

THE RELATIVE INFLUENCES OF LOCAL HABITAT  
HETEROGENEITY AND PRODUCTIVITY ON SPECIES RICHNESS

by

William Justin Cooper  
A Thesis  
Submitted to the  
Graduate Faculty  
of  
George Mason University  
in Partial Fulfillment of  
The Requirements for the Degree  
of  
Master of Science  
Environmental Science and Policy

Committee:

\_\_\_\_\_ Dr. David Luther, Thesis Director  
\_\_\_\_\_ Dr. Thomas Lovejoy, Committee Member  
\_\_\_\_\_ Dr. William McShea, Committee Member  
\_\_\_\_\_ Dr. Tavis Forrester, Committee Member  
\_\_\_\_\_ Dr. Ingrid Visseren-Hamakers, Graduate Program  
Director  
\_\_\_\_\_ Dr. A. Alonso Aguirre, Department Chairperson  
\_\_\_\_\_ Dr. Donna Fox, Associate Dean, Student Affairs &  
Special Programs, College of Science  
\_\_\_\_\_ Dr. Peggy Agouris, Dean, College of Science

Date: \_\_\_\_\_ Fall Semester 2018  
George Mason University  
Fairfax, VA

The Relative Influences of Local Habitat Heterogeneity and Productivity on  
Species Richness

A Thesis submitted in partial fulfillment of the requirements for the degree of Master of  
Science at George Mason University

by

William Justin Cooper  
Bachelor's of Science  
James Madison University, 2013

Director: David Luther, Professor  
Department of Environmental Science and Policy

Fall Semester 2018  
George Mason University  
Fairfax, VA

Copyright 2018 William Justin Cooper  
All Rights Reserved

## **DEDICATION**

This is dedicated to my loving family and friends who have helped me on this journey.

## **ACKNOWLEDGEMENTS**

I would like to thank the many friends, interns, volunteers, and supporters who have made this happen. My two interns, Joel and Sarah, assisted me in the field season and identification of many species in countless hours of recordings. I would also like to thank Drs. McShea, Luther, Forrester, and Lovejoy who were of invaluable help in the planning and writing of this thesis project.

## TABLE OF CONTENTS

	Page
List of Tables .....	vii
List of Figures.....	viii
List of Abbreviations.....	ix
Abstract .....	x
Chapter One: Determining the appropriate scale for measuring habitat heterogeneity and productivity when modeling species richness of different vertebrate taxa .....	1
1. Introduction.....	1
2. Methods.....	4
2.1. Survey location selection.....	4
2.2. Monitoring methods .....	5
2.2.1 Acoustic monitoring: bats, frogs, & birds.....	6
2.2.2 Camera trapping: terrestrial mammals.....	7
2.3. Data processing .....	7
2.3.1 Acoustic data: birds and frogs .....	7
2.3.2 Ultrasonic data: bats.....	9
2.3.3 Camera trap data: mammals .....	10
2.4. Remote sensing data.....	10
2.5. Spatial Autocorrelation of Richness.....	14
2.6 Guild grouping.....	14
2.7 Statistical analysis .....	15
3. Results.....	18
3.1. Survey results.....	18
3.2. Multi-scale performance of occupancy models .....	19
3.3. Differences of scale.....	22
4. Discussion .....	23
4.1. Scale dependence of community-habitat relationships .....	24

4.1.1 Frogs.....	24
4.1.2 Bats .....	25
4.1.3 Birds.....	26
4.1.4 Terrestrial Mammals.....	27
4.2. Patterns across taxa and guilds/inferences from these models .....	28
4.3. Limitations.....	29
4.4. Conclusions.....	30
Chapter Two: The relative influence of habitat heterogeneity and productivity on avian species richness at the community level .....	32
1. Introduction.....	32
2. Methods.....	36
2.1. Survey location selection.....	36
2.2. Monitoring methods .....	37
2.3. Data processing .....	37
2.3.1 Acoustic data .....	37
2.3.2 Remote sensing measures.....	38
2.4 Statistical analysis .....	40
2.4.1 Modeling Approach.....	40
2.4.2 Model Validation.....	42
3. Results.....	43
4. Discussion .....	52
4.1 Total avian richness.....	53
4.2 Guild specific richness .....	55
4.3 Management implications.....	56
4.4 Conclusions.....	58
References .....	59

## LIST OF TABLES

Table	Page
Table 1: Remotely sensed measures .....	13
Table 2: Spatial autocorrelation.....	14
Table 3: Survey summary.....	18
Table 4: Avian model selection results .....	44

## LIST OF FIGURES

Figure	Page
Figure 1: Survey summary .....	5
Figure 2: Peak avian activity .....	9
Figure 3: Comparison of observed richness to NEON surveys.....	19
Figure 4: AUC frogs and bats .....	20
Figure 5: AUC birds.....	21
Figure 6: AUC terrestrial mammals.....	22
Figure 7: Issues of scale .....	23
Figure 8: Patterns of optimal scale across vertebrate taxa .....	29
Figure 9: Selected avian parameter responses .....	46
Figure 10: Averaged predictive comparisons for final avian model.....	47
Figure 11: Species specific and community responses to selected covariates .....	49
Figure 12: Total estimated species richness per site.....	50
Figure 13: Predictive maps using model outputs.....	51
Figure 14: Avian richness model validation.....	52

## LIST OF ABBREVIATIONS

Acoustic Recording Unit .....	ARU
Average Predictive Comparison .....	APC
Credible Interval .....	CI
Enhanced Vegetation Index.....	EVI
Hectare.....	ha
Leaf Area Density .....	LAD
Light Detection and Ranging.....	LiDAR
Meter .....	m
National Ecological Observatory Network .....	NEON
National Landcover Database.....	NLCD
Normalized Difference Water Index.....	NDWI
Smithsonian Conservation Biology Institute.....	SCBI

## **ABSTRACT**

The Relative Influences of Local Habitat Heterogeneity and Productivity on Species Richness

William Justin Cooper, M.S.

George Mason University, 2018

Thesis Director: Dr. David Luther

As natural habitats continue to decrease and become fragmented, pressure increases to better understand the complex systems of species-habitat interactions and the spatial scale at which habitat characteristics are measured. I explored the relative importance of habitat heterogeneity and productivity, at multiple spatial scales, as predictors of species richness in 19 vertebrate guilds across 3 taxonomic classes, birds, frogs, and mammals. Habitat heterogeneity and productivity metrics were derived from LiDAR and hyperspectral data obtained from the National Ecological Observatory Network's airborne observation platform. A combination of passive acoustic monitors and camera traps, provided species occurrence data of birds, frogs, and mammals. Species richness of each group was modeled based on their detectability using a Bayesian multi-species occupancy model. To select the most appropriate scale of habitat characteristics for each guild, I systematically calculated the receiver operating

characteristic area under the curve for each model iteration, quantifying the uncertainty in model predictions with each scale.

Performance of the models depended on the spatial scale at which habitat heterogeneity and productivity were measured, and were different for each taxonomic group. Frog and bat species richness were most strongly related to habitat heterogeneity and productivity measurements within a 20m radius of the survey location. Bird species richness, regardless of guild type, had an optimal scale of an 80m radius. Terrestrial mammal richness was optimal at a 180-meter radius buffer. Results indicated the appropriate scale for each taxon is at, or smaller in area than seasonal or home range areas for these taxa.

The relative influence of habitat heterogeneity and productivity were further investigated for bird species richness with indicator variable methods. Productivity resulted as the most important factor for species richness within bird guilds. Habitat heterogeneity was not influential for guild specific species richness. When all bird species were assessed together habitat heterogeneity and productivity were both important in determining species richness with habitat heterogeneity having a stronger effect overall. The utility of fine resolution measures of habitat heterogeneity and productivity are important determinants of species richness across local landscapes for different taxa and point to key measures for conservation management planning. For birds, focused efforts on increased understory vegetation, heterogeneity in productivity, and vertical structure are predicted to yield higher avian species richness, prioritizing a mosaic of early and late successional habitats with small localized disturbances.

# **CHAPTER ONE: DETERMINING THE APPROPRIATE SCALE FOR MEASURING HABITAT HETEROGENEITY AND PRODUCTIVITY WHEN MODELING SPECIES RICHNESS OF DIFFERENT VERTEBRATE TAXA**

## **1. Introduction**

The continued loss and fragmentation of natural habitats increases the need to better manage, conserve, and restore the remaining ecologically valuable areas that support diverse assemblages of animals (Haddad et al., 2015; Pimm et al., 2014; Barnosky et al., 2011). For effective management of species richness, it is necessary to understand how the occurrence of animal species is related to environmental heterogeneity and productivity gradients (Farrell et al., 2013). The strength of these relationships depends on the spatial scale at which species interact with the environment (Jackson & Fahrig, 2015; Keil et al., 2012). By overlaying the habitat preferences of multiple species at the most appropriate scale, more accurate predictions of species richness can be estimated (Boyce et al., 2006). However, the most appropriate spatial scale must be determined when describing how animals respond to their environment, as heterogeneity and productivity measures vary with the scale of measurement (Holland et al., 2004).

Johnson (1980) developed a general hierarchical method of ranking habitat selection based on scale of habitat use and availability. First-order selection defines the distribution of a species across large areas, second-order selection determines the home

range of an individual within a large area, third-order selection pertains to the selection of habitat patches within an individual's home range, and fourth-order selection describes selection for resources within these patches. Within this framework, important localized heterogeneity and productivity gradients average out when measurement scales are too large, while measurement scales that are too small under sample these important processes (Boyce, 2006). In addition, the most appropriate scale of these influences should vary between vertebrate taxonomic groups with different resource and home range requirements (Wiens, 1989). However, the role of spatial scale is not always considered when modeling habitat selection or estimating total richness, despite the well supported foundation for multi-scale habitat selection modeling (Mayor et al., 2009; McGarigal et al., 2016).

Several studies have demonstrated that habitat selection by animal species is scale dependent (Bissonet et al., 1997; Mysterud et al., 1999; Anderson et al., 2005). For example, Boyce et al. (2003) developed models to characterize elk habitat and found that important selection coefficients, including forest type and vegetation richness, changed in magnitude and even changed between selection and avoidance at different scales. Similarly, caribou have been found to select open woodlands at local scales during calving season but avoided these habitats at landscape scales (Leblond et al., 2011). Scale dependency in environmental variables has also been seen when studying overall richness. Hu et al., (2018) showed that the strength and magnitude of important attributes influencing tree species richness are dependent on the cell-size sampled, where increasing cell-size decreased the strength of significantly positive relationships to non-significant or

even significantly negative relationships. Therefore, it is important to use a range of measurement scales should as study replicates to determine the optimal scales to measure these environment-species relationships (Holland & Yang, 2016).

In this study I use a range of measurement scales for use in multi-species occupancy models to test which scale should be used when linking habitat productivity and heterogeneity to observations of animal richness at local scales. Relationships between habitat measures and multiple vertebrate taxa, including bats, terrestrial mammals, birds, and frogs, were measured across a local landscape (~1800 hectares) in northern Virginia. Based on Johnson's (1980) hierarchical scaling theory, I seek to answer, 1) What spatial scale of productivity and habitat heterogeneity measures is the best predictor for local richness for different vertebrate taxa and 2) Do second- or third-order scales of selection correspond to the best scale of productivity and heterogeneity covariates. I predict that the best spatial scale for relating habitat heterogeneity and productivity to species richness will be different for each taxonomic group due to life history differences, and that the best scale will be related to second-order scales of selection. For taxonomic groups with home ranges larger than the measurement scales used in this study, model performance should increase with increasing scale up to the largest scale. Since home range sizes vary greatly within vertebrate taxa, it was also predicted that the highest performing models would perform better when breaking species communities into guilds that group species sharing similar life histories and resource needs.

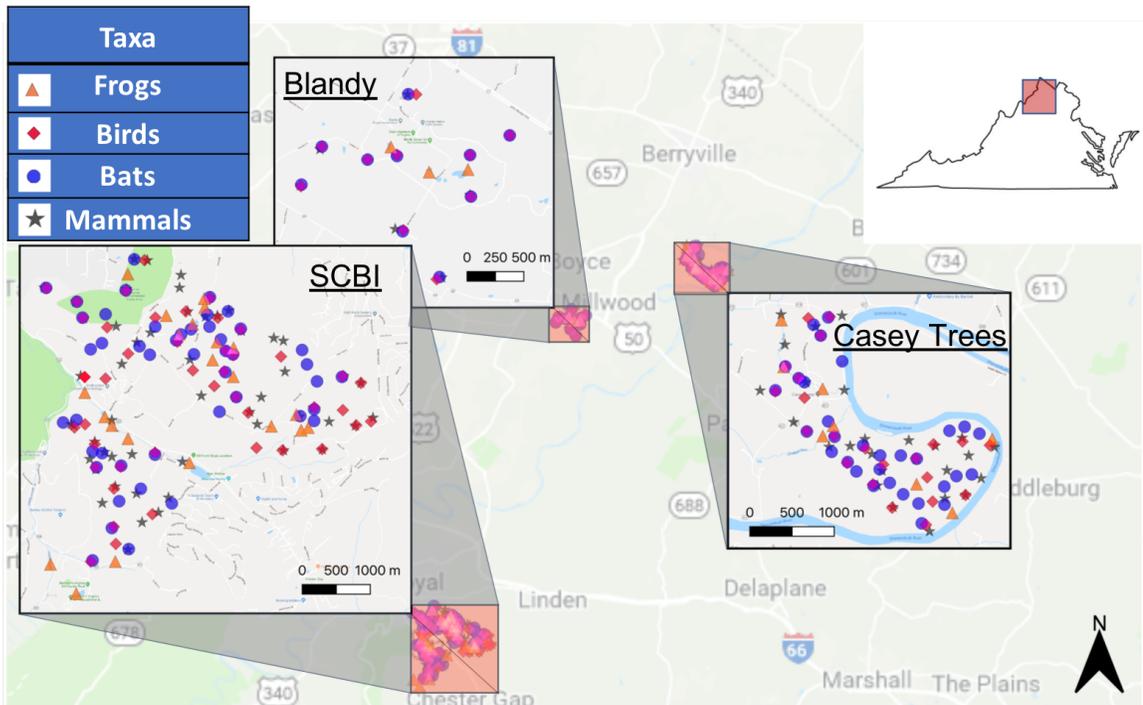
## **2. Methods**

### ***2.1. Survey location selection***

Research took place at three northern Virginia study sites, the Smithsonian Conservation Biology Institute (SCBI) in Front Royal (38°53'18.38" N, 78°09'52.38" W; 1295 hectares), Blandy Experimental Farm in Boyce (39°03'48.72" N, 78°03'46.84" W); 288 hectares), and Casey Trees Farm in Berryville (39°05'25.60" N, 77°58'36.92" W; 295 hectares), which represent a gradient of management areas (for a total of 1878 hectares; Figure 1). These sites were selected to match sampling within the more extensive National Earth Observatory Network (NEON; Domain 2). These sites are representative of mixed agriculture and temperate secondary forest habitats common in the Mid-Atlantic region; all sites included fields used for hay production and abandoned fields as well as mature stands of hardwood forests and distinct edge habitats between fields and forests (Bourg et al., 2005). Ponds, secondary and tertiary streams, and bottomland hardwood stands were also present at all sites.

A randomized grid utilized by NEON at all sites was used to select sample sights for vertebrate richness. The grid utilized a Reversed Randomized Quadrant-Recursive Raster (RRQRR) algorithm to create a spatially balanced random sample grid (Theobald et al., 2007). The algorithm allowed for the flexible addition or subtraction of unwanted locations, such as points in the middle of a road, and allowed for the stratification of land cover data based on the National Land Cover Database 2011 (NLCD) (Homer et al., 2015). The number of forest and field survey locations chosen at each site was representative of the overall ratio of forest to open area and in our classification, forest

was a combination of NLCD classifications for forest, woody wetlands, and shrub/scrub, and open was a combination of NLCD classifications of cultivated and grassland/herbaceous.



**Figure 1:** The three study sites and all camera/recorder locations. The table above summarizes the survey effort and timing for each taxa group’s deployments.

## 2.2. Monitoring methods

The selection of survey locations varied for each vertebrate taxon based on habitat requirements. Frog species were sampled within 10 m of a water source (stream or pond). Bat survey locations were selected within 4 categories: open areas, within 5 m of a road or forest edge, within 20 m of a forested water source or in a forest at least 60 m from a

road. Birds were surveyed at the same locations used by NEON during 2015, with new sites surveyed in 2016. Each bird survey location was within one of 2 habitat categories (open or forested) and separated by > 200 m. Terrestrial mammals were sampled within open and forested habitats with > 200 m between locations.

### *2.2.1 Acoustic monitoring: bats, frogs, & birds*

Wildlife Acoustics' SM3BAT acoustic recording units (ARUs) were used for acoustic surveys of birds, bats and frogs, as the unit records both acoustic and ultrasonic frequencies. I deployed each unit with either a single omnidirectional microphone (flat frequency response between 50-Hz and 20-kHz) for birds and frogs or a single omnidirectional ultrasonic microphone (built in 4-pole high pass filter at 8-kHz) for bats. The gain was standardized for all recording units. I sampled the recordings with 16-bit digitization and a 24-kHz sample rate for birds and frogs and a 256-kHz sample rate for bats. The units saved each recording in a WAV file format (Tierney et al., 2013).

I matched the diel and seasonal timing of ARU deployment to the peak activity for each focal taxon: bats were surveyed from sunset to sunrise during July and August (Skalak et al., 2012); birds were surveyed for three hours starting 30 minutes before sunrise during late May and continuing through June (Wimmer et al., 2013). Frogs were surveyed for 3 hours starting 30 minutes before sunset and again for three hours starting 30 minutes before sunrise from March through May (De Solla et al., 2005). Both birds and frogs were recorded during two rounds of deployments at each location to capture any early and late season differences in species richness. Frogs were surveyed with two 10-day deployments in 2015 and 2016 at 11 locations in 2015, and 22 additional

locations in 2016. Birds were surveyed with two 6-day deployments during mid-May through July in 2015 and 2016. During each active period, the unit recorded one minute out of every 10 minutes. Bat surveys included 6-day deployments from mid-July through August for both 2015 and 2016. The ARUs only recorded sounds when triggered by ultrasonic frequencies (greater than 8 kHz) that reached a threshold of 12 decibels. The recording duration for individual triggers was 3-15 seconds.

I surveyed frogs, birds, and bats by attaching ARUs to a tree approximately 2 m above ground level. Frogs and birds were surveyed with a single acoustic microphone directly attached to the unit (Depraetere et al., 2012). For bats, the ultrasonic microphone was elevated an additional 2.5 m above the ground (total 4.5 m) to increase signal detection of mid- and upper-canopy bats (Rodhouse, Vierling, & Irvine, 2011).

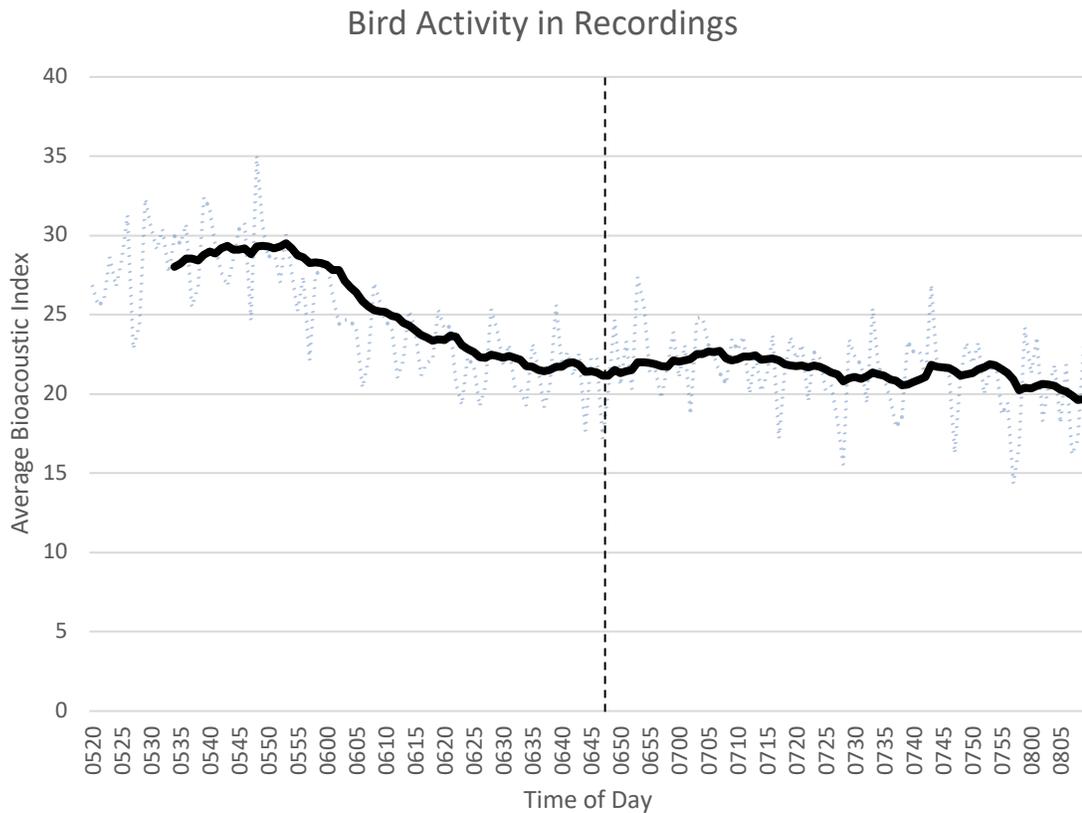
### *2.2.2 Camera trapping: terrestrial mammals*

The mammal community was surveyed with camera traps (Reconyx PC-800) (O'Connell, Nichols, & Karanth, 2011). Cameras were placed approximately 50 cm in height on posts in open field areas and trees in forested areas. I applied commercial carnivore scent lure (Pro's Choice) to a small object 3m in front of the camera to attract nearby predator species. Camera were set to no delay between photos and captured 10 photos per trigger event at a rate of 1 photo per second. The cameras were moved to a new location every three weeks from April to August in both 2015 and 2016 to coincide with peak mammal activity.

## **2.3. Data processing**

### *2.3.1 Acoustic data: birds and frogs*

Sound files from each survey location were first processed to subsample sound recordings. First, files with no frog or bird signals were eliminated using the ‘seewave’ package in R version 3.3.2 (Sueur, Aubin, & Simonis, 2008), which identified all sound files with no signal energy above the background noise. Any frog recordings that resulted with animal signals were listened to and any frog species heard was recorded. To reduce the sheer number of sound clips I identified the peak time of acoustic diversity using ‘soundecology’ in R version 3.3.2 (Villanueva-Rivera and Pijanowski, 2017). and averaged the bioacoustics index, a function of sound level and number of frequency bands used above a 2-kHz threshold, across daily recording times (Boelman et al., 2007). This index showed that the first 1.5 hrs of recordings each day (30-min before sunrise to 1 hour after sunrise) had the most diverse sound scape to estimate species occurrence (see Figure 2). From the recording in the first 1.5 hrs, I randomly subsampled 50 1-minute recordings from each site to determine species richness. I then compared the species richness within these clips to the point count survey results from NEON.



**Figure 2:** The Bioacoustic Index for all morning bird recordings across all recording days in 2015. The black line represents a moving average across 15 minute intervals. The vertical black dotted line represents 1.5 hours after the first recording and a subset of data to the left of the line were used in our analysis.

### 2.3.2 Ultrasonic data: bats

Ultrasonic recordings were processed with Kaleidoscope Pro (version 3.1.4B) to calculate an estimated nightly species presence and absence for each site. Within Kaleidoscope Pro, I specified the maximum duration of the WAV files as 15 seconds. The filter setting specified a signal of interest with at least three pulses between 12 and 120 kHz and 2 and 500 milliseconds. I compared our recording to a library of sounds from bats species found in Virginia, except for the grey bat (*Myotis grisescens*) whose range does not extend into our study sites. To estimate nightly occupancy of each species,

this program uses a maximum likelihood estimation based on the strength of identifications and the known misclassification rates found by Britzke et al. (2002).

### *2.3.3 Camera trap data: mammals*

After retrieving each camera trap, SD cards containing photos and metadata from camera traps were processed and managed using the eMammal web application ([www.emammal.si.edu](http://www.emammal.si.edu)). Each sequence of photos triggered by an animal was manually tagged for name and total number species. The images and metadata were then stored in the eMammal repository and later downloaded for analysis.

### **2.4. Remote sensing data**

Remote sensors are beneficial in performing repeated standardized measurements over a range of scales (Davies and Asner, 2014; Farrell et al., 2013; He et al., 2015). Light detection and ranging (LiDAR) and hyperspectral imagery are two sensors that can measure relationships between habitat selection and ecological gradients with high resolution and accuracy (Müller et al. 2010; Smith et al., 2002). These sensors have been used to measure vertical vegetation structure, environmental productivity, and habitat condition with resolutions less than one meter across large expanses of land (Lefsky et al., 2002; Martinuzzi et al., 2009). These measures have also been used to designate habitats related to the occurrence of individual species (Clawges et al., 2008) and to understand how habitat heterogeneity relates to richness as a whole (Goetz et al., 2007). The information from these sensors provide great potential to investigate relationships between vertebrate richness, habitat heterogeneity, and productivity patterns at both fine

and large scales across landscapes (Farrell et al., 2013), but the scale of measurement in these studies must be biologically justified (Jackson and Fahrig, 2015).

To test a gradient of scales in the occupancy models, I averaged scale-dependent measurements over buffered areas ranging from a 20 meter radius to a 180 meter radius for birds, bats, and frogs and up to 220 meters for terrestrial mammals with 20-meter increments centered on each survey location. This range of scales was selected to minimize the overlap of data between survey sites at the largest scales and represent the distance that units could definitively survey at the smallest scale.

NEON's Airborne Observation Platform (including a full waveform and discrete-return LiDAR sensor, a hyper-spectral imaging spectrometer, and a high-resolution camera) flew over our three sites in two 100 km<sup>2</sup> flights in August 2016; SCBI in one flight, and both Blandy and Casey Trees in the second flight. Using the classified LiDAR point cloud downloaded from NEON's database, LiDAR height returns were stratified and standard ground metrics were calculated using the "lidR" package in R version 3.3.2 (Roussel & Auty, 2018). Measurements included the leaf area density (LAD) for undergrowth (0-3 meters), understory (3-15 meters), mid-canopy (15-30 meters), and upper canopy (>35 meters), as well as the percentage of LiDAR returns classified as "ground" at each location within a given radius for area (see Table 1). In addition to these vertical habitat measurements, the slope, aspect, and elevation were averaged from the LiDAR data using the same R package.

NEON also produced raster products from their hyperspectral imagery readily available for download (<http://data.neonscience.org/>). NEON's available enhanced

vegetation index (EVI) and normalized difference water index (NDWI) raster products, derived from their hyperspectral imagery, were used to calculate the mean EVI and NDWI for each location using the “raster” package in R version 3.3.2 (Hijmans, 2017) (see Table 1). The averaged EVI represents a surrogate measure of vegetation productivity and health, with high values indicating healthy vegetation (Huete et al., 2002), averaged at each radial distance around each location. Similarly, NDWI is a surrogate for drought stress, with a high value indicating high water content within vegetation and soil (Gao, 1996), averaged at each radial distance around each location.

Occupancy covariates included remote sensing measurements of productivity, heterogeneity, and other explanatory factors. Productivity included undergrowth leaf area density (LAD) (0-3 meters), aboveground LAD (for frogs and mammals; >3 meters), understory LAD (for birds and bats; 3-15 meters), mid-canopy LAD (for birds and bats; 15-30 meters), upper canopy LAD (for birds and bats; >35 meters), EVI, and NDWI. Heterogeneity included measures of horizontal heterogeneity such as the standard deviation in EVI and NDWI, as well as vertical heterogeneity measures such as the standard deviation in vegetation height. Other variables included average slope, aspect, and elevation were added to the model to account for local variance not accounted for by habitat heterogeneity or productivity measures. All covariates were averaged within each of the targeted buffer scales.

Detection covariates varied for each daily survey period included mean daily temperatures, mean daily wind speeds, and total daily precipitation. Daily weather measurements were taken by NEON at each site on a 30-minute basis and downloaded

**Table 1:** List of all metrics used during this study. Measures fall into one of three categories labeled in the left-most column, including productivity, heterogeneity, and other factors.

	<b>Metric</b>	<b>Measurement</b>	<b>Definition</b>	<b>Source</b>
<b>Productivity</b>	Leaf Area Density (LAD)	meter <sup>2</sup> /meter <sup>3</sup>	One-sided leaf area within a given vertical strata. Describes vertical and horizontal structure variances within vegetation across different height intervals	Bouvier et al., 2015
	Enhanced Vegetation Index (EVI)	No unit	Remote sensing indicator sensitive to vegetation health and productivity while correcting for atmospheric conditions. Calculated from near infrared, red, and blue reflectance patterns.	Huete et al., 2002
	Normalized Difference Water Index (NDWI)	No unit	Remote sensing indicator of drought stress, sensitive to water content in leaves and environment. Calculated from near infrared and shortwave infrared reflectance patterns.	Gao, 1996
<b>Heterogeneity</b>	STD of vegetation height (cRough)	Meters	Standard deviation of height values	Huang et al., 2014
	STD of EVI	No Unit	Standard deviation in the EVI within a buffered radius	
	STD of NDWI	No Unit	Standard deviation in the NDWI within a buffered radius	
<b>Other</b>	Avg. Slope	Angle in Degrees	The angle of the ground surface inclined from a horizontal line	
	Avg. Aspect	Classified (North, East, South, West)	The positioning of the given area in a specific cardinal direction	
	Avg. Elevation	Meters	Distance above sea level	
	% of Ground	Percentage	Percentage of returns classified as "ground"	
	Dist. To Development	Meters	The distance from a survey location to the nearest developed open area	
	Dist. To Water	Meters	The distance from a survey location to the nearest standing or flowing body of water	

from their online database (<http://data.neonscience.org/>). The LAD at the height of the camera or ARU (LAD from 0-3 meters for mammals, frogs, and birds or 3-15 meters for bats) was also used as a detection covariate, as obstruction of vegetation around the acoustic and camera devices can limit detections.

### ***2.5. Spatial Autocorrelation of Richness***

Spatial independence was assessed with a Moran’s I test for each study site. The tests were performed using the coordinates of the survey locations, the number of nearest neighbor locations, and the species richness at each survey location. Moran’s I p-values and correlation values were obtained using the R package “lctools” (Kalogirou, 2017) and an alpha value of 0.05 (Table 2).

**Table 2:** Results of Moran’s I tests for spatial autocorrelation at each site for each target vertebrate group. Moran’s p-values indicate no significant relationship exists between species observed and the distance between sites. “-” Indicates too few sites sampled for testing.

<b>Group</b>	<b>SCBI</b>		<b>Blandy</b>		<b>Casey Trees</b>	
	<b>r-value</b>	<b>Mantel p-value</b>	<b>r-value</b>	<b>Mantel p-value</b>	<b>r-value</b>	<b>Mantel p-value</b>
Frogs	-0.172	0.131	-	-	-0.088	0.292
Birds	-0.069	0.542	-0.103	0.916	-0.075	0.761
Bats	-0.100	0.423	-0.080	0.600	0.039	0.393
Mammals	0.034	0.439	0.021	0.056	0.057	0.304

### ***2.6 Guild grouping***

To investigate any differences between functional groups within each taxon, guilds were created with distinct assemblages of species linked by shared attributes. Guilds were formed based on shared habitat needs, foraging behaviors, and body size traits to test if modeled richness within these guilds out performed overall richness.

Mammals were split into four guilds based on diet and body size. There was insufficient natural history data to break frogs into guilds, so all frog species were grouped together during analysis. Bats were divided in two guilds including species that forage in densely vegetated areas (high clutter) and species that forage in open areas (low clutter). Avian species were classed in three separate guild configurations based on habitat, foraging, and nesting behavior. Habitat classifications included forest, grassland, and edge guilds. Foraging classifications included aerial, bark, foliage, and ground guilds. Nesting classifications included, cavity nests, cup nests in trees, and cup nests in shrubs guilds.

## ***2.7 Statistical analysis***

The Bayesian hierarchical model is a multi-species approach to obtain complex information about communities by estimating individual species occurrence possibilities (Dorazio and Royle, 2005). Hierarchical multi-species occupancy models have previously been used to investigate relationships between habitat selection and avian species richness (Jones et al., 2012), linking component occupancy models for individual species to make inferences at the community level while accounting for imperfect detection. The benefit to using this type of model includes this ability to model spatially replicated detection data across sites where data from common species can be used to better estimate the occupancy of rare species. Using estimated occupancy at multiple sites, multi-species hierarchical models can be used to estimate how communities of species respond to environmental variables, such as habitat heterogeneity and productively (Russel et al., 2009).

A two-step approach was used to evaluate the appropriate scale and guild grouping strategy for each taxon. First, a Bayesian method of modeling occupancy for multiple species was used to model community responses to habitat heterogeneity and productivity at each scale by estimating individual species occurrence patterns within each sampled taxon (Dorazio & Royle, 2005; Dorazio et al., 2006). Second, the predictive abilities of occupancy models were compared between scales using area under the receiver operating characteristic curve (AUC ROC), which is based on a confusion matrix that summarizes the prediction results in terms of true/false presence/absence as true vs. predicted outcomes (Hanley & McNeil, 1982). AUC ROC values can be calculated in a Bayesian framework from the posterior distribution of predicted values and used for quantitative comparisons between groups by allowing the uncertainty in the quality of predictions to be calculated (Zipkin et al., 2012).

To ensure that a model converges on a reasonable value, three independent Markov chain Monte-Carlo chains were used (van Ravenzwaaij et al., 2018). The initial samples were thrown out as they can be very wrong since they have not been influenced by previous samples within the chain. These initial throw-away samples are called burn-ins. For each model used in this study three separate Markov chains were used with 3000 burn ins and an additional 2000 iterations, or model runs. Convergence was determined using the R-hat statistic, which represents the variance ratio of the MCMC algorithm within and between chains across iterations (Gelman & Hill, 2006). I used an R-hat value of less than 1.1 to indicate convergence (Kéry & Royle, 2018).

To compare between models at different scales with a Bayesian approach, I followed the methods of Zipkin et al. (2012) to calculate AUC values for each scale and guild group. Two models were fit separately for each scale and guild, using occurrence data from survey locations. First, to obtain reliable AUC results, a set of the sites' data were held out for validation, 25% of the frog and bat locations and 30% of the bird and mammal locations. After fitting models, the posterior covariate values were used to predict species-specific latent occupancy estimates for the validation sites. Second, to generate true occupancy values for the validation sites, a second model was fit at each scale sampling from the data at all sites (Zipkin et al., 2012). This second round of models produced true occupancy values for each species at each location to compare with latent occupancy values. If a species was present at least once during the sampling period of those test samples, then  $z=1$  for every draw of the posterior distribution. However, if a species was not observed the occupancy value was based on the detection probability, habitat heterogeneity, and productivity characteristics of that location to account for imperfect detection.

The result of the first step of this two-step approach is a matrix of estimated occurrence probabilities for each species at each location and a matrix of true occupancy values for each species at each location which were used to calculate AUC values for each iteration of the models. For this study, I used the full posterior distribution and the R package ROCR (Version 1.0-7; Sing et al., 2005) to quantify the uncertainty in the model estimates as AUC values and the R package BEST (Version 0.5.1; Kruschke and Meredith, 2018) to calculate the 95% credible intervals of these estimates. Guild models

with the highest mean AUC score were selected as the most appropriate grouping for further analysis. Using the most appropriate guild grouping, I considered the most appropriate scale to be the model that resulted in the maximum mean AUC and non-overlapping credible intervals.

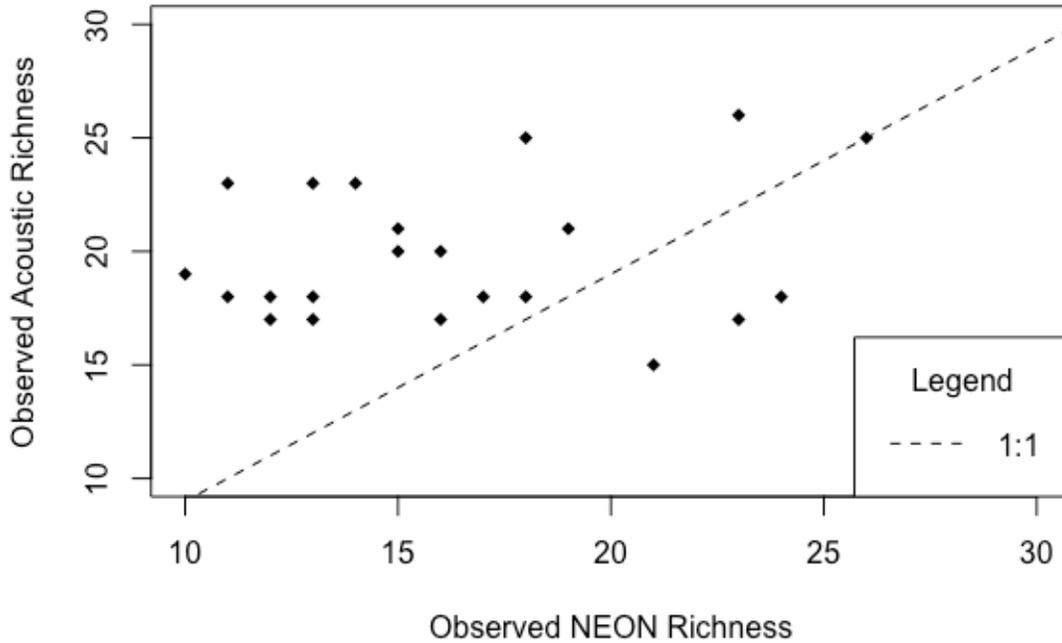
### 3. Results

#### 3.1. Survey results

Species' presence data was sampled from 204 unique locations across the three sites, including 33 frog, 76 bird, 78 bat, and 102 terrestrial mammal survey locations (Table 3). Moran's I test results suggest no significant spatial autocorrelation between species richness and the proximity of survey locations (Table 2). The bird richness at each site calculated from the subsampled acoustic recordings collected in this study was either equal to or exceeded the species richness observed by NEON at 18 of the 22 sites. Larger differences occurred at only 3 sites (see Figure 3).

**Table 3** Summary of acoustic and camera trap surveys with apparent species detected.

<b>Group</b>	<b># Locations</b>	<b>Days Surveyed</b>	<b>Species Detected</b>	<b>Mean Species/location</b>	<b>Range Species/location</b>
Frogs	33	1596	10	2.1	0-7
Birds	76	1933	83	25.3	12-44
Bats	78	1631	7	4.9	1-7
Mammals	102	2049	14	3.5	1-7

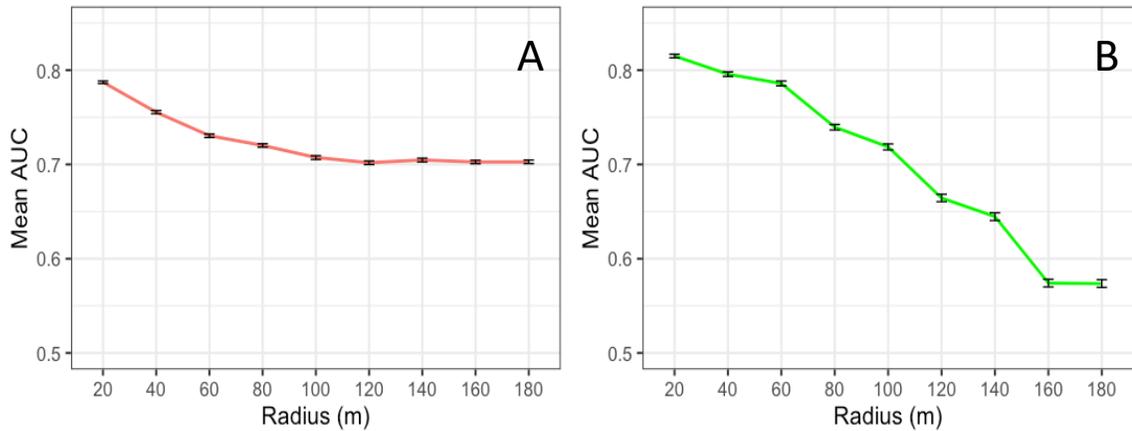


**Figure 3:** Observed richness from acoustic recorders plotted against richness from NEON point count surveys in 2015-2016. The dotted line represents a 1:1 comparison of the two richness measures and each point represents a comparison of richness measures at a site. Points above the line indicate higher observed richness from acoustic recorders compared to NEON point count surveys. Observed richness from 50 random minutes of acoustic recordings during the first 1.5 hours of recording each day was equal or greater than NEON point counts at 19 of 22 sites.

### 3.2. Multi-scale performance of occupancy models

The performance of the frog and bat multi-species occupancy models varied widely depending on the measurement scale. The maximum mean AUC values for both frog and bat models included models using a spatial scale with a 20 m radius around a survey location with no overlap in credible intervals at other scales. For these taxa, there was no difference in optimal scale between the guild models or the whole taxa model.

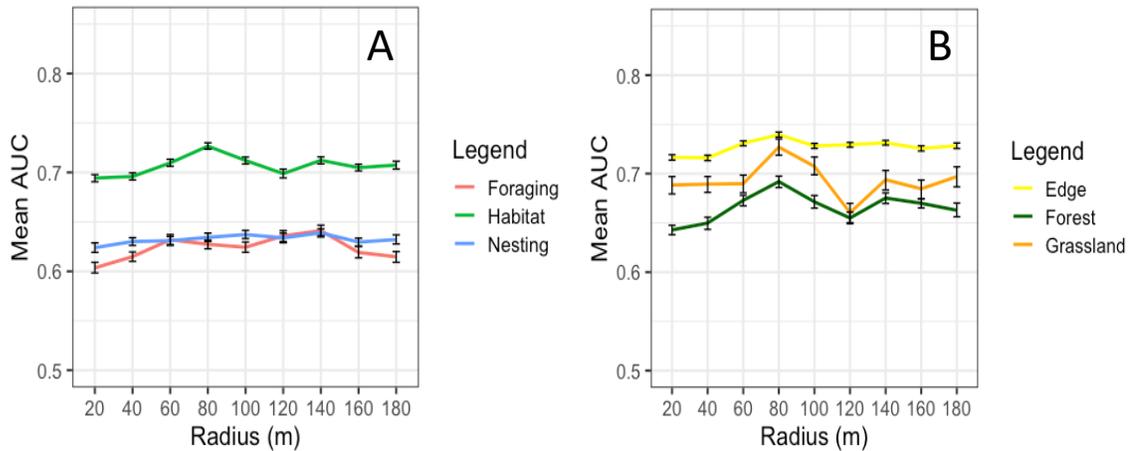
The resulting mean AUC values for the best models were 0.81 (CI: 0.81-0.82) for the frog models and 0.79 ( CI: 0.78-0.79) for the bat models (Figure 4).



**Figure 4:** AUC prediction scores at each scale tested for frogs and bats. Each point represents the mean with dotted lines indicating 95% credible intervals. A) Mean AUC scores for all bat species. B) Mean AUC scores for all frog species.

For birds, the model performance varied depending on both scale and the guild. The mean AUC values were highest for the habitat guilds with a maximum mean AUC = 0.73 with an 80 meter radius ( CI = 0.72-0.73) (Figure 5-A). For the forest birds, the maximum mean AUC value resulted in a mean AUC value of 0.69 ( CI: 0.69-0.70) (Figure 5-B). For the grassland birds, the optimal spatial scale resulted with a mean AUC of 0.73 ( CI: 0.72-0.74) (Figure 5-B). For the edge species, the optimal spatial scale resulted with a mean AUC of 0.74 (CI: 0.73-0.74) (Figure 5-B). For these three guild groups, there was no overlap in the AUC credible intervals at other scales. The mean AUC values for models ran with both the foraging (range 0.60-0.64) and nest (0.62-0.64)

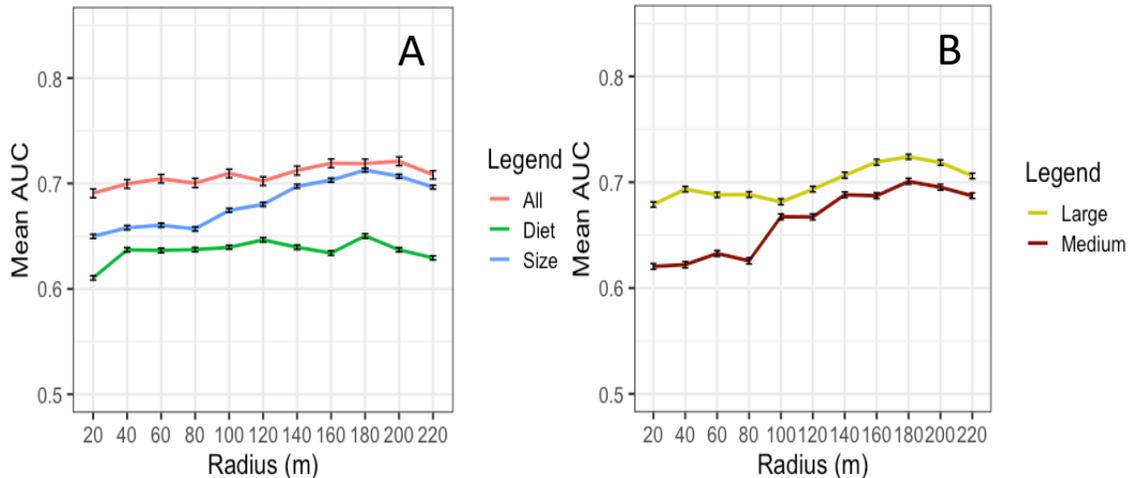
guilds and were much lower than those of models containing habitat guilds (Figure 5-A). The models associated with nesting and foraging classifications were dropped from further analysis due to their lower performance compared to the habitat models.



**Figure 5:** A summary of AUC prediction scores at each scale tested for bird guilds. Each point represents the mean AUC value with error bars indicating 95% credible intervals averaged for all groups within a guild (A). The mean AUC scores and 95% credible intervals for individual groups within the habitat guild (B).

With regards to terrestrial mammals, model performance varied depending on both the measurement scale and the guild. There was no difference between the AUC results of 160 m, 180 m, and 200 m measurement scales when modeling all species together (Figure 6-A). However, there were differences between scale and AUC for terrestrial mammal guilds. Both large body and small body sized mammals resulted in maximum mean AUC values with a 180 m radius and mean AUC scores of 0.72 (CI: 0.72-0.73) and 0.70 (CI: 0.69-0.70) respectively, with no overlap in credible intervals at

other scales (Figure 6-B). The diet guilds performed worse than body sized guilds (Figure 4-A) and were dropped from further analysis in this study.

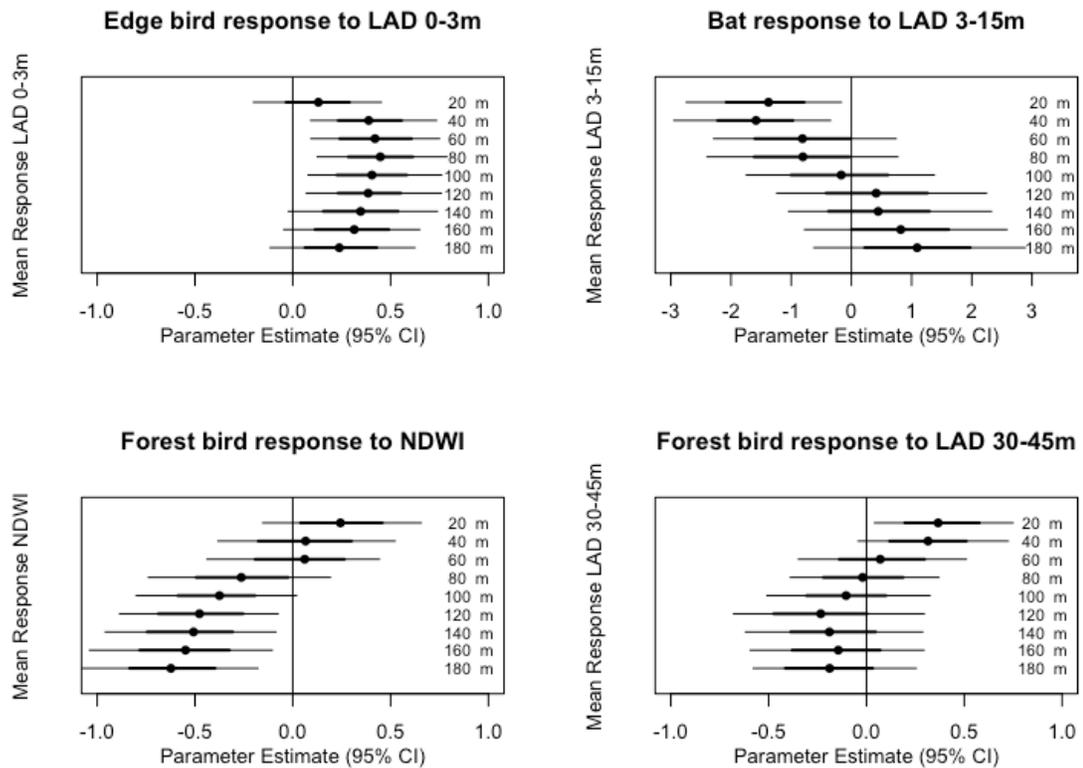


**Figure 6:** A summary table of AUC prediction scores at each scale tested for mammals. Each point represents the mean AUC values with error bars indicating 95% credible intervals averaged for all groups within each guild grouping (A). The mean AUC and 95% credible intervals for individual groups within the body size guild (B).

### 3.3. Differences of scale

The strength and relationship of all model parameters was investigated at each scale. Many of these parameters were scale dependent, changing in magnitude and direction with increasing scale of measure. For example, leaf area density in the upper canopy resulted in a positive relationship, not overlapping zero, when modeling forest bird richness with 20m scaled measurements. However, as the scale of measure increased, the strength of this parameter was steadily reduced to zero with 80m scaled measurements and shifted to a negative relationship with larger scales. Another example resulted from modeling edge bird richness with a 20m scaled measure of understory leaf

area density was not important crossing zero, but the relationship became positive, not overlapping zero, at the 80m scale, and then returning to not important as the measurement scale increases toward 180m. Many other covariates share this wavering trend between positive, neutral, or negative relationships as the scale of measure is increased (Figure 7).



**Figure 7:** Mean bat, edge bird, and forest bird responses to specific covariates across scales. These figures show how the results and interpretations of the results can change depending on which scale is used.

## 4. Discussion

The results of this study indicated that optimal measurement scales can be associated with second- and third-order selection based on habitat heterogeneity and productivity for multiple vertebrate taxa. For frogs and birds these scales were equivalent to the average home range size of each taxonomic group or second-order selection. However, for bats and terrestrial mammals, I found peak performing scales equivalent to areas well within home range sizes or third-order selection. Through the use of continuous high-resolution habitat heterogeneity and productivity measures at a range of scales, models were able to determine the scale that best predicted richness at local levels for each of the vertebrate guilds.

### *4.1. Scale dependence of community-habitat relationships*

#### *4.1.1 Frogs*

Heterogeneity and productivity measurements made within a 20-meter sampling buffer were the best predictors for frog species richness, covering an area of roughly 1257 m<sup>2</sup>. This optimal measurement area is similar to several local frog species home range sizes. Common frog and toad species for this area have home range sizes varying from 751m<sup>2</sup> for wood frogs (SD=±228) (Blomquist & Hunter, 2010), to 688m<sup>2</sup> for American toads (SD=±294) (Forester et al., 2006), and as small as 65m<sup>2</sup> for green frogs (range=20-200) (Martof, 1953). The similarity in frog home range sizes and optimal scale found in this study suggests that habitat heterogeneity and productivity gradients are important for second-order habitat selection according to Johnson's (1980) hierarchical habitat selection framework.

The most predictive scale for frog richness is likely due to the measurement of specific resources needed for amphibian breeding and life history. Frogs depend on moist substrates, increased canopy cover, and complex ground vegetation structure throughout home ranges to satisfy biological needs (Blomquist & Hunter, 2010; Forester et al., 2006). The measures used in this study show a link between these requirements and the scale needed to model frog richness. In addition, relating habitat heterogeneity and productivity measures to these specific requirements could be beneficial to modeling frog richness across larger areas.

#### *4.1.2 Bats*

Habitat heterogeneity and productivity measurements averaged in a 20-meter buffer, or roughly 1257 m<sup>2</sup>, were best predictors of bat occupancy and richness. Models for the two bat foraging guilds were optimal at the same 20-meter scale, indicating that bats using either high frequency or low frequency echolocation calls are responding to habitat heterogeneity and productivity at the same spatial scale, which allowed further modeling to combine all species together at this 20-meter scale.

Unlike frogs, there was little evidence that scale performance is related to the home range size of bat species because performance continued to decrease as the measurement scale increased toward a typical bat's home range (1-3 km from their roost; 65 to > 200 hectares (Owen et al., 2003; Kniowski & Gehrt, 2014). Based on these results, bats rely on fine scale habitat heterogeneity and productivity gradients to select habitat well within their home ranges, linking these measures to third-order selection.

Bat foraging habits offer one possible explanation for the importance of habitat heterogeneity and productivity in third-order habitat selection. Some species have been known to occupy ‘beats’ within 100 m of roost sites for foraging purposes once they are established in an area (Senior, Butlin & Altringham 2005). These “beats” are considered areas within the home range that bats will use more intensively than other areas for periods of time. The optimal scale found in this study is more consistent with similar localized areas of high use where bats travel and forage most frequently within their larger home range. Bellamy, Scott, and Altringham (2013) also arrived at a similar conclusion when testing habitat suitability models for a community of bats with a fine resolution habitat map, finding the finest and best performing scale tested was within a 100-meter buffered area of the survey site. The importance of small-scale habitat factors, such as tree spacing measured at 4 m<sup>2</sup>, has resulted in greater predictivity of bat richness where habitat measures at 4 km<sup>2</sup> were not able to explain variation within bat species (Gehrt & Chelsvig, 2003). Thus, habitat heterogeneity and productivity are linked to third-order selection for bats, possibly based on preferred roosting and foraging areas within home ranges.

#### *4.1.3 Birds*

The best performing scale of habitat heterogeneity and productivity measurements for birds resulted from a radius of 80 m (roughly 2 ha). Regardless of habitat requirements or guild grouping, bird species seem to select habitat based on heterogeneity and productivity at similar scales. The bird species observed in this study have a variety of home range sizes, however the average response was best at scales

within or near most avian home range sizes. This is consistent with other studies that observed the strongest relationships between individual bird species and habitat heterogeneity or structure occurred at scales between 0.2 and 4 ha, smaller than the typical home range of locally observed species (Seavy, Viers, & Wood, 2009; Weisberg et al., 2014). The selection of habitats based on heterogeneity and productivity at approximately 2 ha as an average of all species best relates to second-order selection near home range size of birds (Figure 5). This result suggests resources related to habitat heterogeneity and productivity may be important in defining home range size in birds.

#### 4.1.4 Terrestrial Mammals

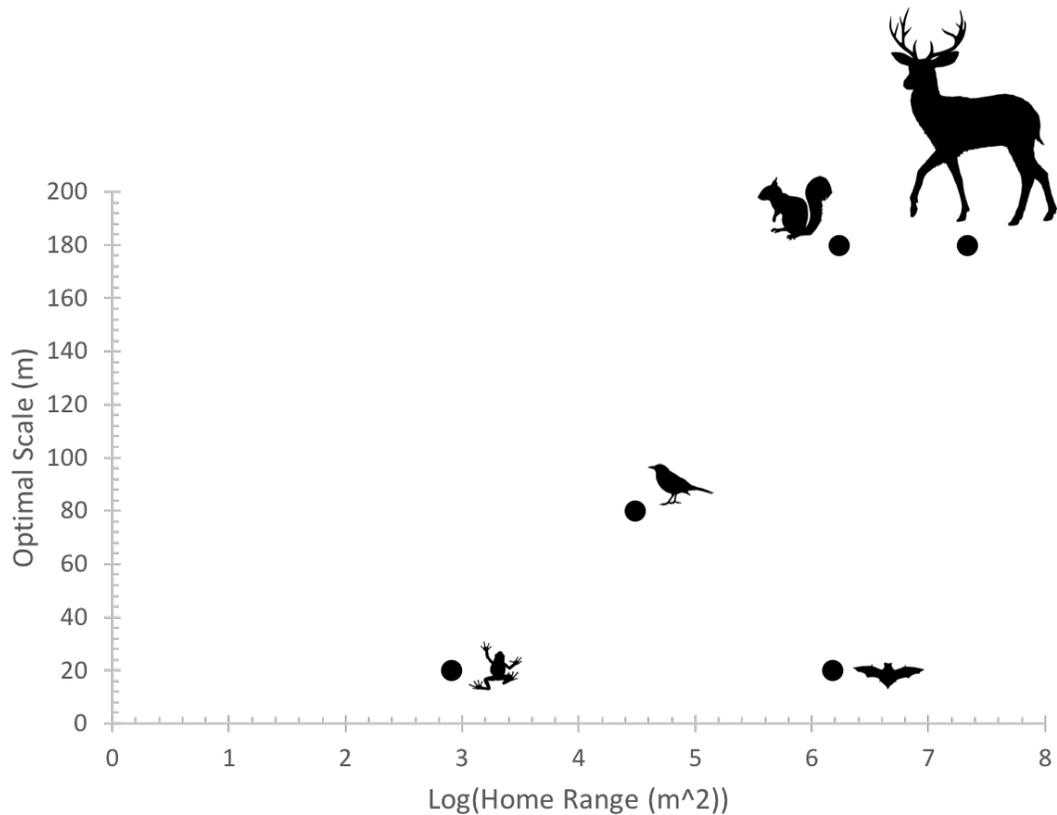
Mammal richness was best predicted by measurements with a radius of 180 meters, much larger in scale compared to other taxonomic groups surveyed. However, this buffered area equivalent to approximately 10 hectares only represents a small percentage of the average home range size for observed mammals. Models that included all species performed better than guild grouping and resulted in the highest performance at 180-meter radius. Both the body size and the diet guilds resulted in this same optimal scale, indicating that mammals are selecting for habitat heterogeneity and productivity at similar scales regardless of body size or diet type.

As with bats, the scale of habitat preference for terrestrial mammals relates to third-order selection including areas well within the average home range which often exceed 10 hectares. For example, the mean home range of a white-tailed deer, *Odocoileus virginianus*, is 196 hectares (Byford, 1970) and the mean home range size of a coyote, *Canis latrans*, is 7598 hectares (Ozaga and Harger, 1966), which is much larger than the

optimal scale for predicting mammal occupancy found in this study. This suggests that habitat heterogeneity and productivity are linked to third-order habitat selection for terrestrial mammals.

#### ***4.2. Patterns across taxa and guilds/inferences from these models***

The use of the correct scale is important in measuring these specific resources, as measurement scales too large could lead to incorrect assumptions and conclusions (Mayor et al., 2009; McGarigal et al., 2016). I found that fine resolution measures of habitat heterogeneity and productivity can be used to model species richness and occurrence for different taxonomic groups at local scales. The influence and strength of these measures varied among taxa and between guilds. By using multiple taxonomic groups for this study, I was able to show that home range may not always be the best indicator of optimal measurement scale. In terms of Johnson's (1980) framework and subsequent reviews (Mayor et al., 2009; McGarigal et al., 2016), the selection of habitat heterogeneity and productivity can be observed at scales equivalent to areas of second- and third-order habitat selection for a range of vertebrate taxa. Habitat heterogeneity and productivity measures for taxonomic groups that utilize the entirety of their home range to satisfy life history requirements are best linked to second-order selection scales, such as birds and frogs. Alternatively, measures used for taxonomic groups that divide their home range into foraging, breeding, and resting areas are better linked to third-order selection.



**Figure 8:** A figure showing optimal scale plotted against the log of average home range size within each taxonomic group. Home range sizes here are represented as the average size within each taxon for common species in found in Northern Virginia. The blue dotted line represents a fitted linear trendline to the data.

### 4.3. Limitations

There were several limitations to this study that were inherent in the sampling methodology. One limitation was the ability to consistently detect animals or signals within a certain range from the sensor. Due to our passive diversity monitoring techniques, I was not able to confidently identify the distance animals were actually recorded from the acoustic recorder or camera trap. Recording units and cameras should detect at least 20 meters under ideal conditions with no obstructions. Due to this, 20 meters was the smallest sampling buffer used to measure habitat heterogeneity and

productivity. Therefore, the most appropriate measurement scale for taxonomic groups such as frogs and bats with optimal scales at 20 meters might be smaller than 1257 m<sup>2</sup>. Future studies should sample for richness within a defined area or even use high temporal resolution movement data to test for habitat selection preferences smaller than 1257 m<sup>2</sup>.

A second limitation within this study was inherent in the study design. With units spaces at least 200 meters apart, my analysis was only able to consider scales out to 200 meters from the survey location without increased spatial autocorrelation. For terrestrial mammals, this means that the highest performing scale might not be 180 meter if larger scales are considered. Future studies should test habitat selection with these measures at larger scales with a broad diversity dataset to test how using larger scales influences the predictivity of these models.

A third important limitation to note from this study was that models were not optimized for scale with each covariate. The methods used here only optimized for overall scale, assuming that the response to habitat heterogeneity and productivity should occur at the same scale regardless of measure used. However, a better performing model might optimize for scale and include measurements made a different scales within one model. The time and resources were not available to test this scale optimization method and should be considered in future studies.

#### ***4.4. Conclusions***

Unfortunately, there is not a consistent pattern in selection order across taxonomic groups, but this study helps to explain possible differences in habitat selection scales between vertebrate taxa. There is potential to use habitat metrics from high resolution

remote sensing data to obtain the habitat measurements needed to accurately model richness across large areas based on habitat selection among species. This approach could allow better downscaling of species richness models that currently poorly predict local richness for many taxa. Approaches that identify richness patterns relative to vegetation conditions using high resolution data can only increase our ability to model species richness in small spatial units and increase our understanding of relationships between habitat selection and species richness, helping support management decisions across large scales (Vierling et al., 2008). Commonly used remote sensing data such as LiDAR also gives us the ability to scale up these models and measurements to apply at larger scales, possibly improved by incorporating other data sources such as movement, occurrence, and citizen science data. By linking large scale vertebrate richness monitoring networks to local habitat heterogeneity and productivity, larger questions can be asked about how scale affects species richness, community richness, and species distributions.

## **CHAPTER TWO: THE RELATIVE INFLUENCE OF HABITAT HETEROGENEITY AND PRODUCTIVITY ON AVIAN SPECIES RICHNESS AT THE COMMUNITY LEVEL**

### ***1. Introduction***

Over the past two decades, management efforts have shifted from the preservation of individual species toward the conservation of functional ecosystems that support diverse assemblages of species (Reid et al., 1998; Myers et al., 2000; Mittermeier et al., 2011; Marchese, 2015). Birds are typically the focal taxa in these studies due to fact that they are highly mobile, allowing species to select the best available habitats needed to support migratory populations, as seen in more than one third of the heterogeneity-diversity studies reviewed by Tews et al. (2004) between 1960 and 2003. Two seminal hypotheses that explain the relationship between ecosystems and bird diversity are the habitat heterogeneity (Currie, 1991) and the productivity-richness hypotheses (Waide et al., 1999). These hypotheses have been tested globally in a variety of ecosystems with differing spatial scales (Stein, Gerstner, & Kreft, 2014). Unfortunately, the coarse scale environmental data used to test these relationships tends to break down at local scales to non-significant relationships (Mittelbach et al., 2001). To find significance in the relationship between species richness and habitat heterogeneity and productivity at local scales, fine resolution habitat data is needed to test these hypotheses across large areas.

The habitat heterogeneity hypothesis predicts that more heterogeneous habitats will support a greater number of bird species by providing a higher density of niches compared to homogenous habitats (MacArthur, 1972). The higher density of niches in complex habitats are associated with a higher diversity of resources which facilitates resource partitioning (Harrison Cornell, & Moore, 2010). A half century ago, MacArthur and MacArthur (1961) first described how heterogeneity in foliage heights was correlated with avian richness and this relationship has been repeatedly shown to be a critical factor influencing bird life histories (Halaj, Ross, & Moldenke, 2000; Kelly, 1993; Robinson & Holmes, 1984). More recently, fine resolution structural heterogeneity metrics captured by remote sensors have proven useful for explaining differences in avian richness across large areas, such as the United States (Huang et al., 2014). Similar vertical heterogeneity metrics have been associated with higher avian richness regardless of foraging, nesting, and habitat requirements (Weisberg et al., 2014). The habitat heterogeneity theory has generally predicted avian species richness significantly better than other theories with fine resolution habitat data (Rahbek & Graves, 2001; Kerr & Packer, 1997).

However, the productivity hypothesis still has widespread support and hypothesizes that as vegetation productivity increases species richness also increases (Rosenzweig, 1995; Waide et al., 1999). Productivity-richness relationships have proven important for avian richness and are positively related at global and regional scales in most cases (Nieto et al., 2015). Simple productivity indices such as the normalized difference vegetation index (NDVI) can explain up to 61% of the variation in avian species richness across North America due to large differences in productivity (Hurlbert

and Haskell, 2003). These measures have shown great promise as surrogates of avian richness across broad scales but have been hard to scale down to regional and local landscapes because of challenges measuring productivity at such relatively small scales across large areas.

Researchers have explored significant relationships between avian richness and habitat characteristics at local scales within individual patches using field based measures and independent sites (MacArthur & MacArthur, 1961). However, scaling results up to larger areas becomes very difficult and labor intensive. In addition, different avian guilds seem to respond differently to these measures at different spatial scales (Weisberg et al., 2014). Since coarse resolution measures of productivity and heterogeneity deteriorate in their ability to predict species richness at smaller local scales, scientists need to distinguish the relative importance of new technologies for determining the significance of relationships between habitat heterogeneity and productivity and species richness at local scales.

Relatively new technologies, such as light detection and ranging (LiDAR) and hyperspectral imagery, have provided information about the three-dimensional structure of habitats across landscapes with finer resolution compared to satellite-based measures (Lefsky et al., 2002; Turner et al., 2003; Vierling et al., 2008). Researchers have used these new methods for fine scale measures of structural heterogeneity and productivity indices, finding moderate correlations with observed avian richness (Clawges et al., 2008; Seavy et al., 2009; Goetz et al., 2007; Swatantran et al., 2012). These fine resolution measures of productivity and heterogeneity are needed to relate avian richness at scales

where conservation efforts are practiced, and can easily be scaled up to measure the effect of productivity and heterogeneity on avian richness at multiple scales (Huang et al., 2014).

The objective of this study was to test how well these hypotheses predict avian species richness at fine scales with measurements from remote sensors. I tested habitat heterogeneity and productivity metrics for independent bird guilds and for all bird species grouped together looking for any major differences in response. Based on the habitat heterogeneity hypothesis, I predicted total avian richness to be positively associated with habitat heterogeneity both vertically and horizontally, as these heterogeneous habitats provide greater environmental pressure to maintain, thus creating more niche opportunities with more specialized needs. Based on the productivity-richness hypothesis, I predicted avian richness would be positively associated with productivity because increased energy and resources provide greater opportunity for more species to inhabit an area with less competition. Individual guilds, such as forest and grassland birds, were predicted to differ in the magnitude of their response to these measures because specific groups of birds vary drastically in the resources needed and behaviors expressed. For example, grassland species were predicted to respond more to heterogeneity than productivity measures, and vice-versa for forest species. Overall, both local habitat heterogeneity and productivity were predicted to be highly influential in estimating avian richness at small spatial scales.

## ***2. Methods***

### ***2.1. Survey location selection***

This study took place at three locations in northern Virginia, including the Smithsonian Conservation Biology Institute (SCBI) in Front Royal (38°53'18.38" N, 78°09'52.38" W), Blandy Experimental Farm in Boyce (39°03'48.72" N, 78°03'46.84" W), and Casey Trees Farm in Berryville (39°05'25.60" N, 77°58'36.92" W). These locations were selected to match areas within Domain 2 of the National Earth Observatory Network (NEON) that represent a gradient of management areas and that matched avian diversity monitoring performed by NEON. All sites included fields used for hay production, abandoned fields, and mature stands of hardwood forests with distinct edge habitats between fields and forests (Bourg et al., 2005). Ponds, secondary and tertiary streams, and bottomland hardwood stands were also present at all sites.

Sites were selected using a spatially balanced randomized grid, utilized by NEON at all survey sites, for avian monitoring (Theobald et al., 2007). During 2015, survey sites for this study were matched to the avian point count survey locations of NEON diversity surveys. In 2016, new survey locations were chosen from the random grid and there was no overlap in survey sites between years. The number of forest and field survey locations chosen at each site was representative of the overall ratio of forest to open area. Forest was considered a combination of National Land Cover Database 2011 (NLCD) classifications for forest, woody wetlands, and shrub/scrub. Open area was considered a combination of NLCD classifications of cultivated and grassland/herbaceous.

## **2.2. Monitoring methods**

Avian richness was surveyed with Wildlife Acoustics' SM3BAT acoustic recording units (ARUs). We deployed each ARU with a single omnidirectional microphone (flat frequency response between 50-Hz and 20-kHz) and standardized gain. I sampled recordings with 16-bit digitization and a 24-kHz sample rate. The units saved each recording in a WAV file format (Tierney et al., 2013). We matched and recorded the diel and seasonal timing of ARU deployment to the peak activity for birds. Each site was surveyed in two 6-day deployments with an ARU that was activated for three hours starting 30 minutes before sunrise during late May and June. During each active period, the unit recorded one minute out of every ten minutes, collecting enough recordings to match standard point count survey results (Cooper et al., in prep 2018).

## **2.3. Data processing**

### *2.3.1 Acoustic data*

Sound files from each survey location were first processed to subsample sound recordings. I used the first 1.5hrs of recordings each day (30-min before sunrise to 1 hour after sunrise), containing the most diverse and active number of frequencies to allow for the best estimate of species occurrence. From these recordings, I randomly subsampled 50 recordings from each site to determine the observed species richness. Each of these one-minute recordings was listened to manually to identify any bird songs and calls, using both aural and visual signatures from spectrograms in Rave Pro 1.4 (version 1.4). Observed species were then categorized into distinct guilds, forest, grassland, or edge. Based on habitat requirements (Rodewald, 2015).

### *2.3.2 Remote sensing measures*

To test a gradient of scales in the occupancy models, I averaged scale-dependent habitat heterogeneity and productivity measurements over a buffered area 80m from each survey location. NEON's Airborne Observation Platform (including a full waveform and discrete-return LiDAR sensor, a hyper-spectral imaging spectrometer, and a high-resolution camera) flew over our three sites in two 100 km<sup>2</sup> flights in August 2016; SCBI in one flight, and both Blandy and Casey Trees in the second flight. Using the classified LiDAR point cloud downloaded from NEON's database, LiDAR height returns were stratified and standard ground metrics were calculated using the "lidR" package in R version 3.3.2 (Roussel & Auty, 2018). Measurements included the leaf area density (LAD) for undergrowth (0-3 meters), understory (3-15 meters), mid-canopy (15-30 meters), and upper canopy (>35 meters), as well as the percentage of LiDAR returns classified as "ground" at each location within a given radius for area (see Table 1). In addition to these vertical habitat measurements, the slope, aspect, and elevation were averaged from the LiDAR data using the same R package.

NEON also produced raster products from their hyperspectral imagery readily available for download (<http://data.neonscience.org/>). NEON's available enhanced vegetation index (EVI) and normalized difference water index (NDWI) raster products, derived from their hyperspectral imagery, were used to calculate the mean EVI and NDWI for each location using the "raster" package in R version 3.3.2 (Hijmans, 2017) (see Table 1). The averaged EVI represents a surrogate measure of vegetation productivity and health, with high values indicating healthy vegetation (Huete et al.,

2002), averaged at each radial distance around each location. Similarly, NDWI is a surrogate for drought stress, with a high value indicating high water content within vegetation and soil (Gao, 1996), averaged at each radial distance around each location.

Occupancy covariates included remote sensing measurements of productivity, heterogeneity, and other explanatory factors. Productivity included undergrowth leaf area density (LAD) (0-3 meters), aboveground LAD (for frogs and mammals; >3 meters), understory LAD (for birds and bats; 3-15 meters), mid-canopy LAD (for birds and bats; 15-30 meters), upper canopy LAD (for birds and bats; >35 meters), EVI, and NDWI. Heterogeneity included measures of horizontal heterogeneity such as the standard deviation in EVI and NDWI, as well as vertical heterogeneity measures such as the standard deviation in vegetation height. Other variables included average slope, aspect, and elevation to account for local variance not included in the heterogeneity or productivity measures.

In addition to previously identified scale-dependent variables, such as percentage ground returns from LiDAR, leaf area density (LAD) of undergrowth (0-3 meters), understory (3-15 meters), mid-canopy (15-30 meters), and upper canopy (>35 meters) measured within an 80m radius around a survey site (Cooper et al., in prep 2018), I evaluated non-scale dependent variables that might help account for variance in the data that might not be explained by habitat heterogeneity or productivity (Table 1). These variables included the distance to the nearest developed area and the distance to the nearest primary water source. Developed areas were defined with the development classifications of NLCD (Homer et al., 2015). Water sources were defined using the U.S.

Geological Survey (2013) as large areas with surface water such as rivers, lakes, or ponds. Distances from survey locations to these areas were measured using the ‘rgeos’ package in R version 3.4.3 (Bivand & Rundel, 2018).

Detection covariates varied for each daily survey period included mean daily temperatures, mean daily wind speeds, and total daily precipitation. Daily weather measurements were taken by NEON at each site on a 30-minute basis and downloaded from their online database (<http://data.neonscience.org/>). The LAD at the height of the ARU (0-3 meters) was also used as a detection covariate, as obstruction of vegetation around the acoustic and camera devices can limit detections.

## ***2.4 Statistical analysis***

### *2.4.1 Modeling Approach*

Bayesian multi-species hierarchical occupancy models estimated total species richness at each site while accounting for uncertainty in detection (Zipkin et al., 2012). These models link occupancy models for individual species to make inferences at the community level while accounting for imperfect detection. The use of spatially replicated sites, as those used in this study, allow these models to use data from commonly detected species to better estimate the occupancy of rarer species. These models can be used to evaluate how whole communities of species respond to environmental variables, such as habitat heterogeneity and productivity (Russel et al., 2009). The averaged response to covariates across all species are thus considered community level parameters. All community occupancy models for each guild and for all species used habitat measurements made at 80m around each survey point (Cooper et al., in prep 2018).

Since info-theoretic model selection techniques (e.g. AIC or BIC) are not valid with Bayesian models, I implemented model selection using posterior model probabilities and the Kuo and Mallick indicator variable statistic (Kuo & Mallick 1998). This method helps refine Bayesian based models (Royle & Dorazio, 2008; O'Hara & Sillanpaa, 2009; Tenan et al. 2014; Hooten & Hobbs, 2015) and allows the expansion of a model to include a set of binary indicator variables, referred to here as  $w_x$  where  $x$  corresponds to each covariate within the model. If  $w_x = 1$ , the associated covariate  $x$  is included for that iteration of the model, but if  $w_x = 0$ , the covariate  $x$  is not included. Model selection was equivalent to estimating the posterior probabilities of each covariate  $x$ , or  $\Pr(w_x = 1)$ . The prior was  $w_x \sim \text{Bernoulli}(0.5)$  to allow for an equal probability of  $x$  being included or not included in the model. To ensure that a model converges on a reasonable value, initial samples were thrown out as they could be wrong since they have not been influenced by previous samples. These initial throw-away samples are called burn-ins. Each model used an indicator variable for each of the occupancy covariates with 10,000 burn-in iterations, after which 5,000 iterations of the model were saved. The selected covariates with the greatest posterior probability were then selected for the final model (Table 4).

Model selection using the Kuo and Mallick indicator variable allowed for the elimination of variables with little influence in the final models. The final models for each guild and all species were built using the combination of covariates with the highest posterior probability for each guild (**Error! Reference source not found.**Table 4). Two covariates were eliminated from all models, the percentage of ground and mean aspect within a 80m radius of the recording site.

To quantify the effect size of the final model covariates in relationship to total avian species richness, I used an average predictive comparisons technique (APC)(Gelman & Pardoe, 2007). Using APC, I evaluated the difference in expected responses for a specified unit increase in an input covariate, using the final fitted model, and averaging over the distribution of all other covariates. Species richness estimates were calculated by summing all species-specific predictions to obtain average expected differences in species count with changes in one variable at a time (Jones et al. 2012). Specified differences for input covariates included a 10% increase in slope, NDWI, EVI, leaf area density at each vertical layer, as well as a 100m increase in distances from water and 500m increase from developed areas, and a 5m increase in the standard deviation of vegetation height (Figure 9).

#### *2.4.2 Model Validation*

To validate models for total species richness, I extrapolated predictions from model outputs across the survey sites and surrounding areas (Kery & Royle, 2018). This produced estimated avian species richness maps at the 160m scale. Rasterized outputs were generated from the LiDAR and hyperspectral data for each covariate measure. The number of species predicted to occupy each cell was summed using occupancy probabilities to estimate total species richness (Dorazio et al., 2011).

Predicted species richness was validated with species richness calculated from point count surveys performed by Virginia Working Landscapes (VWL 2011-2018; Johnson, 2017) within the area covered by NEON's remote sensor. I omitted any flyover species not used in my models, such as hawks, crows, and falcons, to directly compare

VWL survey results to how the final avian species richness model performed. To evaluate the performance of our species richness models, I compared estimated avian species richness against the observed species richness from VWL's point count surveys using linear regression. Performance was then evaluated using the significance and correlation strength of  $R^2$  values (p-value = 0.05) calculated from this linear regression for estimated total species richness across the landscape.

### **3. Results**

Relationships between species richness and measures of both habitat heterogeneity and productivity varied between habitat guilds (Figure 9). Final model selection for each habitat guild indicated large differences in the direction and importance of these measures. For example, leaf area density in the understory (LAD from 0 to 3m) was negatively associated with occupancy in forest guild species, positively associated with edge guild species, and not selected for in the final model of grassland species. The only covariate included in all three habitat guilds was upper story LAD from 15-30m. Occupancy was not only negatively associated with this measure for grassland and edge species, but interestingly this trend resulted with forest species as well. Multiple productivity covariates were included in all final guild models but the only important habitat heterogeneity covariate for these models was the standard deviation in vegetation height for forest species. Heterogeneity in the form of standard deviations in EVI and NDWI were not selected as important occupancy predictors for any guild.

The final model for all species contained thirteen of the fifteen original covariates. Covariates selected for in each guild model were also selected for in the final model of all

avian species. Additionally, the all species model included all horizontal heterogeneity covariates, unlike the guild specific models (Figure 9). The parameters associated with average occupancy across all species varied in strength; however, six of the thirteen selected covariates showed consistent relationships where the 95% credible intervals did not overlap zero. These six covariates included distance from development, EVI, standard deviation of EVI, LAD 15-30m, LAD >30m, and standard deviation of NDWI. Of these, distance to development and standard deviation of EVI were the only positively associated factors influencing occupancy across almost all species. Factors negatively influencing occupancy across most species included EVI, LAD 15-30m, LAD >30m, and standard deviation of NDWI. All other selected covariates were considered important in determining occupancy for individual species and thus included in the final model;

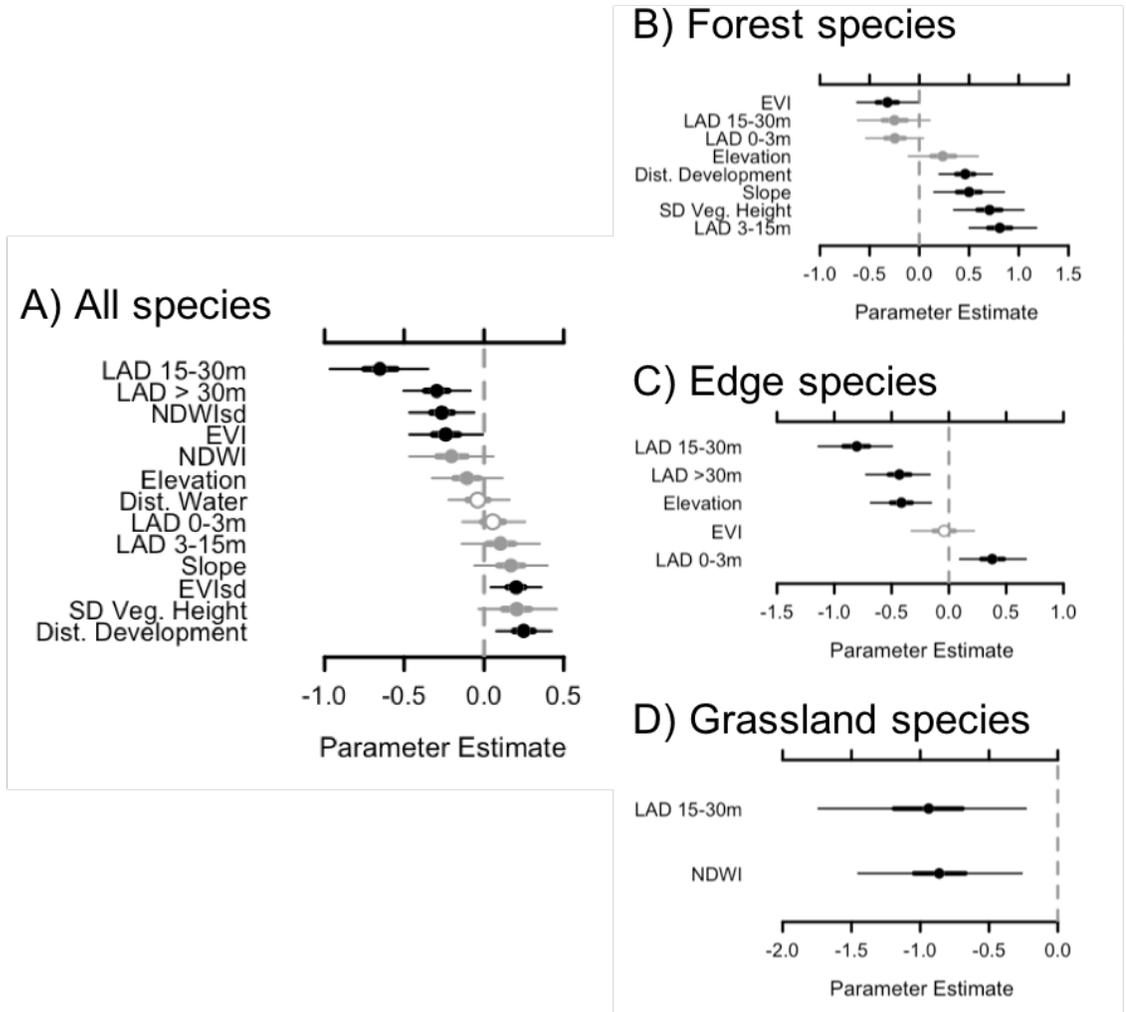
**Table 4:** Model selection using posterior model probabilities and the Kuo and Mallick (1998) indicator variable statistic. All variables marked with X were determined to be related to avian species richness for a given guild.

Guild	Other Factors						Productivity						Heterogeneity		
	Slope	Aspect	Elevation	Dist. To Water	Dist. Development	% Ground	LAD 0-3m	LAD 3-15m	LAD 15-30m	LAD 30-45m	EVI	NDWI	SD Height	SD EVI	SD NDWI
Forest	X				X		X	X	X		X		X		
Grassland									X			X			
Edge			X				X		X	X	X				
All	X		X	X	X		X	X	X	X	X	X	X	X	X

however, the relationship of each parameter was not consistent between species (i.e. positive or negative). This inconsistency averaged across species causes the community parameters to overlap zero and appear insignificant, but they are still considered important in the occupancy part of the hierarchical model for individual species used to estimate total species richness.

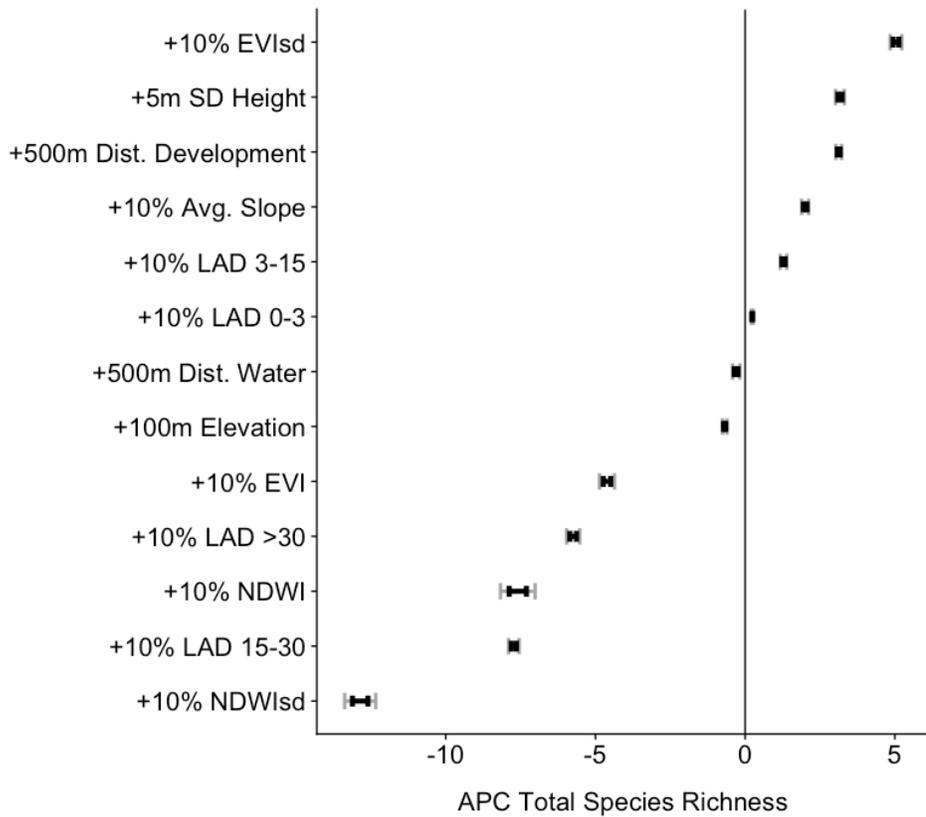
Individual species responses to covariates indicated many avian species respond similarly to certain covariates but oppositely to others. For example, almost all species' occupancy probabilities are predicted to increase as the standard deviation of EVI increases (Figure 11). As indicated earlier, some parameters appear non-important because the response parameters to these factors become averaged out across multiple species. Two examples of this are the responses to vertical heterogeneity and understory leaf area density (LAD from 3-15m). The average occupancy across species does not increase nor decrease with increases in these two measures (Figure 11). This is because occupancy for half of the observed species is negatively associated with increases in these parameters, while occupancy for other species is positively associated with these parameters. This averaging effect in community parameters indicated variables that may be less influential for estimating total avian richness outside of hierarchical frameworks.

APC demonstrated how changes in productivity or heterogeneity potentially affect species richness when all species were modeled together. The largest effects on total avian richness for the all species model were seen with heterogeneity measures (Figure 10). Productivity measure were also important, but had less effect on overall species richness estimated from the all species model. An increase in 10% standard



**Figure 9** Caterpillar plots of species richness for variables in best models when modeling species richness for A) all, B) forest, C) edge, and D) grassland species. Shading represents whether 50% credible interval (gray with open circle), 95% credible interval (gray with closed circle), or neither (black) overlap zero.

deviation of EVI was predicted to increase richness by about 5 species. Alternatively, an increase of 10% in the standard deviation of NDWI was predicted to lower avian richness by almost 13 species. For vertical heterogeneity, a 5m increase in the standard deviation of vegetation height was predicted to increase species richness by almost 4 species. Other

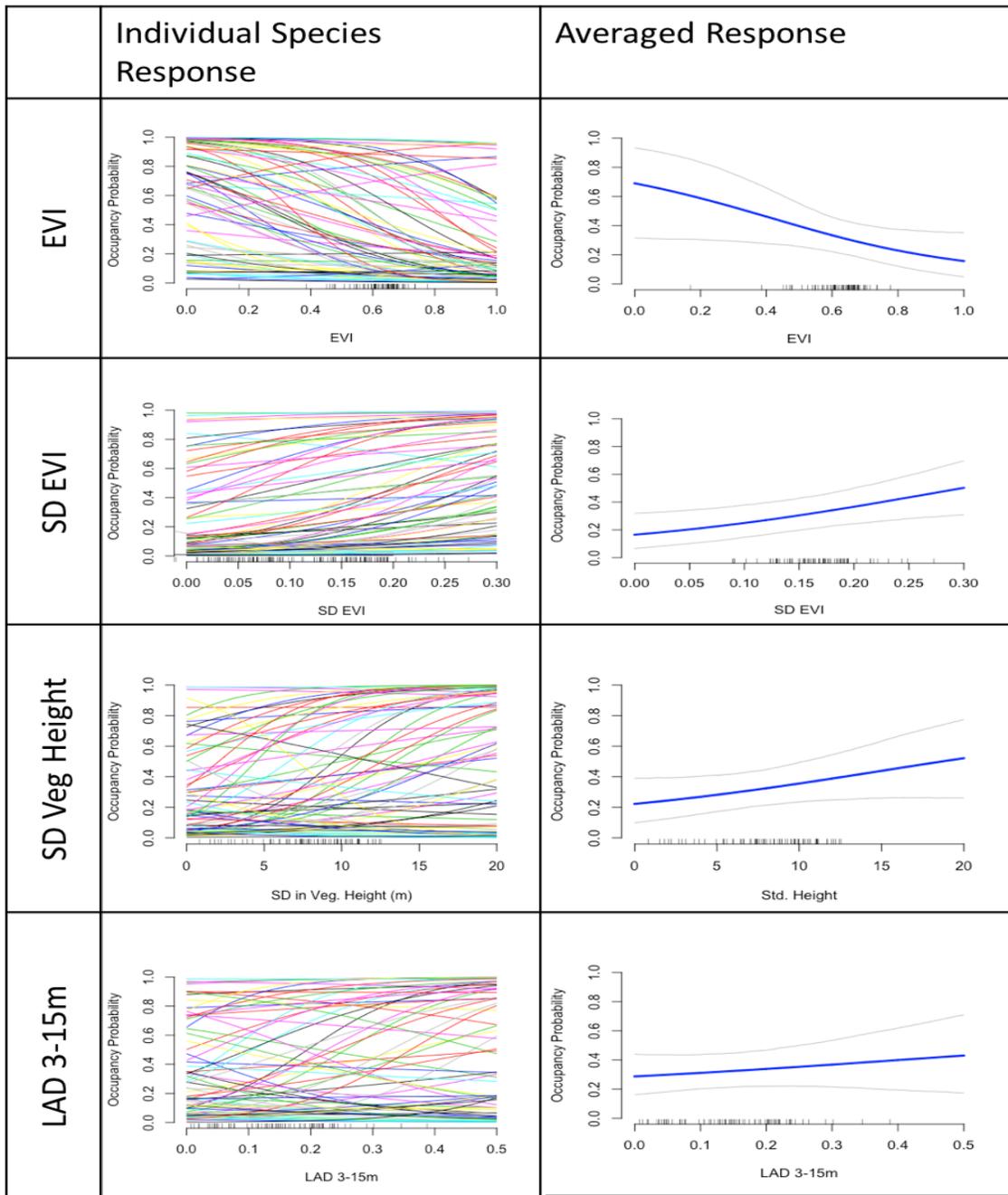


**Figure 10** Average predictive comparisons (+/- 1 and 2 standard errors) for the association between estimated total avian species richness and selected model covariates. A change in the number of species present, represented on the x-axis, are based on a 10% increase in leaf area density at each vertical stratum, a 10% increase in slope and the indices NDWI and EVI, a 10% increase in the SD of NDWI and EVI, a 100m increase in distances from water, a 500m increase from developed areas, and a 5m increase in the standard deviation of vegetation height.

parameters that indicated a gain of species resulted from a 10% increase in LAD from 0m to 15m. Parameters indicating a loss of species included increased EVI, LAD above 15m, and increased NDWI. Results indicated that other factors such as distance to development or water, elevation, and average slope were also considered important in the final model estimating total avian richness but did not show large gains or losses when measures were

increased. Overall, heterogeneity was the greatest predictor of total richness, followed by productivity measures for the all species model.

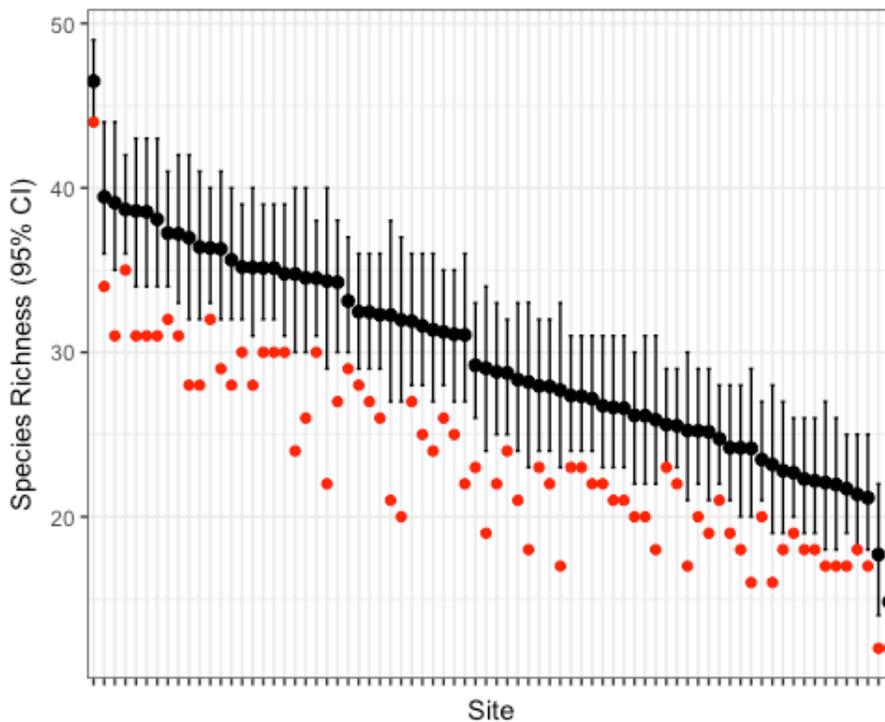
Species richness estimates and maps produced from model outputs showed distinct areas of high and low richness for each guild as well as distinct areas of higher total richness. The final model evaluating total avian richness performed well at any given survey location as sites with high observed richness were predicted to have the highest estimated richness and vice versa with sites of low observed richness (Figure 12). I extrapolated these predictions across the landscape as a map for total richness and for guild specific richness (Figure 13). The forest guild had the highest average richness across the survey area (mean = 15 species) followed by edge guild species (mean = 14 species) and lastly grassland guild species (mean = 2 species). Across survey sites, the average in total richness was roughly 31 species. The largest standard deviation for any single pixel of estimated species richness resulted from forest richness estimates (max SD = +/- 4 species), followed by edge richness estimates (max SD = +/- 3 species), and lastly



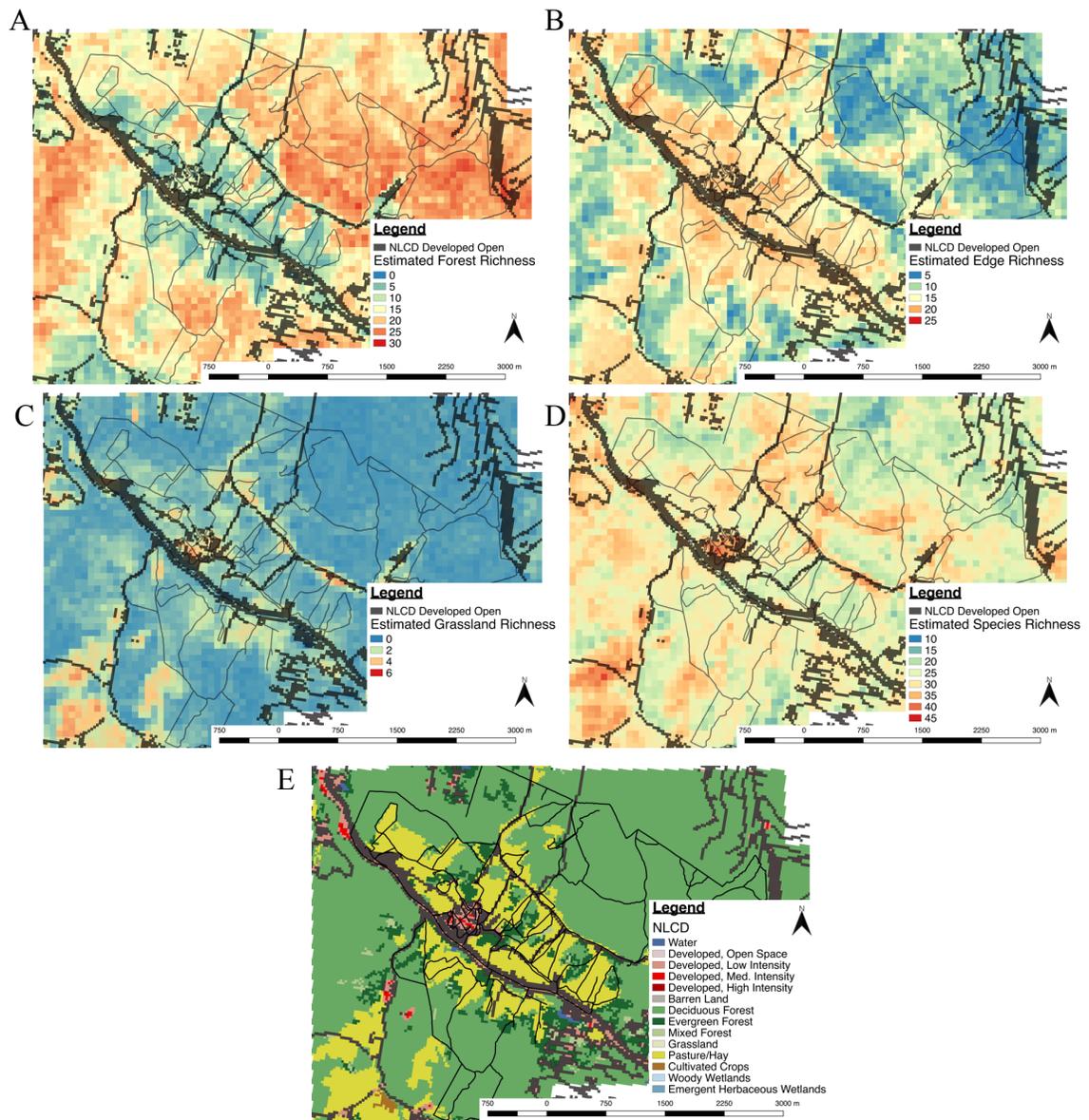
**Figure 11:** Species specific and mean occupancy probabilities of all observed birds based on EVI, SD of EVI, SD of vegetation height, and LAD 3-15m. Elements on the left represent all individual species-level response to changes in these measures. Graphs on the right represent the average occupancy value across all observed species. Gray lines indicate 95% credible intervals. The hash marks on the x-axis indicate actual observations for each respective covariate.

grassland richness estimates (max SD = +/- 2 species). Overall, standard deviations did not vary drastically for individual estimates across the survey areas, indicating that uncertainties in total species richness estimates were fairly uniform.

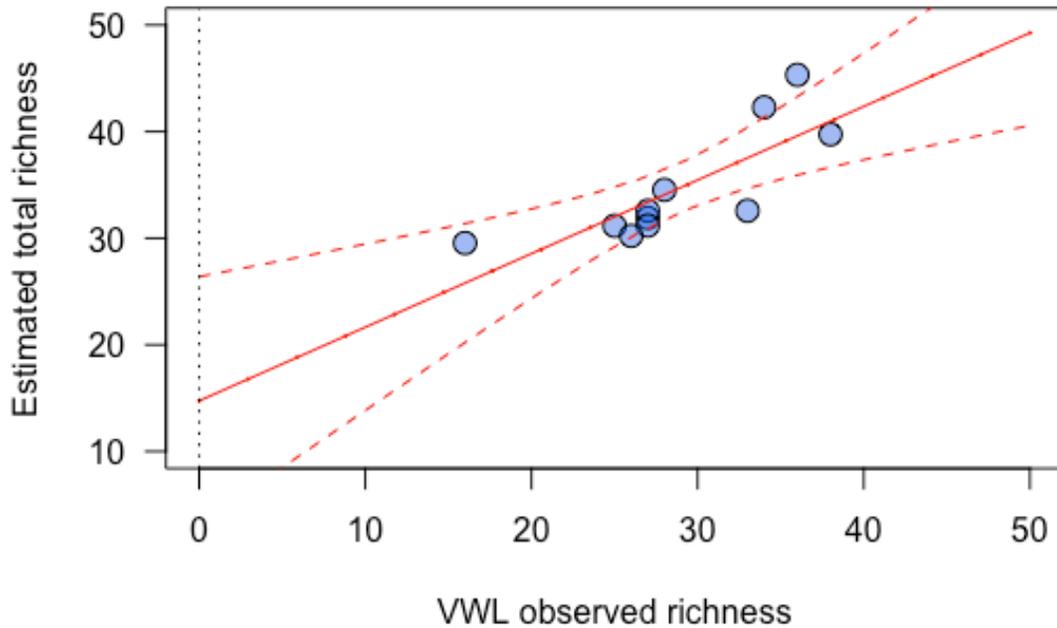
Maps were validated with the estimated total richness within the pixel where each VWL grassland point counts were performed. After removing all species from the VWL data that were not accounted for in my final model as well as flyover observations, validation from VWL's avian point count surveys revealed a significant relationship with moderate predictive power between the point count data and our avian richness estimated from ARD recordings with an  $R^2 = 0.63$  ( $P < 0.01$ ) (Figure 14).



**Figure 12:** Observed richness from ARDs and estimated richness from the final model at each survey location. Red dots indicate actual observed richness, black dots indicate mean predicted richness, and lines represent the 95% credible interval.



**Figure 13:** Maps estimating total forest (A), edge (B), grassland (C), and all (D) avian richness across SCBI. Areas in dark orange representing areas with an estimated higher avian richness for each guild or for all species from predictive models. Blue areas representing areas with lower avian richness. E) A landcover map based on NLCD 2011 data products available for the SCBI area.



**Figure 14:** Observed Virginia Working Landscape (VWL) richness from point count surveys and estimated total richness from my models. Solid red line represents linear model prediction from these data calculated in R software (Version 3.5.1). Dotted lines represent 95% confidence intervals.

#### ***4. Discussion***

While it is highly unlikely that a single mechanism is responsible for driving avian richness, the combination of heterogeneity and productivity measures are important to include compared to using either one alone when modeling avian richness across habitat guilds. The results of this study emphasize the importance of spatial arrangement in vegetation and the role it plays associating the quality and quantity of habitat that provide a diversity of ecological niches which support avian species.

#### ***4.1 Total avian richness***

The productivity-richness hypothesis was only partially supported in this study. Productivity parameters did not result in positive parameters throughout the vertical strata as hypothesized, and the traditional productivity index, EVI, resulted in a negative response with total species richness. For this study, increased productivity in the understory and mid-canopy showed support for the productivity hypothesis, while upper canopy productivity measures failed to support this hypothesis as these productivity covariates were negatively associated with richness parameters. Results from Bae et al. (2018) also show productivity indices and canopy densities were negatively associated with richness in temperate ecosystems, supporting the results from this study. Other studies suggest productivity has a quadratic effect on species richness (Rosenzweig & Sandlin, 1997; Huston, 2001); however much debate has surrounded this idea (Waid et al., 1999; Mittelbach et al., 2001; Whittaker & Heegard, 2003). For this study, quadratic effects were not used due to the relatively small variation in productivity across sampling sites.

The hypothesis that increased habitat heterogeneity would have a positive relationship with species richness was better supported in this study. Increased heterogeneity in productivity and vegetation height were associated with positive richness parameters stronger than all productivity and other covariates used for this all species model. Increased standard deviation in EVI and in vegetation height had the largest positive influences on total avian richness. Bae et al. (2018) also found that increased variability in both vertical structure and productivity indices such as NDVI are associated

with increased richness, supporting results found in this study. It is clear that a single aspect of habitat heterogeneity or productivity does not dictate the number of species within a given area, but there is benefit to using both types of habitat characteristics when estimating species richness.

As expected, habitat characteristics prove to have both positive and negative influences on total species richness. Positive factors for species richness in this study included increased heterogeneity in vegetation height and productivity (cRough and EVI<sub>sd</sub>) as well as increased leaf area densities in the understory and mid-canopies (LAD 0-3 and LAD 3-15m). These positive factors are indicative of early successional habitats or localized disturbances. Negative factors included increased heterogeneity in water content and upper leaf area densities (NDWI<sub>sd</sub> and LAD 15-30m) as well as increased productivity (EVI), indicative of late successional habitats.

Traditionally, successional habitats are thought to influence species movement, interaction, and mortality within a community just as much as they do population dynamics (Fagan, Cantrell, & Cosner, 1999). Considering the intermediate disturbance hypothesis (Connell, 1978), patterns of successional productivity and structural heterogeneity should be considered throughout the vertical strata of an environment to account for shifting habitats supporting a varying number of species overall. The three dimensional habitat characteristics captured by fine resolution remote sensing tools, such as LiDAR, help identify key attributes of these successional gradients and ultimately allow for a better understanding of the factors influencing avian richness. From these results, a mosaic of habitats including early successional growth and localized

disturbances can be key areas supporting higher levels of species richness, while late successional areas support fewer overall species. As the models indicated, late successional habitats are still considered important to supporting many specialist species, even though community parameters show a general negative relationship with richness. For example, the cerulean warbler, a species of concern for the area, was identified to use only high elevation mature habitats and avoid successional and open habitats. The potential to use this complex information in new modeling frameworks will hopefully allow ecologists and conservationists to better understand how these selection preferences can be used to model total avian richness at localized gradients across broad scales.

The benefit of using a hierarchical multi-species model is the fact that individual species identities are retained, allowing users to see individual species' responses such as endangered species or species of concern in addition to all other species observed from sampling. This important information can be separated from the overall model as independent occupancy models when needed to inform more specific conservation decisions. In addition these models are able to improve occupancy estimates of these rare or threatened species using the collective data on all species observed during sampling. This allows for unobserved species, especially rare or threatened species, to be accounted for in the total richness estimate based on occupancy probabilities at other sampling sites (Dorazio et al., 2006).

#### ***4.2 Guild specific richness***

Individual avian habitat guilds were best predicted by specific measures of productivity and habitat heterogeneity that described the habitat characteristics required

for each guild. More productivity covariates were important to forest and edge guild species compared to grassland guild species. Since only 6 grassland specialist species were observed, the results from the grassland guild model don't give much information about these species. For example, the two most common grassland species, such as the brown headed cowbird and eastern bluebird, were found in almost all fields and did not show preference for certain fields over the others. The basic requirements were open dry spaces with no upper canopy vegetation. As for forest species, results show that this guild is negatively associated with common productivity indices such as EVI, meaning that increased forest species richness might be associated with areas of lower productivity. In addition, forest species are negatively associated with increased leaf area density in the upper canopy but are positively associated with lower canopy leaf area density. These conclusions are of little use for grassland management purposes and suggest that all-inclusive models, pulling information from all 73 observed species, are more useful than modeling individual guilds with regard to habitat heterogeneity and productivity.

#### ***4.3 Management implications***

The results presented in this study are useful for local land management and conservation efforts, underscoring the need for selective management strategies that take into account long term goals. For example, removing large areas of resources at a time would be detrimental to avian richness as this would decrease heterogeneity and support even aged successional growth. Instead, managing for a mosaic of habitat types would be most beneficial to richness by promoting early successional habitats with patches of late successional forests to sustain areas of high diversity while maintaining areas for

specialist species. By removing upper canopy biomass in select areas, light would be provided to the forest floor, allowing shrubs, seedlings and saplings to grow slowly and increase productivity in the lower and middle canopies, thus increasing the standard deviation of EVI and in turn increasing species richness. As for grassland management, more remote sensing data and surveys are needed in other locations to make management recommendations.

Habitat heterogeneity and productivity covariates demonstrated contrasting effects on species richness. From the hierarchical model, results show that covariates such as EVI and the standard deviation in vegetation height have opposite effects on species richness indicate from the community parameters. However, individual species responses show that some species are oppositely associated with each covariate compared to the community parameter. Benefits of using this model allow users to see that general diversity patterns may not capture the effect on species of interest. This is important when utilizing the results of such models for management and conservation decision making. Other modeling strategies generalize these effects and attribute trends toward species richness without accounting for individual species preferences. It is vital to think about these species that are not represented well with community level parameters when making management decisions because these species might potentially be rare or threatened, dependent on specific habitat characteristics not supporting high avian diversity as indicated by some community parameter.

#### ***4.4 Conclusions***

As the use of these three-dimensional measures become widely available, datasets characterizing structural attributes of habitats will proliferate in the ecology and conservation fields. This new information will become increasingly useful for biodiversity and management applications. My study shows the strength of habitat heterogeneity and productivity measures from these fine resolution remote sensing platforms as they provide a wealth of information to help improve species distribution, occupancy, and diversity models. While acknowledging the complexity of these datasets, research has barely scratched the surface of what can be inferred from these high resolution remote sensing data. It is therefore imperative to explore the roles of habitat heterogeneity and productivity at these local scales with regards to species richness in other locations as well as other taxonomic groups with these new technologies. Furthermore these types of studies need to be repeated in both similar environments and in other ecosystems globally as data become available to validate the results from this study and begin answering larger questions about what drives localized gradients of species richness.

## REFERENCES

- Anderson, D. P., Turner, M. G., Forester, J. D., Zhu, J., Boyce, M. S., Beyer, H., & Stowell, L. (2005). Scale-dependent summer resource selection by reintroduced elk in Wisconsin, USA. *Journal of Wildlife Management*, *69*(1), 298–310. [http://doi.org/10.2193/0022-541X\(2005\)069<0298:SSRSBR>2.0.CO;2](http://doi.org/10.2193/0022-541X(2005)069<0298:SSRSBR>2.0.CO;2)
- Bae, S., Müller, J., Lee, D., Vierling, K. T., Vogeler, J. C., Vierling, L. A., ... Thorn, S. (2018). Taxonomic, functional, and phylogenetic diversity of bird assemblages are oppositely associated to productivity and heterogeneity in temperate forests. *Remote Sensing of Environment*, *215*, 145–156. <http://doi.org/10.1016/j.rse.2018.05.031>
- Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., ... Ferrer, E. A. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, *471*(7336), 51–57. <http://doi.org/10.1038/nature09678>
- Bellamy, C., Scott, C., & Altringham, J. (2013). Multiscale, presence-only habitat suitability models: Fine-resolution maps for eight bat species. *Journal of Applied Ecology*. <http://doi.org/10.1111/1365-2664.12117>
- Belmaker, J., & Jetz, W. (2010). Cross-scale variation in species richness-environment associations. *Global Ecology and Biogeography*, *20*(3), 464–474. <http://doi.org/10.1111/j.1466-8238.2010.00615.x>
- Belmaker, J., & Jetz, W. (2012). Regional Pools and Environmental Controls of Vertebrate Richness. *The American Naturalist*, *179*(11), 512–523. <http://doi.org/10.1086/664610>
- Bissonette, J. A., Harrison, D. J., Hargis, C. D., & Chapin, T. G. (1997). The Influence of Spatial Scale and Scale-Sensitive Properties on Habitat Selection by American Marten. In *Wildlife and Landscape Ecology* (pp. 368–385). New York, NY: Springer New York. [http://doi.org/10.1007/978-1-4612-1918-7\\_15](http://doi.org/10.1007/978-1-4612-1918-7_15)
- Bivand R., & Rundel C. (2018). rgeos: Interface to Geometry Engine - Open Source ('GEOS'). R package version 0.3-28. <https://CRAN.R-project.org/package=rgeos>

- Blomquist, S. M., & Hunter, M. L. (2010). A multi-scale assessment of amphibian habitat selection: Wood frog response to timber harvesting. *Écoscience*, *17*(3), 251–264. <http://doi.org/10.2980/17-3-3316>
- Boelman, N. T., Asner, G. P., Hart, P. J., Martin, R. E., & Martin<sup>1</sup>, R. E. (2007). Multi-Trophic Invasion Resistance in Hawaii: Bioacoustics, Field Surveys, and Airborne Remote Sensing. *Ecological Applications*, *17*(8), 2137–2144. <http://doi.org/10.1890/07-0004.1>
- Bourg, N. A., McShea, W. J., & Gill, D. E. (2005). Putting a Cart before the Search : Successful Habitat Prediction for a Rare Forest Herb. *America*, *86*(10), 2793–2804.
- Bouvier, M., Durrieu, S., Fournier, R. A., & Renaud, J. P. (2015). Generalizing predictive models of forest inventory attributes using an area-based approach with airborne LiDAR data. *Remote Sensing of Environment*, *156*(January), 322–334. <http://doi.org/10.1016/j.rse.2014.10.004>
- Boyce, M. S. (2006). Scale for resource selection functions. *Diversity and Distributions*, *12*(3), 269–276. <http://doi.org/10.1111/j.1366-9516.2006.00243.x>
- Boyce, M. S., Mao, J. S., Merrill, E. H., Fortin, D., Monica, G., Fryxell, J., ... Fortin, D. (2003). Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Écoscience*, *10*(4), 421–431.
- Britzke, E. R., Murray, K. L., Heywood, J. S., & Robbins, L. W. (2002). Acoustic identification. *The Indiana Bat: Biology and Management of an Endangered Species*, 221–225.
- Byford, J. L. (1970). Telemetrically determined movements of two white-tailed deer fawns in southwestern Alabama. *Proc. Southeastern Assoc. Game Fish Comm*, *24*, 57-63.
- Clawges, R., Vierling, K., Vierling, L., & Rowell, E. (2008). The use of airborne lidar to assess avian species diversity, density, and occurrence in a pine/aspen forest. *Remote Sensing of Environment*, *112*(5), 2064–2073. <http://doi.org/10.1016/j.rse.2007.08.023>
- Connell, J. H. (1978). Diversity in Tropical Rain Forests and Coral Reefs. *Science*, *199*(4335), 1302–1310. <http://doi.org/0304394096125714>
- Cooper, W., McShea W., Luther, D., Forrester, T. (2018). Determining the appropriate scale for measuring habitat heterogeneity and productivity when modeling species richness of different vertebrate taxa. Manuscript in preparation.

- Culbert, P. D., Radeloff, V. C., Flather, C. H., Kellendorfer, J. M., Rittenhouse, C. D., & Pidgeon, A. M. (2013). The Influence of Vertical and Horizontal Habitat Structure on Nationwide Patterns of Avian Biodiversity. *The Auk*, *130*(4), 656–665. <http://doi.org/10.1525/auk.2013.13007>
- Currie, D. J. (1991). Energy and large-scale patterns of animal- and plant- species richness. *The American Naturalist*, *137*(1), 27–49.
- Davies, A. B., & Asner, G. P. (2014). Advances in animal ecology from 3D-LiDAR ecosystem mapping. *Trends in Ecology and Evolution*, *29*(12), 681–691. <http://doi.org/10.1016/j.tree.2014.10.005>
- De Solla, S. R., Shirose, L. J., Fernie, K. J., Barrett, G. C., Brousseau, C. S., & Bishop, C. A. (2005). Effect of sampling effort and species detectability on volunteer based anuran monitoring programs. *Biological Conservation*, *121*(4), 585–594. <http://doi.org/10.1016/j.biocon.2004.06.018>
- Depraetere, M., Pavoine, S., Jiguet, F., Gasc, A., Duvail, S., & Sueur, J. (2012). Monitoring animal diversity using acoustic indices: Implementation in a temperate woodland. *Ecological Indicators*, *13*(1), 46–54. <http://doi.org/10.1016/j.ecolind.2011.05.006>
- Donovan, T. M., & Flather, C. H. (2002). Relationships among North American Songbird Trends, Habitat Fragmentation, and Landscape Occupancy. *Ecological Applications*, *12*(2), 364. <http://doi.org/10.2307/3060948>
- Dorazio, R. M., & Royle, J. A. (2005). Estimating size and composition of biological communities by modeling the occurrence of species. *Journal of the American Statistical Association*, *100*(470), 389–398. <http://doi.org/10.1198/016214505000000015>
- Dorazio, R. M., Gotelli, N. J., & Ellison, A. M. (2011). *Modern Methods of Estimating Biodiversity from Presence-Absence Surveys*. (G. Venora, O. Grillo, & J. Lopez-Pujol, Eds.) *Biodiversity Loss in a Changing Planet*. InTech. <http://doi.org/10.5772/23881>
- Dorazio, R. M., Royle, J. A., Söderström, B., & Glimskär, A. (2006). Estimating species richness and accumulation by modeling species occurrence and detectability. *Ecology*, *87*(4), 842–854. [http://doi.org/10.1890/0012-9658\(2006\)87\[842:ESRAAB\]2.0.CO;2](http://doi.org/10.1890/0012-9658(2006)87[842:ESRAAB]2.0.CO;2)
- Fagan, W. F., Cantrell, R. S., & Cosner, C. (1999). How Habitat Edges Change Species Interactions. *The American Naturalist*, *153*(2), 165–182. <http://doi.org/10.1086/303162>

- Farrell, S. L., Collier, B. a., Skow, K. L., Long, a. M., Campomizzi, a. J., Morrison, M. L., ... Wilkins, R. N. (2013). Using LiDAR-derived vegetation metrics for high-resolution, species distribution models for conservation planning. *Ecosphere*, 4(3), 1–18. <http://doi.org/10.1890/ES12-000352.1>
- Forester, D. C., Snodgrass, J., Marsalek, K., & Lanham, Z. (2006). Post-Breeding Dispersal and Summer Home Range of Female American Toads ( *Bufo americanus* ). *Northeastern Naturalist*, 13(1), 59–72. Retrieved from <http://www.jstor.org/stable/4131006>
- Gao, B. (1996). NDWI—A normalized difference water index for remote sensing of vegetation liquid water from space. *Remote Sensing of Environment*, 58(3), 257–266. [http://doi.org/10.1016/S0034-4257\(96\)00067-3](http://doi.org/10.1016/S0034-4257(96)00067-3)
- Gehrt, S. D., & Chelsvig, J. E. (2003). Bat Activity in an Urban Landscape : Patterns at the Landscape and Microhabitat Scale. *Ecological Applications*, 13(4), 939–950. Retrieved from <http://www.jstor.org/stable/4134734>
- Gelman, A., & Pardoe, I. (2007). Average Predictive Comparisons for Models with Nonlinearity, Interactions, and Variance Components. *Sociological Methodology*, 37(1), 23–51. <http://doi.org/10.1111/j.1467-9531.2007.00181.x>
- Gelman, A., & Hill, J. (2006). *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge University Press.
- Gillman, L. N., Wright, S. D., Cusens, J., McBride, P. D., Malhi, Y., & Whittaker, R. J. (2015). Latitude, productivity and species richness. *Global Ecology and Biogeography*, 24(1), 107–117. <http://doi.org/10.1111/geb.12245>
- Goetz, S., Steinberg, D., Dubayah, R., & Blair, B. (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(3), 254–263. <http://doi.org/10.1016/j.rse.2006.11.016>
- Goetz, S. J., Hansen, M., Houghton, R. A., Walker, W., Laporte, N., & Busch, J. (2015). Measurement and monitoring needs, capabilities and potential for addressing reduced emissions from deforestation and forest degradation under REDD+. *Environmental Research Letters*, 10. <http://doi.org/10.1088/1748-9326/10/12/123001>
- Griffiths, G. H., & Lee, J. (2000). Landscape pattern and species richness; regional scale analysis from remote sensing. *International Journal of Remote Sensing*, 21(13+14), 2685–2704. <http://doi.org/10.1080/01431160050110232>

- Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., ... Townshend, J. R. (2015). Supplementary Materials for Habitat fragmentation and its lasting impact on Earth ' s ecosystems. *Science Advances*, *1*(2), 1–10. <http://doi.org/10.1126/sciadv.1500052>
- Halaj, J., Ross, D. W., & Moldenke, A. R. (2000). Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. *Oikos*, *90*(1), 139–152. <http://doi.org/10.1034/j.1600-0706.2000.900114.x>
- Hanley, J. A., & McNeil, B. J. (1982). The Meaning and Use of the Area under a Receiver Operating Characteristic (ROC) Curve. *Radiology*, *143*(1), 29–36. <http://doi.org/10.1148/radiology.143.1.7063747>
- Harrison, S., Cornell, H., & Moore, K. A. (2010). Spatial niches and coexistence: testing theory with tarweeds. *Ecology*, *91*(7), 2141–2150. <http://doi.org/10.1890/09-0742.1>
- He, K. S., Bradley, B. A., Cord, A. F., Rocchini, D., Tuanmu, M.-N., Schmidtlein, S., ... Pettorelli, N. (2015). Will remote sensing shape the next generation of species distribution models? *Remote Sensing in Ecology and Conservation*, *1*(1), 4–18. <http://doi.org/10.1002/rse2.7>
- Hijmans, R. J. (2017). raster: Geographic Data Analysis and Modeling. R package version 2.6-7. <URL: <https://CRAN.R-project.org/package=raster>>
- Holland, J. D., Bert, D. G., & Fahrig, L. (2004). Determining the Spatial Scale of Species' Response to Habitat. *BioScience*, *54*(3), 227–233. [http://doi.org/10.1641/0006-3568\(2004\)054\[0227:DTSSOS\]2.0.CO;2](http://doi.org/10.1641/0006-3568(2004)054[0227:DTSSOS]2.0.CO;2)
- Holland, J. D., & Yang, S. (2016). Multi-scale Studies and the Ecological Neighborhood. *Current Landscape Ecology Reports*, *1*(4), 135–145. <http://doi.org/10.1007/s40823-016-0015-8>
- Homer, C. (2015). Completion of the 2011 National Land Cover Database for the Conterminous United States-Representing a Decade of Land Cover Change Information Landsat-based mapping project View project National Land Cover Database View project. *Photogrammetric Engineering & Remote Sensing*, *81*(5), 345–354. <http://doi.org/10.14358/PERS.81.5.345>
- Hooten, M. B., & Hobbs, N. T. (2015). A guide to Bayesian model selection for ecologists. *Ecological Monographs*, *85*(1), 3–28. <http://doi.org/10.1890/14-0661.1>

- Hu, Y.-H., Johnson, D. J., Mi, X.-C., Wang, X.-G., Ye, W.-H., Li, Y.-D., ... Cao, M. (2018). The relative importance of space compared to topography increases from rare to common tree species across latitude. *Journal of Biogeography*, (November 2017), 1–13. <http://doi.org/10.1111/jbi.13420>
- Huang, Q., Swatantran, A., Dubayah, R., & Goetz, S. J. (2014). The influence of vegetation height heterogeneity on forest and woodland bird species richness across the United States. *PLoS ONE*, 9(8). <http://doi.org/10.1371/journal.pone.0103236>
- Huete, A., Didan, K., Miura, T., Rodriguez, E. ., Gao, X., & Ferreira, L. . (2002). Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment*, 83(1–2), 195–213. [http://doi.org/10.1016/S0034-4257\(02\)00096-2](http://doi.org/10.1016/S0034-4257(02)00096-2)
- Hurlbert, A. H., & Haskell, J. P. (2003). The effect of energy and seasonality on avian species richness and community composition. *American Naturalist*, 161(1), 83–97. <http://doi.org/10.1086/345459>
- Huston, M. A., Balmford, A., Moore, J., Brooks, T., Burgess, N., Hansen, L. A., ... Rahbek, C. (2001). People and Biodiversity in Africa. *Science*, 293(5535), 1591–1592. Retrieved from <https://www.jstor.org/stable/3084591>
- Jackson, H. B., & Fahrig, L. (2015). Are ecologists conducting research at the optimal scale? *Global Ecology and Biogeography*, 24(1), 52–63. <http://doi.org/10.1111/geb.12233>
- Jackson, H. B., & Fahrig, L. (2012). What size is a biologically relevant landscape? *Landscape Ecology*, 27(7), 929–941. <http://doi.org/10.1007/s10980-012-9757-9>
- Jiménez-Alfaro, B., Chytrý, M., Mucina, L., Grace, J. B., & Rejmánek, M. (2016). Disentangling vegetation diversity from climate-energy and habitat heterogeneity for explaining animal geographic patterns. *Ecology and Evolution*, 6(5), 1515–1526. <http://doi.org/10.1002/ece3.1972>
- Johnson, A. E. M. (2017). CONSERVATION AND LAND MANAGEMENT PRACTICES AND THEIR IMPACT ON SUSTAINING BREEDING AND NON-BREEDING GRASSLAND BIRD POPULATIONS IN THE SOUTHEAST. PhD Dissertation, George Mason University.
- Johnson, D. H. (1980). The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology*, 61(1), 65–71. <http://doi.org/10.2307/1937156>

- Jones, J. E., Kroll, A. J., Giovanini, J., Duke, S. D., Ellis, T. M., & Betts, M. G. (2012). Avian species richness in relation to intensive forest management practices in early seral tree plantations. *PLoS ONE*, 7(8). <http://doi.org/10.1371/journal.pone.0043290>
- Kalogirou, S. (2017). lctools: Local Correlation, Spatial Inequalities, Geographically Weighted Regression and Other Tools. R package version 0.2-6. <URL: <https://CRAN.R-project.org/package=lctools>>
- Keil, P., Schweiger, O., Kühn, I., Kunin, W. E., Kuussaari, M., Settele, J., ... Storch, D. (2012). Patterns of beta diversity in Europe: The role of climate, land cover and distance across scales. *Journal of Biogeography*, 39(8), 1473–1486. <http://doi.org/10.1111/j.1365-2699.2012.02701.x>
- Kelly, J. P. (1993). The Effect of Nest Predation on Habitat Selection by Dusky Flycatchers in Limber Pine-Juniper Woodland. *The Condor*, 95(1), 83–93. <http://doi.org/10.2307/1369389>
- Kerr, J. T., & Packer, L. (1997). Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature*, 385(6613), 252–254. <http://doi.org/10.1038/385252a0>
- Kéry, M., & Royle, J. A. (2018). *Applied hierarchical modeling in ecology : analysis of distribution, abundance and species richness in R and BUGS. Volume 1, Prelude and static models*. Elsevier.
- Kniowski, A. B., & Gehrt, S. D. (2014). Home range and habitat selection of the Indiana bat in an agricultural landscape. *The Journal of Wildlife Management*, 78(3), 503–512. <http://doi.org/10.1002/jwmg.677>
- Kruschke, J. K. & Meredith, M. (2018). BEST: Bayesian Estimation Supersedes the t-Test. R package version 0.5.1. <URL: <https://CRAN.R-project.org/package=BEST>>
- Kuo, L., & Mallick, B. (1960). *Variable Selection for Regression Models. Source: Sankhyā: The Indian Journal of Statistics, Series B (Vol. 60)*. Retrieved from <https://www.jstor.org/stable/pdf/25053023.pdf?refreqid=excelsior%3A47856fd04be95098c09ec88eed050a22>
- Leblond, M., Frair, J., Fortin, D., Dussault, C., Ouellet, J. P., & Courtois, R. (2011). Assessing the influence of resource covariates at multiple spatial scales: An application to forest-dwelling caribou faced with intensive human activity. *Landscape Ecology*, 26(10), 1433–1446. <http://doi.org/10.1007/s10980-011-9647-6>

- Lefsky, M. A., Cohen, W. B., Parker, G. G., & Harding, D. J. D. (2002). Lidar Remote Sensing for Ecosystem Studies. *BioScience*, 52(1), 19–30 ST–Lidar Remote Sensing for Ecosystem Stu. [http://doi.org/10.1641/0006-3568\(2002\)052\[0019:LRSFES\]2.0.CO;2](http://doi.org/10.1641/0006-3568(2002)052[0019:LRSFES]2.0.CO;2)
- Lindberg, E., Roberge, J.-M., Johansson, T., Hjältén, J., Balzter, H., Pfeifer, N., ... Thenkabail, P. S. (2015). Can Airborne Laser Scanning (ALS) and Forest Estimates Derived from Satellite Images Be Used to Predict Abundance and Species Richness of Birds and Beetles in Boreal Forest? *Remote Sens*, 7, 4233–4252. <http://doi.org/10.3390/rs70404233>
- MacArthur, R.H. (1972). *Geographical Ecology: Patterns in the Distribution of Species*. Princeton University Press, Princeton, NJ.
- Macarthur, R. H., & Macarthur, J. W. (1961). On Bird Species Diversity. *Ecology*, 42(3), 594–598. <http://doi.org/10.1111/j.1466-8238.2007.00316.x>
- Marchese, C. (2015). Biodiversity hotspots: A shortcut for a more complicated concept. *Global Ecology and Conservation*, 3, 297–309. <http://doi.org/10.1016/j.gecco.2014.12.008>
- Martinuzzi, S., Vierling, L. A., Gould, W. A., Falkowski, M. J., Evans, J. S., Hudak, A. T., & Vierling, K. T. (2009). Mapping snags and understory shrubs for a LiDAR-based assessment of wildlife habitat suitability. *Remote Sensing of Environment*, 113(12), 2533–2546. <http://doi.org/10.1016/j.rse.2009.07.002>
- Martof, B. (1953). Home Range and Movements of the Green Frog , *Rana Clamitans*. *Ecology*, 34(3), 529–543. <http://doi.org/10.2307/1929725>
- Mayor, S. J., Schneider, D. C., Schaefer, J. A., & Mahoney, S. P. (2009). Habitat Selection at Multiple Scales. *Ecoscience*, 16(2), 238–24716. <http://doi.org/10.2980/16-2-3238>
- McGarigal, K., Wan, H. Y., Zeller, K. A., Timm, B. C., & Cushman, S. A. (2016). Multi-scale habitat selection modeling: a review and outlook. *Landscape Ecology*, 31(6), 1161–1175. <http://doi.org/10.1007/s10980-016-0374-x>
- Mittelbach, G. G., Steiner, C. F., Scheiner, S. M., Gross, K. L., Reynolds, H. L., Waide, R. B., ... Gough, L. (2001). What is the observed relationship between species richness and productivity? *Ecology*, 82(9), 2381–2396. [http://doi.org/10.1890/0012-9658\(2001\)082\[2381:WITORB\]2.0.CO;2](http://doi.org/10.1890/0012-9658(2001)082[2381:WITORB]2.0.CO;2)

- Mittermeier, R. A., Turner, W. R., Larsen, F. W., Brooks, T. M., & Gascon, C. (2011). Global Biodiversity Conservation: The Critical Role of Hotspots. In *Biodiversity Hotspots* (pp. 3–22). Berlin, Heidelberg: Springer Berlin Heidelberg. [http://doi.org/10.1007/978-3-642-20992-5\\_1](http://doi.org/10.1007/978-3-642-20992-5_1)
- Müller, J., Stadler, J., & Brandl, R. (2010). Composition versus physiognomy of vegetation as predictors of bird assemblages: The role of lidar. *Remote Sensing of Environment*, *114*(3), 490–495. <http://doi.org/10.1016/J.RSE.2009.10.006>
- Myers, N., Mittermeier, R. a, Mittermeier, C. G., da Fonseca, G. a, & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853–8. <http://doi.org/10.1038/35002501>
- Mysterud, A., Lian, L.-B., & Hjernann, D. Ø. (1999). Scale-dependent trade-offs in foraging by European roe deer ( *Capreolus capreolus* ) during winter. *Canadian Journal of Zoology*, *77*(9), 1486–1493. <http://doi.org/10.1139/cjz-77-9-1486>
- Nieto, S., Flombaum, P., & Garbulsky, M. F. (2015). Can temporal and spatial NDVI predict regional bird-species richness? *Global Ecology and Conservation*, *3*(1), 729–235. <http://doi.org/10.1016/j.rse.2007.08.023>
- O’Hara, R. B., & Sillanpää, M. J. (2009). A review of Bayesian variable selection methods: what, how and which. *Bayesian Analysis*, *4*(1), 85–117. <http://doi.org/10.1214/09-BA403>
- O’Connell, A. F., Nichols, J. D., & Karanth, K. U. (2011). *Camera Traps in Animal Ecology*. (A. F. O’Connell, J. D. Nichols, & K. U. Karanth, Eds.). Tokyo: Springer Japan. <http://doi.org/10.1007/978-4-431-99495-4>
- Owen, S. F., Menzel, M. A., Ford, W. M., Chapman, B. R., & Karl, V. (1972). Home-Range Size and Habitat Used by the Northern Myotis ( *Myotis septentrionalis* ). *The American Midland Naturalist*, *150*(2), 352–359.
- Ozaga, J. J., & Harger, E. M. (1966). Winter Activities and Feeding Habits of Northern Michigan Coyotes. *The Journal of Wildlife Management*, *30*(4), 809–818.
- Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., ... Sexton, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, *344*(6187). <http://doi.org/10.1126/science.1246752>
- Rahbek, C., & Graves, G. R. (2001). Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences*, *98*(8), 4534–4539. Retrieved from [www.pnas.org/cgi/doi/10.1073/pnas.071034898](http://www.pnas.org/cgi/doi/10.1073/pnas.071034898)

- Reid, W. V. (1998). Biodiversity hotspots. *Trends in Ecology & Evolution*, 13(7), 275–280. [http://doi.org/10.1016/S0169-5347\(98\)01363-9](http://doi.org/10.1016/S0169-5347(98)01363-9)
- Robinson, S. K., & Holmes, R. T. (1984). *Effects of Plant Species and Foliage Structure on the Foraging Behavior of Forest Birds*. *The Auk* (Vol. 101). Retrieved from <https://www.jstor.org/stable/pdf/4086894.pdf?refreqid=excelsior%3Ad4fb02986ac3ea523a646f0eb33fa125>
- Rodewald, P. (Editor). 2015. *The Birds of North America*: <https://birdsna.org>. Cornell Laboratory of Ornithology, Ithaca, NY.
- Rodhouse, T. J., Vierling, K. T., & Irvine, K. M. (2011). A Practical Sampling Design for Acoustic Surveys of Bats. *Journal of Wildlife Management*, 75(5), 1094–1102. <http://doi.org/10.1002/jwmg.151>
- Rosenzweig, M. L. (1995). *Species diversity in space and time*. *Species diversity in space and time*. Cambridge University Press.
- Rosenzweig, M. L., & Sandlin, E. A. (1997). Species Diversity and Latitudes: Listening to Area's Signal. *Oikos*, 80(1), 172–176. <http://doi.org/10.2307/3546528>
- Roussel, J. & Auty, D. (2018). lidR: Airborne LiDAR Data Manipulation and Visualization for Forestry Applications. R package version 1.5.1.<URL: <https://CRAN.R-project.org/package=lidR>>
- Royle, J. A., & Dorazio, R. M. (2008). *Hierarchical modeling and inference in ecology : the analysis of data from populations, metapopulations and communities*. Academic Press.
- Running, S. W., Nemani, R. R., Heinsch, F. A., Zhao, M., Reeves, M., & Hashimoto, H. (2004). A Continuous Satellite-Derived Measure of Global Terrestrial Primary Production. *BioScience*, 54(6), 547. [http://doi.org/10.1641/0006-3568\(2004\)054\[0547:ACSMOG\]2.0.CO;2](http://doi.org/10.1641/0006-3568(2004)054[0547:ACSMOG]2.0.CO;2)
- Russell, R. E., Royle, J. A., Saab, V. A., Lehmkuhl, J. F., Block, M., Sauer, J. R., ... Sauer, J. R. (2009). Modeling the Effects of Environmental Disturbance on Wildlife Communities : Avian Responses to Prescribed Fire. *Ecological Applications*, 19(5), 1253–1263.
- Seavy, N. E., Viers, J. H., & Wood, J. K. (2009). Riparian bird response to vegetation structure: a multiscale analysis using LiDAR measurements of canopy height. *Ecological Applications*, 19(7), 1848–1857. <http://doi.org/10.1890/08-1124.1>

- Senior, P., Butlin, R. K., & Altringham, J. D. (2005). Sex and segregation in temperate bats. *Proceedings of the Royal Society B: Biological Sciences*, 272, 2467–2473. <http://doi.org/10.1098/rspb.2005.3237>
- Seto, K. C., Fleishman, E., Fay, J. P., & Betrus, C. J. (2004). Linking spatial patterns of bird and butterfly species richness with Landsat TM derived NDVI. *International Journal of Remote Sensing*, 25(20), 4309–4324. <http://doi.org/10.1080/0143116042000192358>
- Sing, T., Sander, O., Beerenwinkel, N., and Lengauer, T. (2005). ROCr: visualizing classifier performance in R. *Bioinformatics*, 21(20), pp. 7881. <URL: <http://rocr.bioinf.mpi-sb.mpg.de>>.
- Skalak, S. L., Sherwin, R. E., & Brigham, R. M. (2012). Sampling period, size and duration influence measures of bat species richness from acoustic surveys. *Methods in Ecology and Evolution*, 3(3), 490–502. <http://doi.org/10.1111/j.2041-210X.2011.00177.x>
- Smith, A. M., Ollinger, S. V., Martin, M. E., Aber, J. D., Richard, A., & Goodale, C. L. (2002). Direct Estimation of Aboveground Forest Productivity through Hyperspectral Remote Sensing of Canopy Nitrogen. *Ecological Applications*, 12(5), 1286–1302.
- Stein, A., Gerstner, K., & Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, 17(7), 866–880. <http://doi.org/10.1111/ele.12277>
- Sueur J., Aubin T., Simonis C. (2008). Seewave: a free modular tool for sound analysis and synthesis. *Bioacoustics*, 18: 213-226
- Swatantran, A., Dubayah, R., Goetz, S., Hofton, M., Betts, M. G., Sun, M., ... J-P Schumann, G. (2012). Mapping Migratory Bird Prevalence Using Remote Sensing Data Fusion. *PLoS ONE*, 7(1). <http://doi.org/10.1371/journal.pone.0028922>
- Tenan, S., O'Hara, R. B., Hendriks, I., & Tavecchia, G. (2014). Bayesian model selection: The steepest mountain to climb. *Ecological Modelling*, 283, 62–69. <http://doi.org/10.1016/J.ECOLMODEL.2014.03.017>
- Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M., & Jeltsch, F. (2004). Animal Species Diversity Driven by Habitat Heterogeneity/Diversity: The Importance of. *Journal of Biogeography*, 31(1), 79–92. Retrieved from <http://www.jstor.org/stable/3554692>

- Theobald, D. M., Stevens, D. L., White, D., Urquhart, N. S., Olsen, A. R., & Norman, J. B. (2007). Using GIS to generate spatially balanced random survey designs for natural resource applications. *Environmental Management*, *40*(1), 134–146. <http://doi.org/10.1007/s00267-005-0199-x>
- Tierney, G., Mitchell, B., Miller-Rushing, A., Katz, J., Denny, E., Brauer, C., ... Dieffenbach, F. (2013). Phenology Monitoring Protocol Northeast Temperate Network. *Natural Resource Report NPS/NETN/NRR*, 273. Retrieved from [https://www.usanpn.org/files/shared/files/NETN\\_Phenology\\_Protocol\\_final\\_0.pdf](https://www.usanpn.org/files/shared/files/NETN_Phenology_Protocol_final_0.pdf)
- Tuanmu, M.-N., & Jetz, W. (2015). A global, remote sensing-based characterization of terrestrial habitat heterogeneity for biodiversity and ecosystem modelling. *Global Ecology and Biogeography*, *24*, 1329–1339. <http://doi.org/10.1111/geb.12365>
- Turner, W., Spector, S., Gardiner, N., Fladeland, M., Sterling, E., & Steininger, M. (2003). Remote sensing for biodiversity science and conservation. *Trends in Ecology and Evolution*, *18*(6), 306–314. [http://doi.org/10.1016/S0169-5347\(03\)00070-3](http://doi.org/10.1016/S0169-5347(03)00070-3)
- van Ravenzwaaij, D., Cassey, P., & Brown, S. D. (2018). A simple introduction to Markov Chain Monte–Carlo sampling. *Psychonomic Bulletin & Review*, *25*(1), 143–154. <http://doi.org/10.3758/s13423-016-1015-8>
- Vierling, K. T., Vierling, L. A., Gould, W. A., Martinuzzi, S., & Clawges, R. M. (2008). Lidar: Shedding new light on habitat characterization and modeling. *Frontiers in Ecology and the Environment*, *6*(2), 90–98. <http://doi.org/10.1890/070001>
- Villanueva-Rivera, L. J., and Pijanowski, B. C. (2018). soundecology: Soundscape Ecology. R package version 1.3.3. <URL: <https://CRAN.R-project.org/package=soundecology>>
- Waide, R. B., Willig, M. R., Steiner, C. F., Mittelbach, G., Gough, L., Dodson, S. I., ... Parmenter, R. (1999). The relationship between productivity and species richness. *Annual Review of Ecology and Systematics*, *30*(1), 257–300.
- Weisberg, P. J., Dilts, T. E., Becker, M. E., Young, J. S., Wong-Kone, D. C., Newton, W. E., & Ammon, E. M. (2014). Guild-specific responses of avian species richness to LiDAR-derived habitat heterogeneity. *Acta Oecologica*, *59*, 72–83. <http://doi.org/10.1016/j.actao.2014.06.002>

- Whittaker, R. J., & Heegaard, E. (2003). Relationship Between Species Richness and Productivity ? *Ecology*, 84(12), 3384–3390. <http://doi.org/10.1007/s00442-003-1343-z>
- Wiens, J. A. (1989). Spatial Scaling in Ecology. *Functional Ecology*, 3(4), 385–397.
- Wimmer, J., Towsey, M., Planitz, B., Williamson, I., & Roe, P. (2013). Analysing environmental acoustic data through collaboration and automation. *Future Generation Computer Systems*, 29(2), 560–568. <http://doi.org/10.1016/j.future.2012.03.004>
- Zipkin, E. F., Campbell Grant, E. H., & Fagan, W. F. (2012). Evaluating the predictive abilities of community occupancy models using AUC while accounting for imperfect detection. *Ecological Applications*, 22(7), 1962–1972. <http://doi.org/10.1890/11-1936.1>

## **BIOGRAPHY**

William Justin Cooper graduated from Franklin County High School, Rocky Mount, Virginia, in 2008. He received his Bachelor of Sciences from James Madison University in 2013. He was employed as an intern and fellow with the Smithsonian for four years. During three of these years, he also worked as a graduate teaching assistant with George Mason University.