habitats chosen to focus our study on (Figure 1) are three slightly varying hemlock-hardwood swamps; brushy cleared land & deciduous woods; a shrub swamp; and successional upland woods (Edinger *et al.* 2002). The habitat site names are Aleck Meadow Exclosure, the Stone House, Mineral Springs, Aleck Meadow Roadside, Jim's Pond, and Two Gates, and they will hereafter be referred to as Hom 1, Hom 2, Hom 3, Het 1, Het 2, and Het 3, respectively (Table 1).

Table 1: Observation-based, qualitative habitat description of the six study sites at BRF. Codes will be used in subsequent figures to refer to habitats.

Site	Code	NYS Ecological Community Type (Edinger *et al.* 2002)	Perceived Structural Vegetation Complexity	Vegetation Description
Aleck Meadow Exclosure	Hom 1	Hemlock-hardwood swamp	Homogeneous	Largely Hemlock forest with American Beech and other tree species as a minor component. Herb and shrub layers range from poorly developed to nonexistent. Stream is near edge of plot.
Stone House	Hom 2	Brushy cleared land & deciduous woods	Homogeneous	Well-developed herb layer with patches of shrubs and trees, located next to a small stone house; periodic burns to maintain openness.
Mineral Springs	Hom 3	Hemlock-hardwood swamp	Homogeneous	Largely Hemlock forest with American Beech and Sugar Maple as a minor component. Herb and shrub layers range from poorly developed to nonexistent. Stream just beyond edge of plot.
Aleck Meadow Roadside	Het 1	Hemlock-hardwood swamp	Heterogeneous	Largely Hemlock forest with Yellow Birch as a minor component and patches of shrubs on rocky outcrops. Herb and shrub layers range from poorly developed to nonexistent. Stream bisects plot.
Jim's Pond	Het 2	Shrub swamp	Heterogeneous	Well-developed tree, shrub, and herb layers in a variety of stand ages, adjacent to open water.
Two Gates	Het 3	Successional upland woods	Heterogeneous	Well-developed tree, shrub, and herb layers; mosaic of different aged successional patches. Stream near edge of plot.

Songbird Censuses

At each of the six sites a bird point count location with a 50-meter radius was established. Point counts are the preferred method when studying birds in relation to habitat characteristics (Bibby *et al.* 2000), which is an objective in this study. Each point count survey was 5 or 10 minutes in duration (Bibby *et al.* 2000). Surveys were conducted multiple times during May,

June, and July of 2011 and 2012 for a total of 100 minutes per site in order to build a robust bird richness list. Thus, each site's bird richness list was based on 100 minutes of surveying spread over two breeding seasons. Species richness was determined as well as the abundance of each taxon. Point counts were performed with double observers to minimize error and personal bias and each count did not begin until at least two minutes after the observers arrived on the site to allow for settling.

Aerial vegetation cover and DBH

At each site, three plant survey subplots were randomly placed within the 50 m radius of the bird point count (Figure 2a). In these 100 m^2 circular plots tree species identification and diameter at breast height (DBH) measurements were made to provide an index of forest type and maturity (Bibby *et al.* 2000). Herb and shrub species richness and percent ground cover were determined using the Braun-Blanquet technique (Braun-Blanquet 1932, Poore 1955) within four 1 m^2 plots randomly placed in each of the three 100 m^2 circular plots. Only four quadrats were measured following the species-area curve rule (Cain 1938).

Vertical Canopy Complexity

Vertical canopy complexity was assessed using a vegetation complexity board modeled after Nudds (1977). A piece of cloth 3 m tall by 0.5 m wide was affixed to PVC pipe that was t-shaped in order to be able to hold the cloth vertically. The cloth was painted in a grid of decimeter squares, switching colors every half-meter (Figure 2b). While one or two people held

the board steady, two observers viewed the board from 15 m away. For every 0.5 m canopy height increment the observers counted how many decimeter squares were covered (50% or more) by vegetation. For each point, the board was viewed from 4 random bearings. These points were the same center points that were used for 100 m^2 circular plots in the vegetation surveys (n=12 per habitat). The average number of squares that were covered by 50% or more for each canopy height increment was then defined as the vertical density index. For ease of representation, canopy height increments were later combined to represent 1 meter as opposed to 0.5 meters. We then classified the habitats as either structurally heterogeneous or homogeneous (Table 1).

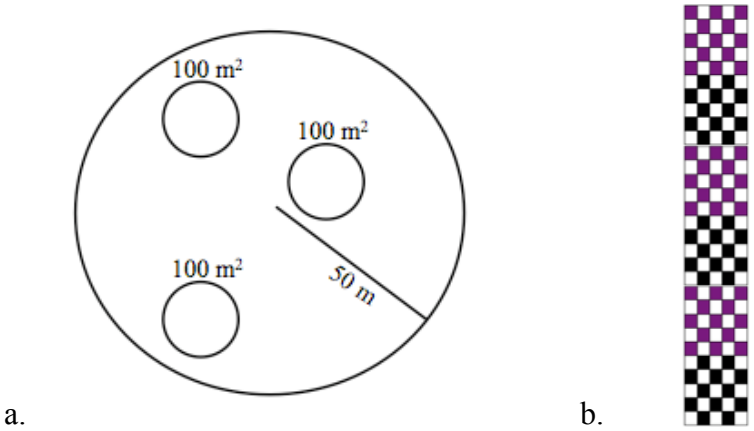


Fig. 2: a. A diagram of the vegetation survey subplots within the 50 m radius plot. b. The 3m by 0.5m density cloth with checkerboard pattern colors alternating every 0.5m.

Statistical Analysis

One-way analysis of variance (ANOVA) was used to test for overall differences among homogeneous and heterogeneous habitats for bird abundance, bird species richness, plant species richness, and the vertical density indices. Differences were considered significant at $P \leq 0.05$. Linear regressions and Pearson Product Moment Correlation were used to determine relationships between selected pairs of measured variables.

RESULTS

The fifteen most abundant bird taxa found across all sites were American robin, red-eyed vireo, American crow, veery, cedar waxwing, common yellowthroat, gray catbird, chipping sparrow, scarlet tanager, American goldfinch, great-crested flycatcher, American redstart, Baltimore oriole, yellow warbler, and eastern towhee. In general, the average number of birds per minute and bird species richness follows the same trend in each habitat (Figure 3).

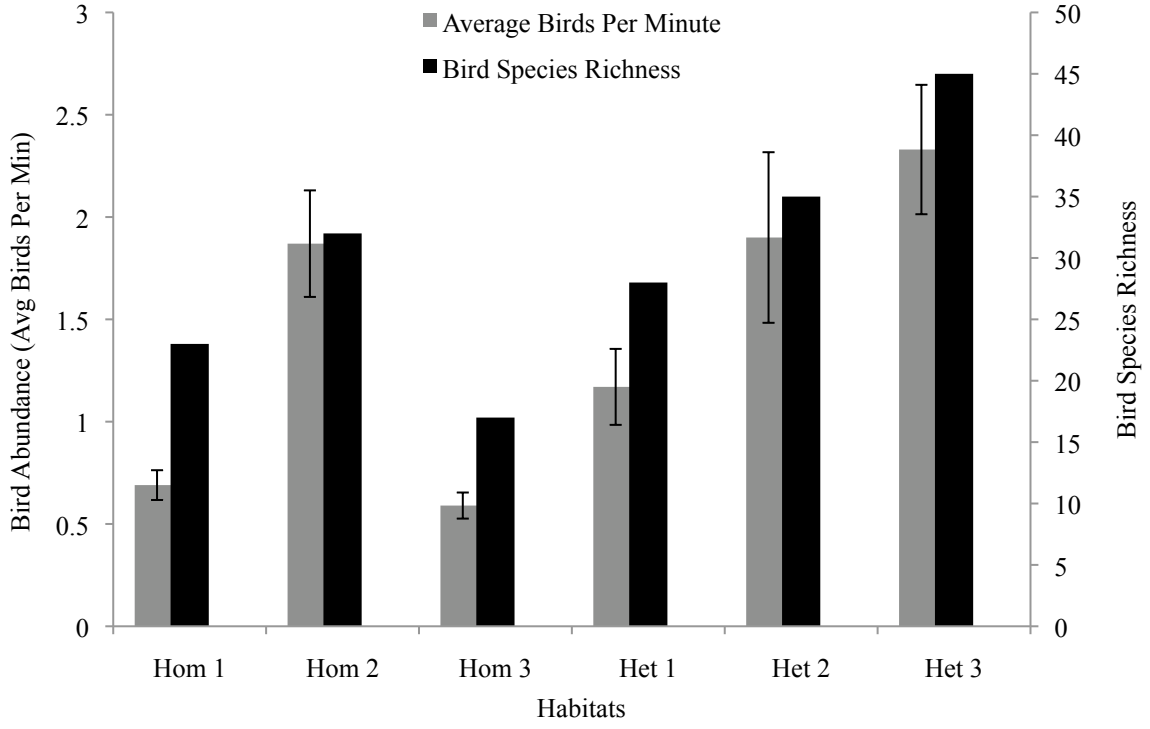


Fig. 3: Average number of birds per minute at each site based on 100 survey minutes spread over two breeding seasons. Error bars were calculated as the standard error from the mean. Observed bird species richness was determined by taking the average of birds per minute on each sampling day for each habitat.

The three homogeneous habitats are significantly different from each of the three heterogeneous habitats in terms of vertical density index and plant species richness (Figure 4). The vertical density index values for the heterogeneous habitats are nearly twice as high as the

homogeneous sites; however, the relative proportions of density in each of the three one-meter sections is very similar among all six study habitats. This means that no individual canopy height increment is completely lacking vegetation in the homogeneous habitats, but that the vegetation is just sparse in all canopy height increments.

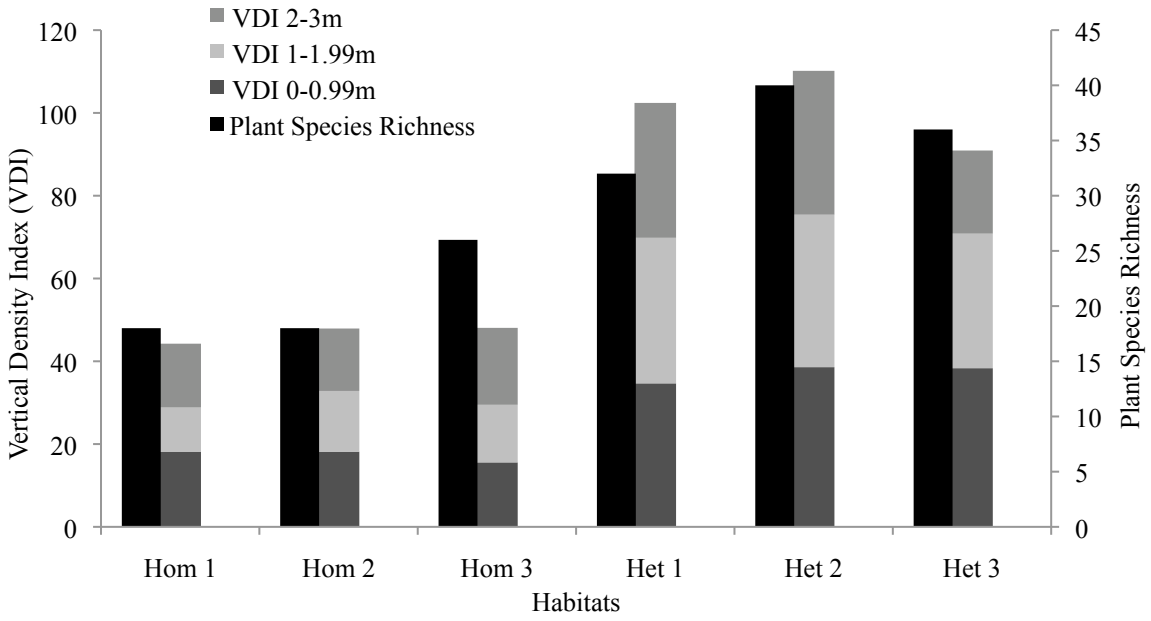


Fig. 4: Vertical vegetation density, as measured by a vertical density index, at each habitat, in three 1-meter sections (0-0.99m, 1-1.99m, 2-3m). The index represents the sum of density cloth value of each section. Observed plant species richness determined by the species lists for each habitat resulting from the vegetation surveys is also shown.

There were statistically significant differences between homogeneous and heterogeneous habitats in plant species richness and vertical density index, but not in bird species richness or bird abundance (Figure 5). There is only 86% confidence that bird species richness is different for each habitat category ($p=0.14$) and is therefore not significant. In addition, songbird species richness was weakly positively correlated with both plant species richness and the vertical density index (Figure 6). The Pearson Product Moment Correlation did not yield results with certainty greater than 90% ($p=0.11$ and $p=0.13$, respectively).

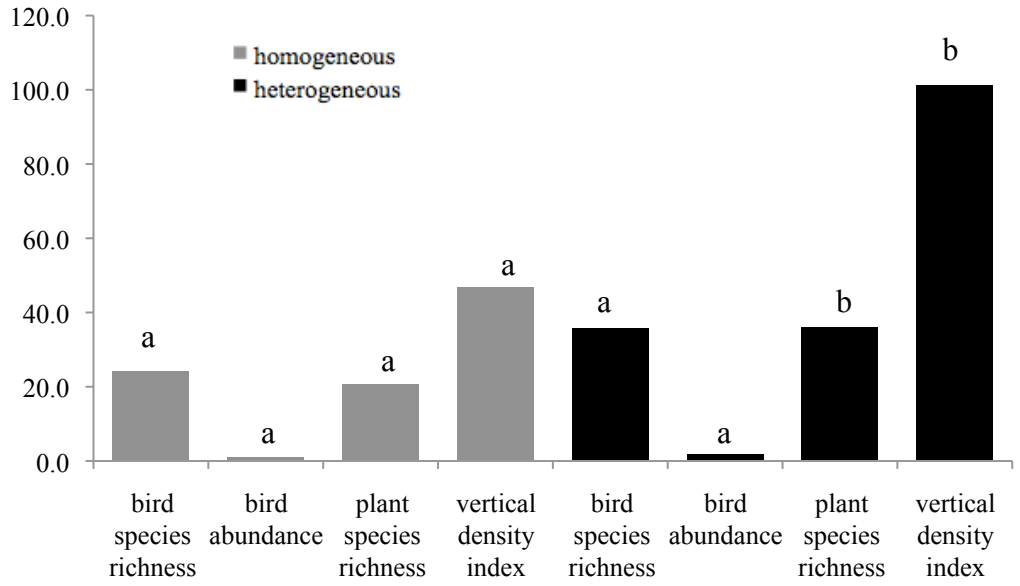


Fig. 5: Averages of bird species richness, bird abundance, plant species richness, and vertical density index for homogeneous and heterogeneous habitats. Metrics labeled "a" in homogeneous habitats and "b" in heterogeneous habitats are significantly different ($p \leq 0.05$).

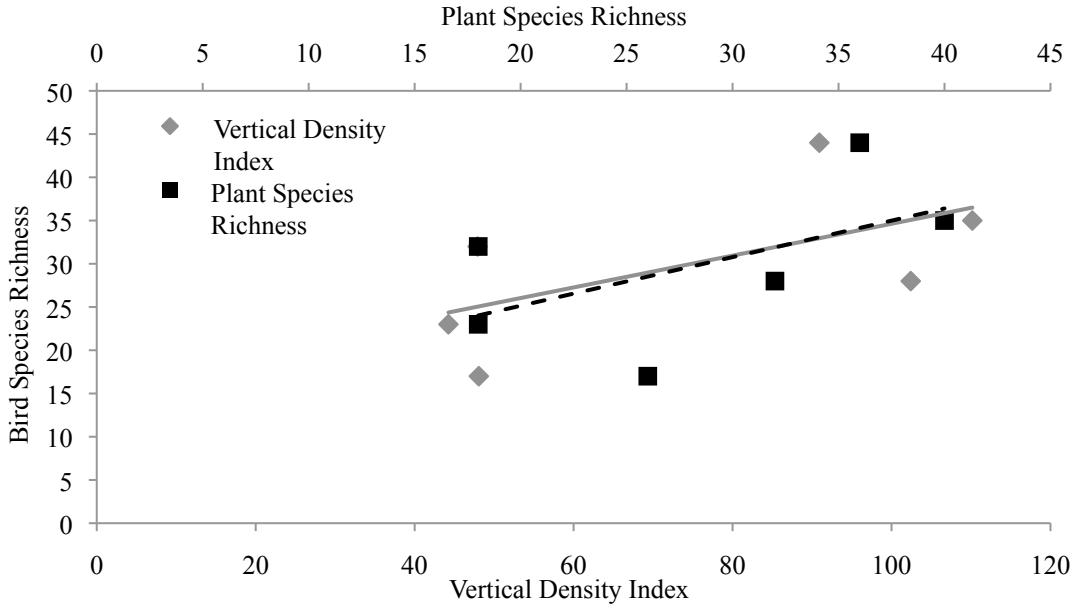


Fig. 6: Relationship of both plant species richness and the vegetation vertical density index to bird species richness. R^2 values were 0.30 and 0.35, respectively, which indicates weak, but present, positive correlations.

DISCUSSION

We found that the structurally homogeneous and heterogeneous habitats were, in fact, significantly different in terms of the vegetation metrics. Plant species richness and vertical vegetation density in homogeneous habitats are both significantly lower than in the heterogeneous habitats. Plant species diversity alone can be a good predictor of bird species diversity, but this is often because plant species diversity is high when vertical vegetation density is high (MacArthur & MacArthur 1961). When this accounted for, plant species data provides no additional knowledge of bird species diversity (MacArthur & MacArthur 1961). This colinearity explains, in part, why we are unable to make a case for or against our hypothesis that vertical canopy complexity is more important to songbird community size and richness than plant species richness.

We found only weak correlations between birds and vegetation. Bird species richness is moderately lower in homogeneous habitats compared to heterogeneous habitats, but songbird abundance was less significant. This leads us to ask, what exactly is it that makes certain habitats more appealing to birds? One study found that structural complexity of habitats had a greater effect on biodiversity in areas that were energy rich (Verschuyl *et al*. 2008). They stated their finding to be in accordance with the hypothesis that suggests that higher levels of heat, energy, or greater food caused by enhanced ecosystem productivity allow more individuals in populations, fewer population extinctions, and more species in a community. Thus, incorporating an examination of forest productivity in a follow-up study could prove to be valuable in explaining some of our results. Habitat patchiness is also something worth more consideration. MacArthur *et al.* (1962) found the variety of patches of vegetation within a

habitat to be a good determinant of the bird species breeding there and Flather & Sauer (1996) found that too many small patches supported a relatively lower abundance of migratory songbirds. Thinking about these patches is also important in terms of understanding habitats on a local scale, which can give more insight to the bird communities than current landscape-scale methods (Lichstein *et al.* 2002, Donovan & Flather 2002). In the future, the use of LiDAR may prove useful in predicting the effects of landscape characteristics and local-scale habitat characteristics on bird communities (Goetz *et al.* 2007).

The most widely abundant bird species of a forest community are usually the generalist species that can thrive in a variety of habitats, including those that have been disturbed (Julliard *et al*. 2006). Specialist species, on the other hand, are categorized as having low dispersal abilities, are less able to cope with environmental stochasticity, and tend to benefit from homogeneous environments (Julliard *et al*. 2006, Devictor *et al.* 2008). One of BRF's generalist species, the red-eyed vireo, was found at all survey sites in the forest, while other species were found reliably at only one or two of the habitats studied. For example, the Acadian flycatcher was found exclusively in the hemlock stands and the chestnut-sided warbler at low, early successional woodlands. In accordance with the theory of niche evolution, specialist species have been found to respond more negatively to habitat fragmentation and disturbance than generalist species (Devictor *et al.* 2008). The presence of these specialist species at BRF highlights the importance of maintaining a mosaic of habitats and continuous forest tracts in order to conserve bird diversity. This may be challenging considering the current threat to hemlocks by the hemlock woolly adelgid. It has been predicted that continued infestation of this aphid-like insect from Japan will lead to an unprecedented loss of hemlocks in the northeastern United States, regardless of individual site conditions (Orwig *et al.* 2002). For the chestnut-sided

warbler we speculate that the lack of fire as a disturbance agent could also pose a problem for the species over the years unless a management regime is put into place. Other species that favor the early seral habitats also face decline due to aging stands and clear cutting (Ellis & Betts 2011).

CONCLUSION

As the climate and our landscapes change there will be a greater need for proactive biodiversity management for birds and many other taxa. A common strategy of forest management for bird biodiversity is the maintenance of structural complexity within stands and providing a variety of seral stages across landscapes to give more patchiness (Verschuyl *et al*. 2008). This is important because the quality and quantity of different habitats within a landscape reflects songbird abundance and vice versa (Lichstein *et al.* 2002).

Even though our study did not show with great significance the connection between songbird species richness and vegetation characteristics, it does suggest that other local habitat or landscape-scale characteristics should be considered in the future when studying eastern New York forest habitats. We identified the importance of vertical canopy complexity as a signifier of different habitats and discussed the importance of this and habitat heterogeneity to bird species richness. Our results could have possibly been more significant if we had been able to survey more habitats.

Another way to improve this study could be to add a wider variety of vegetation metrics to the analysis. There are many different aspects to studying vegetation, which could all be useful in establishing causal relationships between habitat characteristics and fauna.

Understanding these local-scale factors may be more useful in predicting the presence of bird species, but until more is known about landscape-scale signifiers it has been recommended that large forest tracts be protected as opposed to fragmented conservation (Robinson &Wilcove 1994, Vance *et al.* 2003).

Heterogeneous habitats may support higher bird species richness, but the homogeneous habitats are equally as important for specialist species. Thus, the continued presence of a mosaic of habitats at BRF will be crucial in maintaining high forest-wide bird biodiversity in the future.

ACKNOWLEDGEMENTS

I would first like to thank my research mentor and my thesis adviser for allowing this project to come together. I would also like to thank the staff and volunteers of Black Rock Forest, namely Bill Schuster and Katie Pavlis, for all their continued help and support. This project was made possible with funding from the Tow Foundation and the Barnard College Department of Environmental Science.

REFERENCES

Bibby, C.J., N.D. Burgess, D.A. Hill, and S.H. Mustoe. 2000. Bird Census Techniques, 2nd ed. Academic Press, New York.

Borgmann, K.L., and A.D. Rodewald. 2004. Nest predation in an urbanizing landscape: the role of exotic shrubs. Ecological Applications 14(6):1757-1765.

Braun-Blanquet, J. 1932. Plant sociology (Transl. G. D. Fuller and H. S. Conrad), 1st ed. McGraw-Hill, New York.

Brose, U. 2003. Bottom-up control of carabid beetle communities in early successional wetlands: mediated by vegetation structure or plant diversity? Oecologia 135:407-413.

Cain, S.A. 1938. The Species-Area Curve. American Midland Naturalist. 19(3): 573-581.

deCalesta, D.S. 1994. Effect of white-tailed deer on songbirds within managed forests in Pennsylvania. The Journal of Wildlife Management 58(4):711-718.

Dennis, P., M.R.Young, and I.J. Gordon. 1998. Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. Ecological Entomology 23(3):253-264.

Devictor, V., R. Julliard, and F. Jiguet. 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. Oikos 117(4):507-514.

Donovan, T.M, and C.H. Flather. 2002. Relationships among North American songbird trends, habitat fragmentation, and landscape occupancy. Ecological Applications 12(2):364-374.

Edinger, G.J., D.J. Evans, S. Gebauer, T.G. Howard, D.M. Hunt, and A.M. Olivero, editors. 2002. Ecological Communities of New York State. Second Edition. A revised and expanded edition of Carol Reschke's Ecological Communities of New York State. (Draft for review). New York Natural Heritage Program, New York State Department of Environmental Conservation, Albany, NY.
http://www.dec.ny.gov/docs/wildlife_pdf/terrestrial_subterranean.pdf

Ellis, T.M. and M.G. Betts. 2011. Bird abundance and diversity across a hardwood gradient within early seral plantation forest. Forest Ecology and Management 261:1372-1381.

Flather, C.H., and J.R. Sauer. 1996. Using landscape ecology to test hypotheses about large-scale abundance patterns in migratory birds. Ecological Society of America 77(1):28-35.

Freemark, K.E. and H.G. Merriam. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. Biological Conservation 36:115-141.

Goetz, S., D. Steinberg, R. Dubayah, and B.Blair. 2007. Laser remote sensing of canopy habitat heterogeneity as a predictor of bird species richness in an eastern temperate forest, USA. Remote Sensing of Environment 108:254-263.

Holmes, R.T. and T.W. Sherry. 2001. Thirty-year bird population trends in an unfragmented temperate deciduous forest: importance of habitat change. The Auk 118(3):589-609.

Hostetler, M.E. and M.B. Main. 2008. Florida Monitoring Program: Point Count Method to Survey Birds. http://edis.ifas.ufl.edu

Julliard, R., J. Clavel, V. Devictor, F. Jiguet, and D. Couvet. 2006. Spatial segregation of specialists and generalists in bird communities. Ecology Letters 9:1237-1244.

Keesing, F., L.K. Belden, P. Daszak, A. Dobson, C.D. Harvell, R.D.Holt, P. Hudson, A. Jolles, K.E. Jones, C.E. Mitchell, S.S. Myers, T. Bogich, and R.S. Ostfeld. 2010. Impacts of biodiversity on the emergence and transmission of infectious diseases. Nature 468**:**647-652.

Lichstein, J.W., T.R. Simons, and K.E. Franzreb. 2002. Landscape effects on breeding songbird abundance in managed forests. Ecological Applications 12(3):836-857.

MacArthur, R.H. and J.W. MacArthur. 1961. On bird species diversity. Ecology 42(3):594-598.

MacArthur, R.H., J.W. MacArthur, and J. Preer. 1962. On bird species diversity II: Prediction of bird census from habitat measurements. The American Naturalist 96(888):167-174.

Marquis, R.J. and C.J. Whelan. 1994. Insectivorous Birds Increase Growth of White Oak Through Consumption of Leaf-chewing Insects. Ecology 75(7):2007-2014.

McGowan, K.J. and K. Corwin, editors (2008). The Second Atlas of Breeding Birds in New York State. Cornell University Press. Ithaca and London.

Murdoch, W.M., F.C.Evans, and C.H. Peterson. 1972. Diversity and pattern in plants and insects. Ecology 53(5):819-829.

Nudds, T.D. 1977. Quantifying the Vegetative Structure of Wildlife Cover. Wildlife Society Bulletin 5(3):113-117

Orwig, D.A., D.R. Foster, and D.L. Mausel. 2002. Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. Journal of Biogeography 29:1475-1487.

Pidgeon, A.M., V.C. Radeloff, C.H. Flather, C.A. Lepczyk, M.K. Clayton, T.J. Hawbaker, and R.B. Hammer. 2007. Associations of forest bird species richness with housing and landscape patterns across the USA. Ecological Applications 17(7):1989-2010.

Poore, M.E.D. 1955. The Use of Phytosociological Methods in Ecological Investigations: III. Practical Application. The Journal of Ecology 43(2):606-651.

Robinson, S.K. and D.S. Wilcove. 1994. Forest fragmentation in the temperate zone and its effects on migratory songbirds. Bird Conservation International 4:233-249.

Saab, V.A., and H.D.W. Powell. 2005. Fire and avian ecology in North America: process influencing pattern. Studies in Avian Biology 30:1-13.

Sekercioglu, C.H, G.C. Daily, and P.R. Ehrlich. 2004. Ecosystem consequences of bird declines. PNAS 101(52):18042-18047.

Smith, C.R. and P.L. Marks. 2008. Land-use Changes and Breeding Birds. In: The Second Atlas of Breeding Birds in New York State pages 59-68. Eds K. J. McGowan and K. Corwin. Cornell University Press. Ithaca and London.

TIngley, M.W., D.A.Orwig, R. Field, and G. Motzkin. 2002. Avian response to removal of a forest dominant: consequences of hemlock woolly adelgid infestations. Journal of Biogeography 29:1505-1516.

Turnbull, M.H., D. Whitehead, D.T. Tissue, W.S.F. Schuster, K.J. Brown, V.C. Engel, and K.L. Griffin. 2002. Photosynthetic characteristics of canopies of *Quercus rubra, Quercus prinus,* and *Acer rubrum* differ in response to soil water availability. Oecologia 130:515-524.

Vance, M.D., L. Fahrig, and C.H. Flather. 2003. Effect of reproductive rate on minimum breeding habitat requirements of forest-breeding birds. Ecology 84(10):2643-2653.

Verschuyl, J.P., A.J. Hansen, D.B. McWethy, R. Sallabanks, and R.L. Hutto. 2008. Is the effect of forest structure on bird diversity modified by forest productivity? Ecological Applications 18(5):1155-1170.