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Where Birds Chill: An Assessment of the Habitat Preferences of Birds Overwintering in Hudson Valley Forests

Elizabeth Claire Axley
Bard College

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An Assessment of the Habitat Preferences of Birds Overwintering in Hudson Valley Forests

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by
Elizabeth Axley

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Abstract

Many avian species overwinter in eastern North America; however, studies on bird populations are rarely undertaken during this critical survival time, and little is known as to their habitat preferences and foraging behavior. In this observational study, we performed a survey of birds overwintering in the Hudson Valley's temperate, primarily-deciduous forests, assessing avian populations' habitat preferences through the vegetative structural variables surrounding overwintering birds as they forage. Our results suggest that high canopy cover is critically important to predicting overwintering bird occupancy on a microhabitat scale. Moreover, overwintering birds preferentially occupy forest plots *not* dominated by sugar maples, in spite of the fact that sugar maples were the most prevalent tree species surveyed. While shrub and forb cover is not predictive of individual bird occupancy, higher understory cover does influence abundance, suggesting flocking bird species are selective of high ground cover microhabitats. Our results provide critical data on seasonal avian habitat preferences in the face of globally declining avian populations and shifting anthropogenic land use patterns. These results have numerous indications on effective bird conservation over the fall-to-winter season; with further implications in the fields of forest management and white-tailed deer control.

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Contents

1   Background

1.1   Birds in Decline

For the past several decades, alarming trends of bird species in rapid population declines have been noted across ecological circles (Wilcove & Terborgh, 1984; Ballard et al., 2003). Obligate deep-forest breeding migratory birds have especially been found to suffer deep declines in recent record (Askins, 2014b). Through the use of globally integrated databases, both shorebirds and habitat specialist birds have both been shown to display falling populations worldwide (Butchart et al., 2010). Even populations of migratory bird species with no outright phenological response to climate change have recently been noted to be in decline (Møller et al., 2008). Despite beneficial increases in the designation of protected areas covering avian hotspots and biologically important species-specific regions, the rate of biodiversity loss to birds (and across all studied organisms) does not appear to be slowing (Butchart et al., 2010).

Such alarming trends can be viewed not only as having negative implications on the current state of avian biodiversity, but also as greater indicators of the Earth's ecosystem health and stability (Butchart et al., 2010). Hypotheses for these precip-

itously declining avian trends are primarily based on the subtle to drastic manners in which humans have altered the Earth's climate and landscape (Wormworth & Şekercioğlu, 2011). As many avian species are especially sensitive to alteration, they may be regarded as a bellwether for how anthropogenic changes are affecting natural ecosystems and wildlife (Barnagaud et al., 2012; Møller et al., 2008). These trends make birds of prime importance for conservation efforts, and thus understanding their cause(s) is paramount for effective conservation.

1.1.1   Climate Change

Although only covered here in brief, anthropogenically-induced climate change is a salient factor in declining avian populations globally. Avian species ranges are largely climatically determined; specifically, northern range limits tend to be influenced by latitudinal cold temperature, and southern range limits by heat and water availability, along with climatically-produced biotic factors (Böhning-Gaese & Lemoine, 2004). Climate change and its cascade of abiotic and biotic effects have been observed to disrupt these variables and thereby alter or limit the ranges of many bird species, providing some explanation for recent species declines (Böhning-Gaese & Lemoine, 2004). Specifically, birds display differentiation through climatic niches, which climate change has the potential to impede (Matthews et al., 2011; Barnagaud et al., 2012); many of its niche-shifting, -contracting, and -decaying effects have already been begun to be observed (Kissling et al., 2010; Barnagaud et al., 2012; Post, 2013; D'Amen et al., 2013). Birds that occupy high-elevation niches are expected to suffer particularly precipitous declines due to climate change's niche-eliminating effects: modelling of current climate trends produces estimated declines of up to 61% in high-elevation

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bird populations by 2050 (Harris et al., 2014).

Moreover, roughly half of all avian species are migratory for their breeding season, a subset of birds on which climate change can be particularly disruptive due to inherent and environmental phenological variables (Matthews et al., 2011; Wood & Kellermann, 2015). The precise environmental resource phenologies migratory birds are evolutionarily in expectancy of are often not maintained in the face of a changing climate (Menzel et al., 2006), resulting in ecological mismatch at arrival (Saino et al., 2011); this in turn contributes to avian population declines (Visser et al., 2006; Saino et al., 2011). Large-scale climate cycles can disproportionately disrupt long-distance migrants (Ballard et al., 2003): migratory bird species, in a wide-scale attempt to adapt or respond to changing environmental inputs, have generally been observed to be migrating earlier each year, often to uncertain resources and competition upon arrival (Hedenström et al., 2007; Gienapp et al., 2007; Saino et al., 2011). Phenological mismatch can, in turn, disrupt the timings of previously-maintained reproductive processes in birds; for instance, climate change has largely shifted laying dates of bird species forward, on both a micro- and macro-geographic scale (Møller, 2008; Both et al., 2004). This earlier shift in breeding can in turn alter nesting success rates,[1] altering population dynamics on a wider scale (Møller, 2008).

1.1.2   Anthropogenic Habitat Alteration

Notwithstanding its global significance, on a local scale, the deleterious effects of climate change on avian biodiversity and richness may lose primacy to the highly

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[1]This change in nest success may be caused by phenologically altered food supply available to breeding pairs rearing chicks at the time of nesting; however, study has not conclusively substantiated this theory.

disruptive effects of local anthropogenic alterations to landscapes, habitats, and ecosystems.[2] Direct habitat loss poses itself as a particularly dangerous adversary to both non-migratory and migratory bird species. Deforestation, residential development/paving, and the conversion of wild areas to agricultural land describe some of the major contributors to habitat loss for avian species, which are all directly linked with local population declines (Bélisle et al., 2001; Germaine et al., 1998; Peach et al., 1999). Deforestation alone is expected to reduce mid-elevational avian populations by one fifth over the next 30 years (Harris et al., 2014). Even more alarming, at current rates of deforestation, 16 species in the Brazilian Amazon alone are expected to be driven to complete extinction by deforestation in the same time frame, with 80% of those extinctions irretrievably eminent from latent effects of already currently deforested regions (Wearn et al., 2012). Habitat loss may disproportionately constrict niche availability, rendering some niches nonexistent or heavily depleted across a landscape (Swihart et al., 2006). As a result, current levels of forest loss have been shown to have increasingly destructive effects on the abundances of more progressively heavily specialized bird species by habitat (Zurita et al., 2017).

Yet even when habitat is not altogether lost, its fragmentation, degradation, simplification, and isolation can pose interacting exogenous and endogenous threats to birds (Fischer & Lindenmayer, 2007). Habitat fragmentation creates more edges around the perimeter of forests, which many deep-forest breeding birds are intolerant of; thus, populations of these species (ex. Kirtland's Warbler) have exponentially declined in the Northern Hemisphere as forests have become increasingly fragmented

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[2]Of course, climate change and habitat alterations are not so much two distinct adversarial factors to bird populations as they are synergistic potentiators of species declines; their complex, bidirectional relationship, though, is not our primary object of study.

(Probst, 1986; Nelson & Buech, 1996; Robinson & Wilcove, 1994). Habitat fragmentation has been hypothesized as the primary driver behind the increase of brown-headed cowbirds in North America (Whitmore, 1977). Based on their brood-parasitic reproductive nature, in which cowbirds lay their own eggs in other species' nests and parasitically out-compete the host's chicks in nest success, cowbirds are regarded as a major impetus behind the noted declines of forest songbirds across North America (Brittingham & Temple, 1983; Gates & Giffen, 1991). In fact, the effect of increased brown-headed cowbirds may be responsible for reducing avian biodiversity on the continent as a whole (Barnagaud et al., 2015; Kelly & DeCapita, 1982; Strausberger & Ashley, 1997). Habitat fragmentation forcibly creates an increase in edge habitats, providing exponentially increased domains in which cowbirds thrive and seek prospective host nests (Arcese et al., 1996; Barnagaud et al., 2015). Habitat fragmentation's logical consequence of increased edges and decreased protected central forest areas thus forces more forest songbirds into potentially parasitized ranges across a landscape (Ballard et al., 2003; Barnagaud et al., 2015).

Furthermore, niche alteration and destruction is an increasingly observed natural consequence of habitat degradation and fragmentation (Swihart et al., 2003; Layman et al., 2007). Resource partitioning has been found to be strategically wielded by birds through niche diversification in undisturbed sites; however, when human disturbance (such as excessive logging or grazing) is introduced, bird species once stratified are forced to overlap niches, novelly competing for resources and consequently experiencing depleting species richness (Lara et al., 2015). Moreover, human reduction of continuous forest area may lead to altered abiotic conditions (such as wind force or moisture content) within the remaining forested area (Askins, 2014b). After such

alterations, the insect community profile of the remaining forest may be altered in response to these changed abiotic variables, which can in turn strip insectivorous and semi-insectivorous bird species of their natural arthropodic prey (Askins, 2014b). This eliminates the resource-provisional niches previously found in forest tracts, rendering the birds that fill these niches unable to locally compete and/or survive.

Similarly, these compromised areas can also become isolated from nearby forested regions if corridors are not left between fragments, which may pose particular danger for populations left behind on such isolated habitat. These isolated patches of avian habitat, dubbed "forest islands", may be subject to island-like effects, in which insular biota on islands face high extinction rates[3] and populations are not readily replaced by newly colonizing species in order to evade extinction (Howe, 1984; Estrada et al., 1993; Askins, 2014a) Species on isolated forest patches are thus insecure in preserving their regional populations: although some forests may be retained in developed areas, these are "forest islands in a suburban sea", with few replacement individuals making such a trek to unknown isolated habitat areas (Estrada et al., 1993; Askins, 2014a). Even more indicative of the multiplicative means by which habitat alteration factors into avian decline, trends of population declines in bird species can be observationally noted even in unfragmented temperate deciduous forests across North America; study of this phenomenon suggests that subtle habitat change, with anthropogenic disturbances altering woody plant species composition and structure, could be a major factor in loss of avian biodiversity in such regions (Holmes & Sherry, 2001).

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[3]Often, these high extinction rates exist because they are more vulnerable to natural disasters and disease based on low population numbers and a low genetic pool by which to recover from individual losses. See *The Theory of Island Biogeography*, 1967, MacArthur & Wilson for more detail on island effects.

1.2 Relationship Between Birds and Vegetative Structure & Cover

1.2.1 Niches and Vegetative Structure

Avian species have an intimate evolutionary relationship with their environment, due to the stratification of species across multiple habitat types. Common knowledge allows us to recognize that different classes of birds use different vegetative habitats across a geographic scale: waterbirds occupy a fundamentally different habitat than grassland birds, which inhabit an intrinsically different habitat than Arctic tundra-rearing birds, etc. Within a given habitat type, bird species stratify their occupancy and resource use even further, occupying different microhabitat-determined niches (Peterson & Holt, 2003; Barnagaud et al., 2012). These niches can exist on a heavily local scale, based on the specific vegetative composition, type, cover, and structure these species specifically are evolutionarily compatible with; this relationship is often reliant on species-specific resource usage influencing morphological features (Carrascal et al., 1990). This evolutionary strategy, here described as niche partitioning, has led to diverse populations of birds with highly specified resource use strategy co-existing within the same habitat, each using the surrounding vegetation in unique manners (Lara et al., 2015). This theory is supported by observational data at undisturbed sites, which suggests niche partitioning via vegetative structure and cover naturally leads to resource segregation among competitive birds, existing as an evolutionary strategy to reduce competition (Lara et al., 2015).

One way in which differing habitat niches are occupied and diversified is the ver-

tical stratification of bird species across canopy gradients; this trend is found in both temperate and tropical forests (Walther, 2002). Niche partitioning can further be found in temperate forests through the structuring of bird populational assemblages within canopy cover levels based primarily on differing resource use (Böhm & Kalko, 2009). Breeding birds are known to differentiate through habitat niches, creating ordinal relationships between species and the vegetative structures determining their niche breadth (James, 1971). When creating assessments for the distribution, abundance, and niche breadth of birds, scale must be taken into account, so as to account for the ecological contexts by which birds diversify (Brändle & Brandl, 2001). Interestingly, niche adoption seems to be partially gained through socialized learning[4] (Slagsvold & Wiebe, 2007). Nevertheless, the niche concept is so effective, niche-based modelling can improve the sampling of rare species in the field, specifically through the identification of vegetative cover and structural patterns (Guisan et al., 2006).

1.2.2   Theories on Selective Cover Use and Birds

The relationship between birds and the vegetative cover they use within their niche has been investigated for behavioral trends. Avian diversity has generally been shown to be sigmoidally positively related to percent vegetative cover found across a landscape (Karr & Roth, 1971). High percentages of native vegetative cover in particular attracts bird species, with aggregate avian biodiversity increasing with increasing native vegetation cover over multiple spatial scales over time (Cunningham et al., 2014). Bird species richness at site scale was also related positively to the amount of vegetation cover in the surrounding landscape (Cunningham et al., 2014). The greatest

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[4]Yet this study notes this must be in part evolutionarily ingrained, eg. cowbird populations reared in host nests seek out edge niches as adults.

gains in avian biodiversity were found at relatively low increases in vegetation cover, indicating that even small gains in vegetative cover can drastically improve avian biodiversity at the site scale (Cunningham et al., 2014). Species richness of woodland birds in particular has also been found to be significantly related to habitat coverage of a region, with sites displaying higher habitat cover gaining higher avian species richness in modeled observational trials (Radford et al., 2005).

There are a variety of theories explaining such a positive correlation between vegetative cover rates and avian microsite usage. These suggest that birds may select areas of increased cover within their habitat niche because these areas provide a) increased protection from aerial and ground predators; b) increased protection from environmental forces; c) increased food sources; and d) cryptic areas for the storage of food caches.

Predator Protection   Cover may be used by bird species as protection from being sighted and/or killed by predators. Birds tend to increase their occupancy of higher-cover habitat during the post-breeding season, when juveniles who are inexperienced at flight and inept at escaping from predators are most vulnerable; furthermore, adults have diminished flight capacities due to molting patterns (Vitz et al., 2007). Birds in the post-breeding season have therefore been found to preferentially select areas with greater vertical structure (i.e. medium density understory and high density, tall canopy) compared to other forest microsites as the best protection from both aerial and ground predators (Vitz et al., 2007). In this study, it is noted that understory cover must be dense enough to provide protection from ground-dwelling predators, but not so dense as to decrease available escape flight movements or provide cryptic areas for predators to evade detection (Vitz et al., 2007). Protection from

aerial predators has been shown to be increased when vegetative cover is available for smaller avian species, and thus cover was utilized in the escape take-off strategies of birds under simulated threat from red-winged hawk predation when such higher-cover areas were available to them (Kullberg & Lafrenz, 2007). For overwintering birds, proximity to cover further influences feeding behavior at feeders under varying predation risks, with the vigilance behavior of passerine species found to be significantly higher when feeding far from nearby branches of foliage cover (Carrascal et al., 2006). Moreover, although the thermal benefits of direct sunlight would be advantageous to cold-sensitive overwintering birds, in observational contexts birds have been shown to avoid direct sunlight and prefer covered areas due to the protection from predator detection that cover grants (Carr & Lima, 2014). Several avian species have also been found to specifically utilize vegetative cover during nest-building in order to successfully reduce nest predation (Dwernychuk & Boag, 1972; Haensly et al., 1987; Jones & Hungerford, 1972).

Environmental Elements Protection Covered areas may also provide protection to birds against environmental forces, such as weather events of varying extremities. Thermal heat loss is risky in small vertebrates, particularly warm-blooded birds (Carr & Lima, 2014). The thermal heat loss from wind poses a particularly dangerous threat to birds (Wolf & Walsberg, 1996), and birds in the wild have been shown to preferentially choose microclimates with high cover in order to reduce wind speed battery (Wachob, 1996). Moreover, vegetative cover can act as protection from extreme weather events, such as hailstorms, and thus birds who choose to occupy patches with higher cover have decreased mortality rates in such extreme events (Hall & Harvey, 2007). Moreover, higher vegetative cover ratios may be of use to birds in habitats

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with extremely high summer temperatures, as suggested by roadrunners' heavier usage of high shrub- and litter-covered areas during extreme summer temperature events (Montalvo et al., 2014).

Resource Proxy Vegetative cover can also act as a deterministic proxy for food source allocation calculations by birds searching food. As previously discussed, birds occupy different niches across habitats and thus will preferentially choose varying structures based on species-specific indicators; however, within their preferred vegetative structure niche, some trends are notable. Forest structure has been shown to be a deterministic factor in foraging behavior in many passerine avian species. For example, American redstarts, an ecologically plastic species generally elastic in niche filling, will tend to forage at higher canopy altitudes in areas with less vegetative cover, and at lower canopy heights when denser cover pervades (Seidel & Whitmore, 1982). Across several species, birds have been found to more intensely use areas with higher percentages of cover within their niche; specifically, high crown density in trees at the canopy level is associated with high resource use for selected canopy-residing species (Böhm & Kalko, 2009). This may be due to high cover areas possessing substrate characteristics which offer more microhabitats for arthropods, thus providing a higher prey density for insectivorous or semi-insectivorous avian species (Böhm & Kalko, 2009). Moreover, abundance of foliage-gleaning insectivorous avian species has been seen to be highly correlated with foliage density across seasonal changes (Martin & Karr, 1986). Regarding the feeding habits of frugivorous birds, greater usable fruit resource abundance has been found in areas of more highly concentrated understory cover, which in turn were found to be more abundant in areas of lower canopy cover (Martin & Karr, 1986). Thus, frugivorous birds are more likely to find

easily available fruit in areas with generally higher cover, and this may explain higher occupancy of heavily covered areas in the post-breeding season (Vitz et al., 2007). Fruit availability and forest cover may in fact synergistically interact to create long-term, complex landscape effects in order to determine frugivorous birds habitat use (Martínez & García, 2015). Specifically, canopy gap areas, which display higher fruit and foliage-consuming insect abundance, are more highly used by both insectivorous and frugivorous avian species over a studied spring-to-fall timeline (Martin & Karr, 1986).

Cache Site Protection   Finally, vegetative cover, especially ground cover, may be selected for its utility in the protection of birds' caching sites, especially during the winter months when caching is most highly utilized (D. R. Petit et al., 1989; Woodrey, 1991; Johnson et al., 1997). Across avian species that exhibit caching behavior, the floristic and physiognomic characteristics of vegetation, including cover assessments, are used in determining cache sites (D. R. Petit et al., 1989). In nuthatches, social dominance is used as a determiner of which birds can obtain the highest cover patches, specifically those with high rugosity, which are most sought after for caching purposes (Woodrey, 1991). Moreover, even in species that make use of a wide variety of covered-to-uncovered patches, such as blue jays, patches in regenerating wood-lots with high ground cover characteristics are generally preferred and utilized at the highest frequency (Johnson et al., 1997). The use of areas with high ground cover for caching purposes, especially bird choices of high ground cover areas in regenerating woodland lots, may have long-ranging effects on seed germination and tree demography in these habitats, and thus may constitute an ecological service by birds in restoring regenerating woodlands (Johnson et al., 1997).

Various other trends between vegetative cover and avian behavior/survival rates have also been recorded, not including those above noted. For instance, birds take more time in flight and were less likely to successfully return home as forest cover decreased in the landscape, with no other variation found to be determinative in homing time and success (Bélisle et al., 2001). Moreover, some studied avian species have been found to intensely rely on ground and litter cover for nesting purposes (beyond predation protection, as previously discussed). For example, experimental use of complete herbicide to eliminate ground and litter cover reduced the nest success of Common Terns, with no accompanying change in food resource use or predation noted to account for this trend (Cook-Haley & Millenbah, 2002).

1.3 Factors Affecting Cover

Cover can be affected by a number of factors, ranging from naturally varying conditions to human-induced structural changes.

1.3.1 Naturally Variable Factors

Naturally, cover can vary for a variety of reasons. In winter, conifers will usually provide higher cover than deciduous trees, due to not shedding their leaves en masse as deciduous trees do. Thus, in winter, deciduous-coniferous mixed forests will tend to display variable cover percentages across forest patches, dependent on the predominant tree species in certain patches (Bianchini et al., 2001). Moreover, among deciduous trees, differing species display differing levels of canopy cover, and thus cover naturally varies throughout mixed forests (Köble & Seufert, 2001). Because of

these species-specific ranges in cover granted, dispersal variables can affect ensuing vegetation cover over newly populated patches (Gurnell et al., 2006). Woody plant seeds have more highly restrictive microclimate requirements for germination than for adult woody plant survival (Hardegree et al., 2013). Thus, in regenerating forests, the microclimates surrounding dispersed seeds can play a significant role in determining species-specific germination rates and seed success, and therefore is a salient factor in determining the eventual composition, structure, and cover of regenerating forest lots (Holl, 1999). Natural events, such as fire or strong storms, can also have significant effects on canopy cover found within forests, with resulting ground cover effects found over a longer term (Lloret, 1998; Askins, 2014b). These large-scale natural events can thereby markedly shape the habitat structure of forested ecosystems: for example, a natural forest fire can completely reshape a forest ecosystem, altering biodiversity, species composition, growth rates, and a range of cover variables across the board (Lloret, 1998).

Moreover, old-growth and young-growth forests have been experimentally shown to have different habitat structures, and thus different canopy and ground/shrub cover ratios (Donoso & Nyland, 2005). In fact, this correlation is so strong, understory coverage can be used as a metric for determining disturbance history, with young-growth disturbed forests being identified through their increased understory cover metrics (Nowacki & Abrams, 1997). This most likely arises from the pattern found of percent canopy cover inversely determining percent ground cover in forests (Beatty, 1984). As a trend, patches with high canopy cover will generally allow fewer shrub and ground-covering species to grow, and areas with patchy canopy cover generally generate more growth of ground-covering species (Beatty, 1984). Tree diversity has thus been linked

to directly predict ground cover in deciduous forests (Vockenhuber et al., 2011). In a further test of this theory, understory cover patterns have been found to be highly dependent on dominant canopy tree species (Augusto et al., 2003). Specifically, how much light and throughfall precipitation is allowed in by tree canopies can determine success of ground cover colonization, with throughfall precipitation playing the primary deterministic role (Anderson et al., 1969). This pattern may play a role in the production of edge effects, due to increased light and precipitation fall on edges.

1.3.2   Anthropogenically-Linked Factors

A number of factors affecting cover are tied to human activity, some more directly than others. Both forb/understory and canopy cover can be affected by habitat fragmentation, and the resulting effects on edges that inhabit those areas. A direct result of human land use, habitat fragmentation leads to an increase in the perimeter or surface area of forest plots; in other words, more edges are created (Haddad et al., 2015). "Edge effects" can describe the set of community structure changes seen at the boundary of two habitat types, eg. the abrupt transition between a forest and a human disturbance, such as a road or agricultural site (Murcia, 1995). Resulting edge effects on forests are caused by a change in the abiotic and biotic conditions, which have knockdown effects on cover in those areas (Murcia, 1995). Generally, cover trends found in the field indicate the reduction of canopy cover near edges, and the increase in understory cover at edges and fragmented sites (Murcia, 1995). Canopy cover in particular has been shown to be directly affected by edge effects, as it displays a reducing gradient of heights and percent coverage found in trees at the perimeter of edges in forested plots fragmented by roads (Fischer & Lindenmayer,

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2007). The understory is particularly responsive to edge effects, especially those from habitat fragmentation: the cover of the understory drastically increases around edges as compared to central forests (Murcia, 1995). In temperate zone studies on forest edges, edges have been found to typically contain more shrubs and other types of ground cover than central forests (Fleming & Giuliano, 1998; Gates & Giffen, 1991).

Grazing   Cover can further be affected by grazing, especially the grazing practices of human-raised ungulates (Zhang, 1998). Specifically, ground cover percentage in forested areas can be negatively affected by grazing, decimating the amount of ground cover found in forests where grazing occurs (den Herder et al., 2003). These effects were shown not to be caused only by the removal through consuming ground cover species while grazing, but also the trampling that accompanies this practice by grazing animals (den Herder et al., 2003). Moreover, grazing can have implications on the survival of tree species that would go on to provide canopy cover in grazed regions. Grazing can thereby affect tree species diversity and composition, which has knockdown implications on cover found at grazed sites (Zhang, 1998). Grazing practices can further facilitate the successional invasion of non-native tree species into forested regions, thereby reducing the relative and overall cover of native tree species (Relva et al., 2010). Such changes alter forest composition over the long term (Relva et al., 2010).

Particularly notable in Eastern North American ecosystems, the explosion of white-tailed deer populations has created major vegetative structural changes across forest and edge habitats, primarily due to these species' browsing and grazing practices (Nudds, 1977; Russell et al., 2001; Rooney & Waller, 2003). White-tailed deer overpopulation trends have been primarily attributed to direct and indirect an-

thropogenic factors that facilitate increased deer reproduction, including structural changes to the North American landscape and the elimination or reduction of large carnivorous predators such as wolves (Rooney & Waller, 2003; Wolverton et al., 2007). In such predator-free forests, the densities of seedlings and canopy-creating trees are severely structurally altered by herbivore grazing, directly due to the lack of top-down predation maintaining ecosystem balance (Terborgh et al., 2001). This process can lead to an ecological meltdown, with excessive grazing exponentially selecting for unpalatable canopy species to over-dominate forests and excessive loss of biodiversity (Terborgh et al., 2001). White-tailed deer have been found to decrease forb cover in forests, suppressing the cover of and regeneration of woodland herb species (Whigham, 2004). Across patches, sensitive native understory herbs can be driven to elimination or unsustainably low cover rates by the cumulative effects of white-tailed deer grazing (Augustine & Frelich, 1998). Furthermore, white-tailed deer can decrease the biodiversity of ground cover found in forest plots (Whigham, 2004). In regards to canopy cover, white-tailed deer browsing has been found to alter the composition and structure of forest canopy tree species, altering forest structure and resulting canopy coverage (Anderson & Loucks, 1979). Specifically, both heavy and light deer browsing was found to lead to the selective replacement of hemlocks by sugar maples in a hemlock-predominant forest, significantly decreasing hemlock reproduction rates and area biodiversity (Anderson & Loucks, 1979). Overabundant deer herds have moreover been found to generally repress forest regeneration through intensive browsing, thereby creating alternate stable states in forest plant communities (Stromayer & Warren, 1997). Thus, deer may suppress advanced regeneration and succession that normally would restock a site following a release of the overstory, altering woody

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vegetation canopy cover in forests, a trend is thought to be intensifying over time (Stromayer & Warren, 1997).

Human Disturbance Cover can moreover directly be affected by anthropogenic activity. As previously discussed, habitat fragmentation, which is often caused by human-induced structural landscape alterations, can alter vegetative structural patterns and cover. Consistent human disturbance can lead to diversity loss in both ground/understory and canopy tree species, creating altered vegetative cover patterns, even leading to the point of leading to structural ecosystem collapse in tropical and temperate forests (MacDougall et al., 2013). Anthropogenic disturbances alter the species structures of forests, lowering canopy tree diversity (Ramírez-Marcial et al., 2001). This process leads to lowered canopy cover as a direct result of anthropogenic disturbance (Ramírez-Marcial et al., 2001). Human disturbance is theorized as a primary factor in the overall decline of native ground cover in temperate woodlands, with a significant proportion of deciduous forest woodland herb species rendered rare, threatened, or in significant decline in recent decades (Whigham, 2004). Like grazing animals, humans roaming forest landscapes can trample ground-covering species, lowering their survival rates and impacting their resulting cover (Monz, 2002; Pescott & Stewart, 2014).

Humans also play a role in the management of forests, which can affect cover in subtle or drastic manners. Forestry management practices can deleteriously affect the cover of the canopy due to the selective removal of trees, which can have knockdown effects on understory growth and cover rates (Heynen & Lindsey, 2003). This is a direct alteration of structural patterns within forested landscapes. Native canopy cover remaining after intervention can thus even be used as a proxy for the determination

of the success of forestry management practices, as forest management which creates drastic cover change is ineffective due to the host of resulting effects major cover change incurs (Heynen & Lindsey, 2003). Although forestry management's goal is to maintain and encourage natural ecosystem structure, this is not always effectively employed.

1.4 Overwintering Birds

Winter is a critical survival time for temperate birds, due to the perilous hazards associated with either overwintering in a hostile cold environment, or enduring a long distance migration (Karr et al., 1990). Here, we focus on birds that have evolutionarily chosen not to migrate and endure such a cold environment, the overwintering birds of a particular region.[5] Birds overwintering in temperate climates comprise a particularly under-studied subset of avian species as opposed to their long-distance migrational counterparts (Hardy et al., 2013); however, studies on overwintering populations have provided some illumination on their contextual relationship with this seasonal shift. Overwintering birds in the Northern hemisphere are particularly in danger of a changing climate, as temperature shifts are outrunning geographic community shifts at large; without migration as a resource to functionally alter geographic range, overwintering communities are in peril of range exclusion (Santangeli & Lehikoinen, 2017). Low over-winter survival rates can contribute to species declines on a regional scale, negatively impacting biodiversity, thus highlighting the importance of winter

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[5]This term also includes the boreal birds that migrate short distances south into the temperate zone for less harsh wintering conditions. The trends described in this section generally apply to this subset of birds equally, however, the local existence of this subset of bird populations varies across studied regions.

resource ecological study (Peach et al., 1999).

Overwintering birds have been found to have differing survival rates based on food sources available to them; namely, the supplemental food offered by bird feeders increases survival overwinter (Brittingham & Temple, 1988). Beyond granivorous birds, overwintering birds appear to prey on insects inhabiting trees independently of foraging on supplemental food sources, or alternatively different species of birds forage on tree insects compared to those that visit feeders (Teachout et al., 2017).

2 Introduction

Overwintering birds' relationship with the habitat they occupy during this seasonal shift has been relatively absent from study, besides a few key insights. Ectomorphic features have been found to influence habitat-situated foraging behavior in wintering bird populations, with morphology correctly predicting realized niche breadth and overlap (Carrascal et al., 1990). Moreover, overwintering passerines tend to preferably choose feeders with lowered latent predation risk, making use of vegetative habitat cover nearby to the feeders in their foraging patterns (Carrascal et al., 2006). Overwintering birds increased their relative use of one studied tree species during winter as opposed to summer, suggesting winter microhabitats for foraging differ from summer microhabitats due to seasonal resource shifts (Morrison et al., 1985). And grassland overwintering bird species have been associated with microhabitat niches, such as ordinational associations with vertical grass height and shrub density (Ruth et al., 2014).

And study has correlated some individual overwintering North American forest bird species' occupancy in forests with vegetative structural patterns: white-breasted nuthatches and western bluebirds were negatively correlated with dense woodlands, occurring at the highest density in widely-spaced oak forests with sparse understory; while ruby-crowned kinglets and Hutton's vireos were positively associated

with dense, floristically diverse woodland, with a structurally complex understory (Hardy et al., 2013).

Yet Hardy et al. (2013) was not able to broaden these trends to local overwintering bird populations as a whole: this is our aim, to create a broad-scale association of overwintering forest birds with forest characteristics, including the vegetative structure of the microhabitats they occupy. We have particular interest in measuring the response of overwintering bird forest occupancy to vegetative cover, based on the trends between birds and cover seen in 1.2.2 and given the fluxing nature of vegetative cover during the fall-to-winter timeline.

This assessment is especially important given the changing human use of landscape, and the alterations upon it that may impact bird communities. As covered in (habitat change and birds) section, anthropogenic changes can fragment, isolate, and degrade forests in particular, negatively affecting bird populations. In eastern North America specifically, forests have gone through a centuries-long battle with human populations, and have markedly changed in species composition since European colonization (Thompson et al., 2013). With these changing forest dynamics, the result of anthropogenically-driven processes markedly shaping our landscape, avian response is crucial to be investigated.

3   Methods

3.1   Data Collection

3.1.1   Forest Selection

This study aims to create a survey of bird occupancy of forest transects in the Hudson Valley region, specifically relating avian occupation and abundance in chosen transects to microhabitat cover, structure, and composition. For the purposes of this study, a forest was defined as a land area of at least $200m^2$ whose topographic structure is dominated by an assemblage of trees. As a major goal of this study is to observe how birds located in any particular forest are choosing which sections within that forest in which to reside/occupy, forests known to be relatively abundant with birds were selected for survey in this study, as such areas would be likely to have both occupied and unoccupied sections for comparison. These forests known to contain relatively high bird abundance, i.e. "hotspots", were chosen through a variety of measures. Primarily, forested hotspots were recommended both through personal field experience birding in the area (both independently and in Field Ornithology class) and through suggestion from area birders (chiefly via my advisor, Bruce Robertson). To supplement these familiar forests, hotspots listed in the book Birding in the Hudson Valley

by Kathryn Schneider and hotspots listed on the Dutchess County and Columbia County sections of the Cornell Lab of Ornithology's birding resource ebird.org were considered and ultimately chosen for study if a) the hotspot's vegetation structure fit within the study parameters as a forested area; and b) travel was practical from Bard College. New areas were continuously brought up for investigation throughout the course of the study.

3.1.2 Site Selection

Once forests were selected for study, a random section of that forest was chosen as the general study site. Random sections were created by creating a grid overlay of the forest over its total area as displayed on Google Maps (maps.google.com). Each grid square was assigned an ascending unique number, and then a random number was generated via the in-built RNG on iPhone (as accessible by Siri). The corresponding number's plot of area would be travelled to through the most accessible direction, and once a grid's edge was approximately reached via Google Maps positioning, a flag was placed down and surveying for birds would begin. Travelling towards the center of the grid square, we would record the path taken, and a transect (see 3.1.3) was begun at the first bird spotting and a flag was placed at its start. After all survey transects were complete, the previous 50 meter section of the route unoccupied by birds in between the two aforementioned flags was marked as an available empty vegetation plot (see 3.1.3).
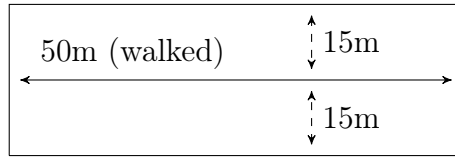
50m (walked)	↕ 15m
	↕ 15m

Figure 3.1.1: Transect Geometry

3.1.3 Transects

Bird Count Methodology

Transects were conducted as 50 m long linear paths of forest with 15 m along each side (see Figure 3.1.1). Transect length, width, and procedure was based on similar/commonplace ornithology procedure among birding studies, including reference to Buler et al. (2007), Fleming and Giuliano (1998), Ruth et al. (2014), and Tingley et al. (2009). In the field, 50 m was measured as 74 steps (because, based on my personal average stride length, on average 74 steps is approximately equal to 50 meters). Walking at a slow and even pace for 50 meters, all birds seen or heard occupying the transect length and width were counted and their species type recorded. If several species were present at once (usually because these birds were in a flock), we paused walking until all could be identified and counted, then resumed until the 50 m was complete. Species IDs for visually seen birds were based on prior birding knowledge (from personal study and the Field Ornithology curriculum), and Sibley's Guide to Eastern Birds was carried in case of identification failure. Species IDs for heard birds were partially based on prior knowledge, and supplemented and verified through the apps Bird Song/SongSleuth when necessary, in which known recorded calls were repeated to confirm species type. Flyovers were not counted due to these birds not "using" or occupying forested tracts.

Bird(s) present; continue	No birds; stop survey

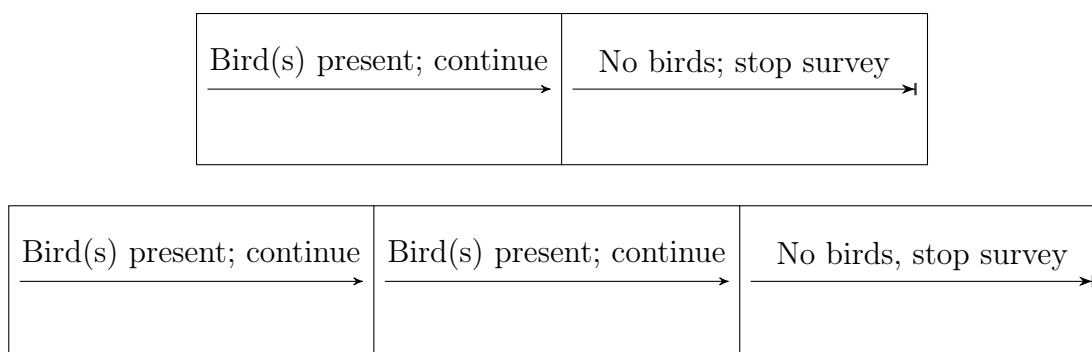| Bird(s) present; continue	Bird(s) present; continue	No birds, stop survey

Figure 3.1.2: Transect pattern

After 50 m was traversed, a flag was placed at its end and another transect of 50 m would begin. We would repeat the transect protocol as many times as necessary until no more birds were contained in a transect, leaving the final, unoccupied transect as a comparative vegetation plot for presence/absence analysis (see Figure 3.1.2). In cases in which repeating or completing a transect would cause leaving the defined forest, a random direction would be chosen and a complete transect would begin in that direction. All transects were marked by flags at both start and end in order to later collect vegetation plot data.

Vegetation Methodology

Vegetation data was taken in both occupied and unoccupied transects for comparative measure. Vegetation structure was measured by four means: canopy density, ground vegetation cover, tree number along transect length/tree density, and dominant tree species composition.

Canopy cover was measured through spherical crown densiometer readings at 5m, 15m, 25m, 35m, and 45m points along the length of the travelled transect. Densiometer use was following the guidelines as given by Lemmon (1956). After leaf fall,

densiometer methods were adjusted to account for lack of leaf coverage within the densiometer viewfinder. At this time, the quartered grid section of the densiometer was considered filled if more than three branches existed within the reading viewfinder.

Ground vegetation was measured as percent cover as estimated at 5m, 15m, 25m, 35m, and 45m points along the length of the travelled transect. For both canopy and ground cover data, the average of the 5m, 15m, 25m, 35m, and 45m data points was taken and each transect was thereby assigned an average canopy and ground cover structure.

Tree density was measured as the counted number of individual tree trunks greater than 10cm diameter at breast height along the linear path of transect walked. The number was counted by spanning a measuring tape for the length of 50 meters between the flags, and all tree trunks within 10 cm of the measuring tape were counted.

Finally, the species composition was based on the identification of the primary tree species in the 50m x 30m transect area. Tree species were identified using a variety of methods, including prior knowledge from Plant Ecology curriculum, Sibley's Guide to Trees and Bark: A Field Guide to Trees of the Northeast by Michael Wojtech. Each transect's predominant species was recorded as an identifying feature of this transect. Dominant tree species was drawn as an estimation as the species which contributed most fully to the transect's canopy by area.

In some cases, vegetation plot data was not able to be collected immediately; in these cases, the flags were not removed upon transect completion, and we returned to the area later in the day when vegetation plot data was able to be completed. In all cases, vegetation plot data was collected in the same day as bird counts.
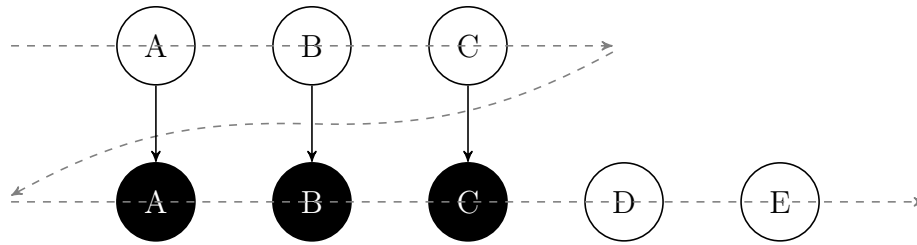
Figure 3.1.3: Sites (ex. A, B, C) with data collected before leaf-fall can be re-examined after leaf-fall; however, novel sites (ex. D, E) are continually examined.

Site Revisitation

At a midpoint in the study, we realized that re-examination of the same sites both before and after leaf-fall, and potentially with and without snow-fall, could be valuable for comparison. Repeating transect areas in different stages of vegetation cover could help achieve Before-After-Control-Impact (BACI) study design, and therefore resurveying areas was undertaken to the best of my ability with respect to previous site specificity.

3.2   Data Analysis

Although a BACI study design was originally intended to examine the data statistically, following data collection completion, we concluded, however, that a) the body of data did not contain enough revisited sites for thorough comparison and b) proper control sites were not generated by the body of data in order to perform a proper BACI analysis. Instead, all transects were treated as independent samples of bird populations, which is not ideal but is partially accounted for in 3.2.2.

3.2.1 Variable Treatment

Some variables were treated as categorical binary variables in order to pursue confident data analysis. The assignment of categories is explained below.

Treatment of Tree Species

During the data analysis stage, we realized that the dominant tree species sampling had greatly varied in terms of species found across transects, and thus specific tree species' sampled numbers were relatively low; moreover, each individual tree species had been found to be dominant in plots at radically different rates, produce irregular sample sizes. Thus, we realized the difficulty in drawing robust conclusions about bird preferences to specific tree species, given the small and unevenly distributed collected species-specific samples. In order to draw more confident conclusions about the data, we compared transects as a binary factor of whether their dominant tree species was the most prevalent tree species sampled, *Acer saccharum* (common name sugar maple). Thus, for all modelling methods employed, tree species was treated as a binary yes/no factor of whether the dominant tree species in that transect was the sugar maple.

Treatment of Fall-to-Winter Timeline

Similar binary treatment was given to the fall-to-winter variable of time of sampling as falling into the category of "fall" or "winter". This decision was based around the final leaf-fall date observed over the course of the studied timeline: the final leaf-fall date was considered December 5, based on the end of general leaf-fall for the final tree to shed its leaves, the *Acer rubrum* (common name: red maple). Unpublished data

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collected on species-specific leaf-fall date in an independent study by Bruce Robertson within the same Hudson Valley area was used as verification of this leaf-fall date for *Acer rubrum* specifically. Thus, all statistical analysis involving time of year as a mitigating variable used this speccific December 5 cutoff point in its assessment of seasonality.

The logic behind this treatment was that leaf-fall was particularly important to this study because of its canopy cover implications, one of the measured vegetative variables on which bird sightings could depend. This dependency is hypothesized from the known use of birds and cover detailed in 1.2.2, but its response to leaf-fall is unknown. Thus leaf-fall logically follows as the proxy for determining seasonal changes in microhabitat cover variance and bird's response to changing cover over time.

3.2.2   Statistical Analysis

The data were assessed and modelled in two primary regards: the measured variables' ability to predict the presence vs. absence of birds in a transect, and their ability to predict realized bird abundance. The logic behind this choice was to separately analyze the factors that predict overwintering bird occupancy in a given microhabitat, as well as the factors influencing groups of higher abundances of birds.

All statistical analyses were run in R (R Core Team, 2019) using the core package `stats`. Generalized linear models (GLMs) were selected as a means of regressing multiple vegetative habitat variables against the bird presence/absence and bird abundances respectively.

Generalized Linear Models

Formulation Given dependent variables $\mathbf{Y}$ and independent variables $\mathbf{X}$, the general formulation of a GLM can be expressed as follows:

$$E(\mathbf{Y}) = g^{-1}(\eta)$$

$$\eta = \mathbf{X}\boldsymbol{\beta}$$

Here, $E(\mathbf{Y})$ is the expected value of $\mathbf{Y}$, $\mathbf{X}\boldsymbol{\beta}$ is a linear combination of the independent variables and their respective, unknown coefficients $\boldsymbol{\beta}$, and g^{-1} is the link function for that family of GLM. For Poisson GLMs, a logarithmic link function is used, leading to the following:

$$E(\mathbf{Y}) = ln^{-1}(\mathbf{X}\boldsymbol{\beta}) = \exp(\mathbf{X}\boldsymbol{\beta})$$

Thus, for a model with one dependent variable and three independent variables, the complete formulation would appear:

$$E(y_1) = \exp(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3)$$

For further information, see Carey (2013).

Analysis We used a type II ANOVA from the R package `car` (Fox & Weisberg, 2011) to analyze the chi-squared residuals of each term in a given model. Additionally, a Pearson's chi-squared test was performed on the residuals for each model to demonstrate goodness-of-fit.[1] This follows guidelines as set by Langsrud (2003).

---

[1] Slightly different formulations were used depending on GLM family; see Appendix (TODO: put a reference here)

Bird Presence/Absence

Because bird presence/absence within a transect is a categorical binary variable, we decided to perform a GLM using the link function of a logistic binomial regression, on the data, as it provides the necessary prediction of a binary categorical variable's likelihood as a function of the inputted regression factors. This logistic binomial regression used the measured factors of canopy cover, ground cover, dominant tree species (see 3.2.1), and forest density in order to predict bird presence within a transect.

These data were supplemented by employing Mann-Whitney U tests on the corresponding vegetative variables in "birds present" vs. "birds absent" transects for each vegetative variable individually. Although, for example, canopy cover density was *roughly* normally distributed (Figure A.2.2) and a t-test could have been employed on the two sampled vegetative cover groups, Mann-Whitney U tests were selected to account for any non-normality in the data sets, and because they are generally found to be nearly as effective as t-tests on samples from normal populations.

The model's individual odds ratios and confidence intervals were generated using the `Publish` package in R (Gerds & Ozenne, 2018).

Bird Abundance

The bird abundance data in response to the measured vegetative and time variables was modelled as a GLM operating under the link function of a Poisson distribution, generating a Poisson regression. This statistical model/regression was chosen because the abundance data, as count data which was heavily zero-bird and one-bird skewed, did not reflect a normal distribution, instead reflecting a Poisson distribution (see

Figure A.2.1). Thus, the GLM was able to effectively model the data around the given variables given this non-normality.

Specifically, we ran this Poisson regression for abundance in response to canopy cover, ground cover, tree density, primary tree species, and season (with the last two as binary variables; see 3.2.1) in order to predict bird abundances within a transect. The model's individual hazard ratios and confidence intervals were again generated using the `Publish` package in R.

3.3 Reference for Interpreting Results

The data was input into R using column headers, which require some translation. Below is a reference table for the variable names as they were input into R. This may additionally be useful in deciphering Figure 4.1.1, Figure 4.1.2, Figure 4.2.1, and Figure 4.2.2.

Term	Variable Name
Ground cover level	`VegGC`
Canopy density	`VegDens`
Forest density	`VegTreeCount`
Fall/Winter	`Fall.Winter [F/W]`
Maples/non-maples	`AcerSacYes.No [M/NM]`

Table 3.1: Terms and variables used in R code

4 Results

We completed 73 transects over 11 unique sites in the Hudson Valley. We encountered a total of 91 individual birds, comprising 17 unique species. Although the transects contained a wide array of tree species, 11 different tree species were classified as dominant within the measured transects.

4.1 Bird Abundance

We fitted a GLM with a Poisson distribution and logarithmic link function to our data, with the target being abundance of birds, and the vegetation data for each transect being the source variables. Our results (Figure 4.1.1) demonstrate that higher ground cover and higher canopy cover positively affect bird abundance ($p < 0.001$, $p < 0.001$). Furthermore, bird abundances observed were higher during the Winter ($p = 0.002$), and in non-maple plots ($p = 0.031$). Forest density did not have a significant effect on bird abundance observed ($p = 0.639$).

After the successful generation of this model, we attempted to generate models exploring the dataset for any interactions between the variables leading to increased abundance found within the data. Specifically, we created models using Fall/Winter and Canopy Cover, Fall/Winter and Ground Cover, Maple/Non-Maple and Canopy

```
# Response variable: Abundance
# Independent variables:
VegGC + Fall.Winter + VegDens + VegTreeCount + AcerSacYes.No
# Results:
      Variable Units HazardRatio        CI.95      p-value signif
         VegGC               1.57 [1.25;1.97]    0.0001207    ***
       VegDens               1.04 [1.02;1.06]    0.0004338    ***
  VegTreeCount               1.02 [0.93;1.12]    0.6386987
   Fall.Winter     F         Ref
                   W         2.56 [1.40;4.70]    0.0023717     **
  AcerSacYes.No     M         Ref
                  NM         1.83 [1.05;3.16]    0.0314769      *
```

Figure 4.1.1: Poisson-family GLM results on bird abundance

Cover, and Canopy Cover and Ground Cover. None of these interactive models had significant results (none with $p = 0.05$ or lower), leading us to believe that no interactions were present within our dataset.

Graphical representations of significant modeled effects are found in figures 4.1.3, 4.1.4; in these figures, the solid line represents the effect of each variable in question in the fitted model, while the shaded area represents a 95% confidence interval around the predicted abundance value.

In Figure 4.1.2, we display the results for a type II ANOVA performed on the model. A majority of the deviance explained by the model (`LR Chisq`) is accounted for by canopy density and ground cover level; their relative predicted effects plots (Figure 4.1.3, Figure 4.1.4) reflect this relation-

```
Analysis of Deviance Table (Type II tests)

Response: Abundance
                LR Chisq Df  Pr(>Chisq)
VegGC            14.9715  1   0.0001091 ***
Fall.Winter       9.3756  1   0.0021990 **
VegDens          12.3514  1   0.0004407 ***
VegTreeCount      0.2204  1   0.6387334
AcerSacYes.No     5.1027  1   0.0238886 *
# Relative to:
Null deviance: 142.10  on 72  DoF
Residual deviance: 109.03  on 67  DoF
```

Figure 4.1.2: ANOVA of model in Figure 4.1.1 vs. null

ship. In line with the p-values derived from the model, forest density does not contribute significantly to the overall deviance.
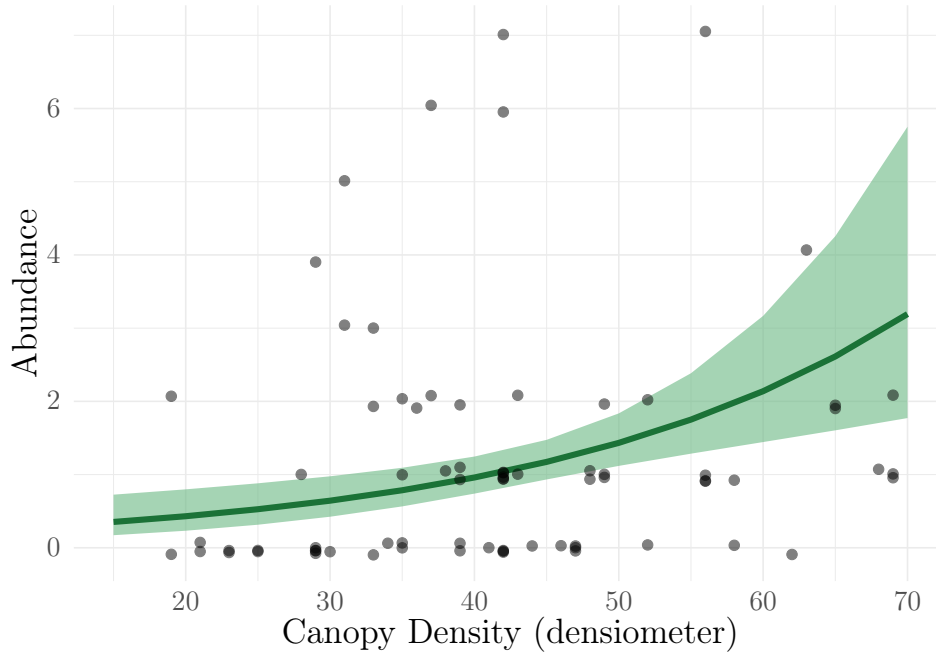

Figure 4.1.3: Partial regression of predicted effect of canopy density on bird abundance. Overlayed with scatterplot of observed bird abundance vs. canopy density; jitter was added on the y axis for better visibility.
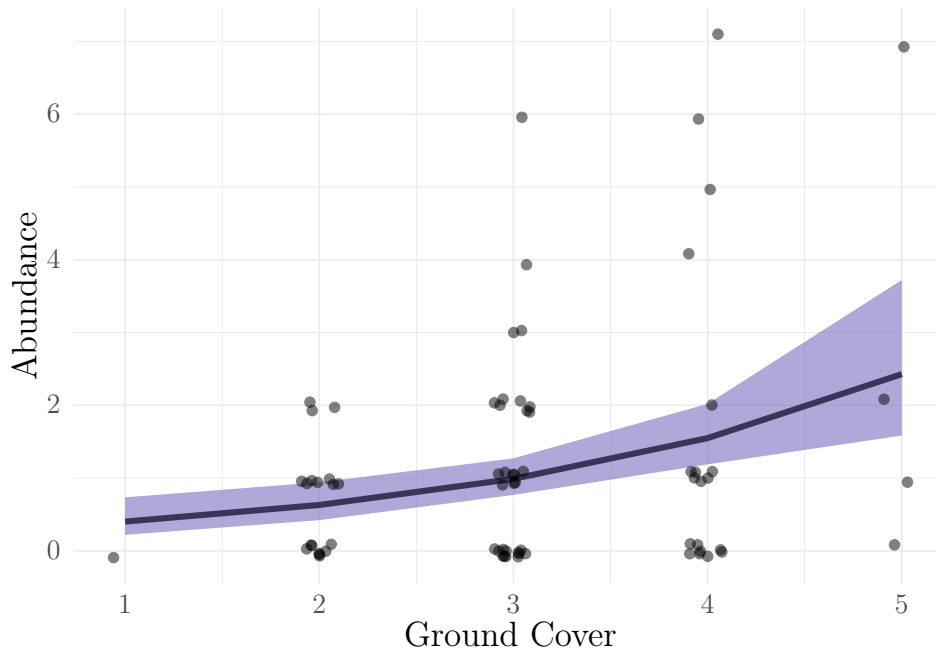
Figure 4.1.4: Partial regression of predicted effect of ground cover level on bird abundance. Overlayed with scatterplot of observed bird abundance vs. ground cover level; jitter was added on both x and y axes.
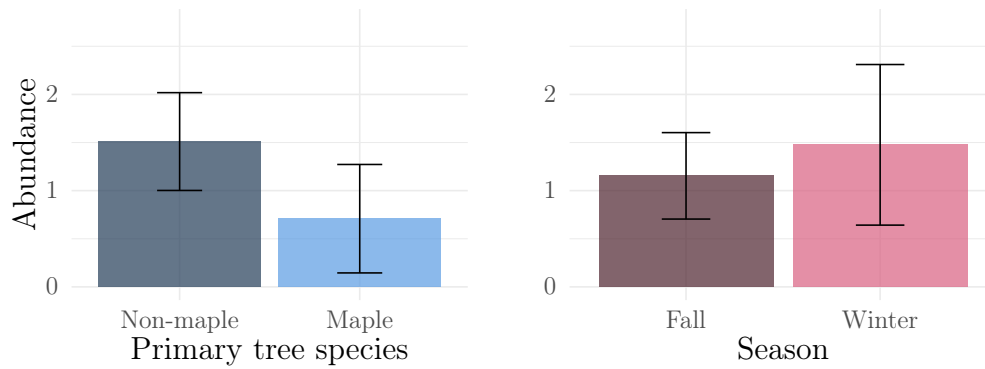

Figure 4.1.5: Average observed abundances across surveyed transects, split by primary tree species and season. Error bars denote 95% confidence interval of the mean. Partial regressions of these observed trends (not pictured) proved to be significant.

4.2 Bird Presence/Absence

We performed a GLM in the form of a binomial logistic regression to analyze specifically the response of bird presence to the factors measured in our data. Our results (Figure 4.2.1) demonstrate that canopy density has a significant effect ($p = 0.003$) on the likelihood of a transect being occupied at all (see Figure 4.2.3). Birds were also more likely to occupy non-maple transects ($p = 0.034$). Ground cover level did not have a significant effect on bird presence ($p = 0.119$), nor did forest density ($p = 0.437$).

```
# Formula:
Bird.NoBird ~ VegDens + VegGC + AcerSacYes.No + VegTreeCount
# Results:
       Variable Units OddsRatio        CI.95    p-value signif
        VegDens             1.08  [1.03;1.13]   0.002801     **
          VegGC             1.69  [0.87;3.27]   0.119103
  AcerSacYes.No     M       Ref
                   NM       3.45 [1.10;10.78]   0.033610      *
   VegTreeCount             1.09  [0.87;1.37]   0.437105
```

Figure 4.2.1: Binomial logistic regression results

As shown in Figure 4.2.2, a majority of deviance explained by the model is accounted for by canopy density.

```
Analysis of Deviance Table (Type II tests)

Response: Bird.NoBird
              LR Chisq Df Pr(>Chisq)
VegDens        11.0033  1  0.0009095 ***
VegGC           2.6274  1  0.1050342
AcerSacYes.No   4.6816  1  0.0304876 *
VegTreeCount    0.6119  1  0.4340803
# Relative to:
    Null deviance: 98.872  on 72  DoF
Residual deviance: 80.307  on 68  DoF
```
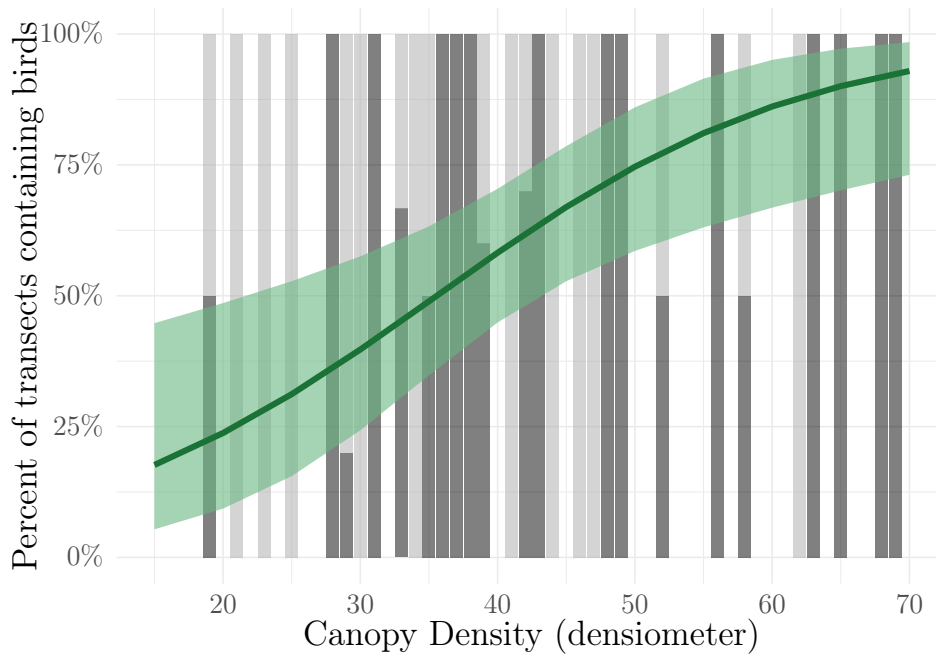
Figure 4.2.2: ANOVA of model in Figure 4.2.1

Figure 4.2.3: Partial regression of predicted bird percentage occurrence based on canopy density. Bars are observed proportions (dark: bird present; light: bird absent) for transects with a particular canopy density.
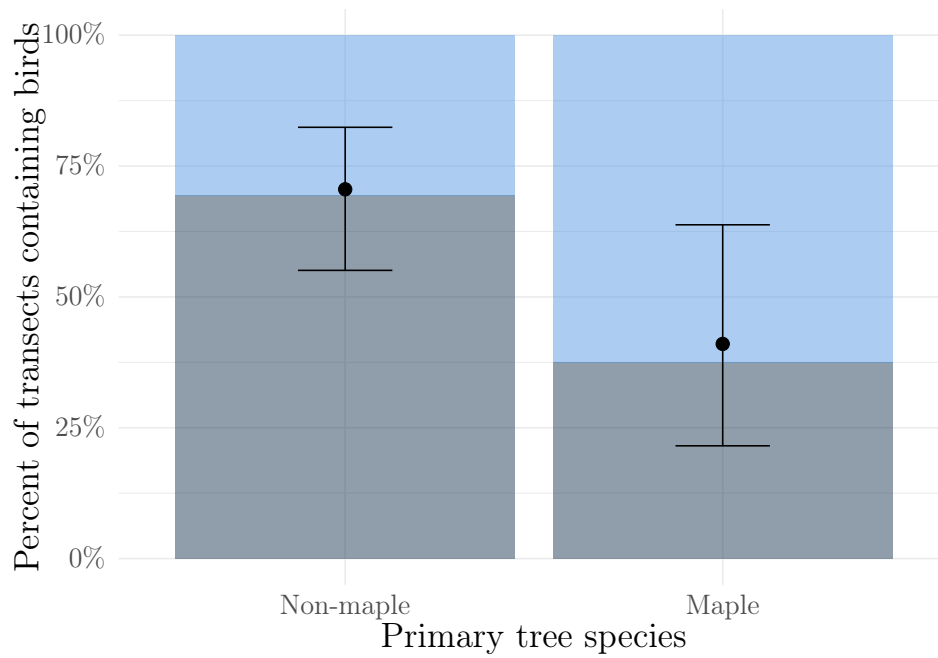
Figure 4.2.4: Partial regressionally predicted bird percentage occurring in sugar maple and non-sugar maple dominated plots (black points, with confidence intervals of 95%). Background bars (blue-grey) are observed proportions of transects containing birds (dark: bird present; light: bird absent).

5 Discussion

The combined results of the two models have novel and interesting conclusions.

5.1 Canopy Cover Preferences

First and foremost, the apparent importance of dense canopy cover for overwintering birds is a key and interesting finding of this study. Both GLM models displayed positive associations between higher levels of canopy cover (based on the densiometer readings recorded in the field) and higher bird observance, both for presence of birds within a transect and higher abundances of birds observed in a transect.

This may substantiate the theories of canopy cover's utility for forest birds in predator evasion (Vitz et al., 2007) and thermal heat loss evasion (Wolf & Walsberg, 1996), as outlined in section 1.2.2, or could signal canopy cover's utility as a proxy for winter foraging resources for insectivorous or partially-insectivorous birds. Cover as a proxy for insectivorous bird resource use has been documented in summer birds in North America (Böhm & Kalko, 2009), but has not had data backing this theory during winter, when vegetative structures change. This naturally contraindicates what studies have suggested on avian perching sites during the breeding season: perch sites during the summer have been shown to be more conspicuous and less covered with

understory shrubs than nesting sites (K. E. Petit et al., 1988). This contraindication makes sense, as in the winter, conspicuous perching sites for breeding visibility are not needed, and thus, choosing perching sites in the canopy for cover protection may be the natural inclination of these species. Overall, this is a novel observance in primarily-deciduous forests in the winter, when the primary vegetative structures granting cover – leaves – are lost to seasonal change. These results indicate the leafless woody branches and stems provided by the canopy of deciduous trees are still preferentially occupied by overwintering forest birds, and this behavioral preference is a new finding that thereby deserves further investigation.

As species-specific canopy cover variations exist (Köble & Seufert, 2001), encouraging the growth of higher winter canopy cover-granting deciduous trees may be beneficial in preserving woodland bird populations, especially those overwintering in forested locales. However, it must be noted that these results are not a broad-scale encouragement of planting high winter canopy-covering trees such as coniferous evergreens, as this study primarily included deciduous forest plots. Thus, although these concepts about overwintering birds and canopy cover may be novel and seemingly far-reaching, they must be contextualized within the study's limits.

As there are no standard methods for measuring canopy cover using a densiometer in the winter, we developed novel methods for making this assessment, thus the replicability of this study would be limited to those who follow our methodology. A further step would be to rigorously test and investigate this winter model of densiometry on barren winter trees, and to come up with a cohesive winter canopy cover assessment methodology beyond what we have employed here.

5.2   Ground/Understory Cover Preferences

Interestingly, higher ground cover predicted higher abundances of birds, but was not significantly predictive of the presence/absence of birds within a plot. Such a diversion among the abundance and presence/absence GLM models indicates understory cover has some influence on flocks of birds that it does not have on solitary birds. In other words, flocks of birds are responsive to shrub cover, yet individual/solitary birds do not have a discernable response to understory cover; this in turn suggests some behavior may be present in flocks but not lone birds, and this behavior would necessitate some interaction with understory cover in order to produce the results found.

A number of theories could explain this correlation. One theory, prime to be investigated in further study based on these results, is that that flocking species are more likely to be purposefully using ground cover for cryptic caching purposes than their solitary counterparts, or indeed that flocking species as a population are more likely to cache food using ground cover as a resource. These hypotheses could help explain some trends found in the field of other studies: black-capped chickadees are known to collectively cache food during the winter and use ground cover as a resource (Fjeld & Sonerud, 1988); and white-breasted nuthaches form pairs during caching seasons, and then seek out covered patches with high rugosity (Woodrey, 1991).

Another theory explaining the diversion between the model results arises when taking into account the canopy cover results discussed above. Canopy cover may be an avian priority and ground cover could be viewed as a less desirable second choice

that is utilized when flocks congregate. When perching in a flock, all of the most desirable covered canopy slots may be occupied by other flock members, and thus the secondary choice of understory cover may then be secondarily utilized for perching and foraging under a covered environment. This theory helps to substantiate the mechanisms behind Austin and Smith (1972)'s findings of insectivorous mixed flocks utilizing smaller twigs and branches, especially those in shrubs, for perching while foraging– our findings further suggest that flocks take into account the nature of the group and choose perch sites with higher understory cover acccordingly.

This result, moreover, has multiple ramifications on conservation biology. These results suggest that a wide gradient of vertical structures must be maintained within avian winter habitats to account for multiple species groups: as flocking species prefer denser understory cover while foraging, while solitary species are not associated with ground cover, a wide breadth of structural microhabitats may be the best way to preserve avian biodiversity and foraging sites in conservation forests. These results suggest the homogeneity of forest structure often realized by forest management practices (Ehrlich, 1996; Korb et al., 2007) may be deleterious to avian conservation.

5.3   Sugar Maple Preferences

Based on the findings here, it appears that *Acer saccharum* plots are not preferred for bird occupancy and abundance. The results indicate that sugar maple plots had a lower chance of being occupied by birds, and when they were occupied by birds, the abundances observed were generally lower. These findings may be indicative of a larger-scale trend in avian habitat use, in which sugar maples are not as useful as substrates for avian foraging for resources (such avian foraging tree species-specific

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preferences are not novel, see Holmes and Robinson (1981)); or, that sugar maples trees provide less protective canopy cover in the winter and thus are unpreferred, given the results of canopy cover on bird observance.

The method utilized in generating these results of treating sugar maples as a binary yes/no categorical variable has some advantages, as sugar maples are one of the more common early-successional, fast-growing growth forms of trees; whereas non-sugar maples sampled were generally found to be slower growth forms. Thus, some limited, tentative conclusions about overwintering bird preference of slower-growing, late-successional tree species may be inferred from these results; however, a more robust analysis in this regard would be imperative to be completed to substantiate these findings. This could be employed through the categorical assignment of growth forms as fast or slow given the dominant tree species noted by transect, or at least extending the binary category to include all maples.

This is especially crucial to further investigate given that maples seem to be a much more dominant taxa in the modern era as opposed to the pre-colonial era in northeastern North America (Thompson et al., 2013). Although maple species were present in low levels before colonization, they have risen to dominate northeastern forests today, accounting for 30% of the trees found in modern forests (the largest share of any taxa), up from only 11% in the pre-colonial period, in which a variety of other species dominated forested areas regionally (Thompson et al., 2013). This may be indicative of a long-term pattern of change negatively affecting avian populations, possibly intractable to short-term fixes; however, radical forest management could alter these trends in a manner beneficial to overwintering birds. Thompson et al. (2013)'s findings of this maple over-dominance in the modern era might be caused, or

at least exacerbated, by the increase in white-tailed deer populations, whose grazing habits favor the structural dominance of sugar maples across forests previously dominated by other species (Anderson & Loucks, 1979). To link these plant community trends with avian habitat preference is a novel and deeply impactful conclusion, as it suggests the post-colonial human disturbance to the northeastern North American forested landscape is broadly negatively impacting avian foraging behavior. This far-reaching conclusion must be reined in because of the small sample size of this study and the lack of specificity in dominant tree assignment, and therefore further study into these significant trends is of prime importance.

The findings we have presented here tentatively suggest that management of the overpopulation of white-tailed deer may be important to avian conservation. These results may therefore give some contextualization to the inversely correlational trends found between higher white-tailed deer populations and lowered avian biodiversity in Tymkiw et al. (2013); deCalesta (1994).

The clear, severe limitation of these findings is that the model was generated using only *Acer saccharum* as a binary dominant tree species identifier; more precise results may be found from grouping the data by all maple species collected (including silver maples, red maples, and other observed species within the maple taxa); or indeed by grouping all fast growth forms rather than just *Acer saccharum.* A further limitation is that the dominant tree species by canopy area was not quantitatively measured, rather, it was estimated by eye: a more rigorous approach to this data collection process should be instituted in future studies in order to eliminate any perspective bias on account of the collector.

5.4   Tree Count Density Preferences

One surprising finding was that tree count/ forest density was not considered significant in any model of bird observation. This is especially surprising given Hardy et al. (2013)'s findings which indicate the density of trees within forested areas is a highly significant indicator of avian occupancy when modelling observances, though this analysis was completed on a species-specific level.

As our model is not species-specific, it may be that the individual species' preferences are competing in the model's generation and thus leading to no significant correlations. As Hardy et al. (2013) found that some species prefer denser environments and other species prefer sparser forest environments, perhaps the species we sampled here cancel each other out in the model's generation, and thus no broad-reaching trends can be found. Further, it is possible that the sample size may have been too small to note these associations, especially when these associations are highly species-specific. Another possibility is that a wide enough range of forest densities was not sampled, given the relative homogeneity of forests within the Hudson Valley, and therefore our model was not able to create broad-scale associations with forest density given the measured data.

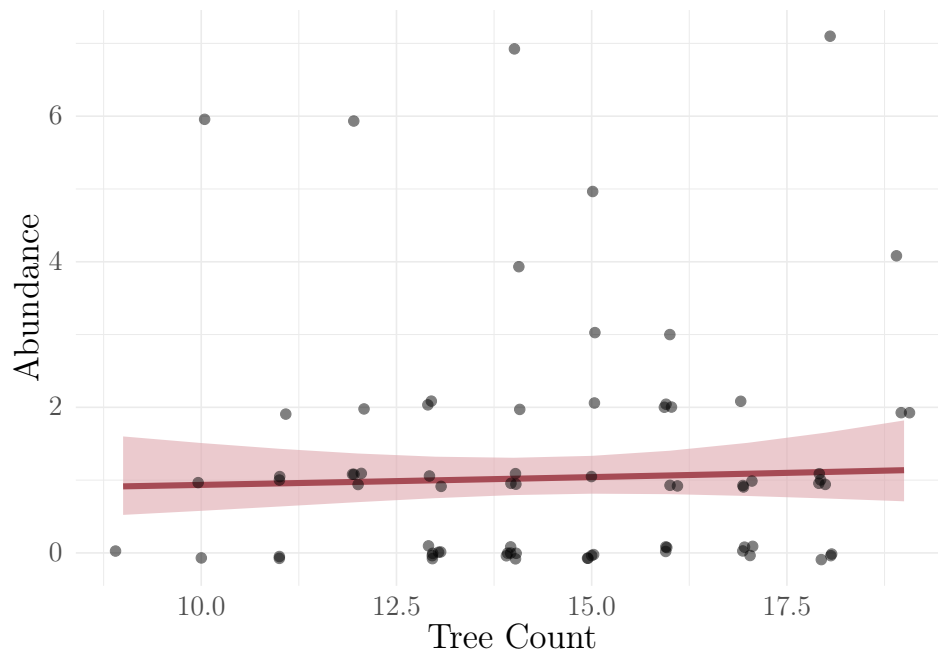# A   Supplementary Figures

A.1   Abundance

Figure A.1.1: Graph of predicted effect of forest density on bird abundance. Overlayed with scatterplot of observed bird abundance vs forest density; jitter was added on both x and y axes.
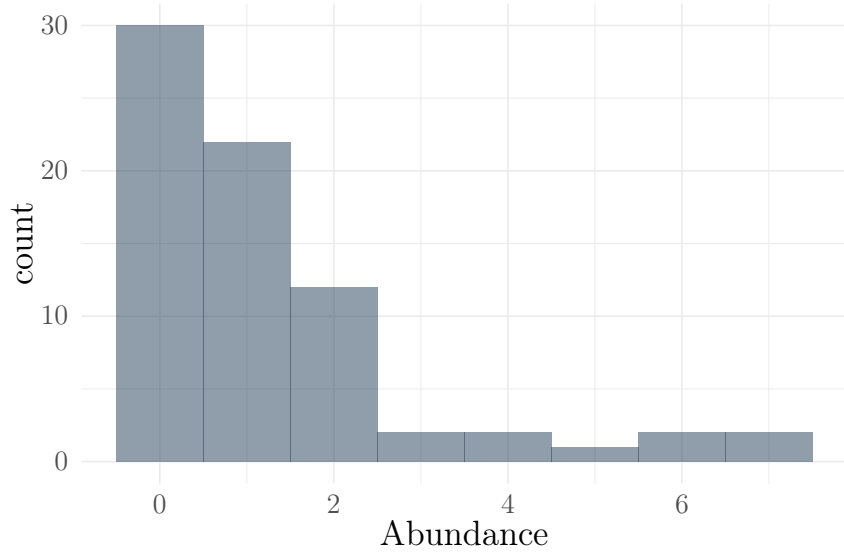
A.2   Histograms
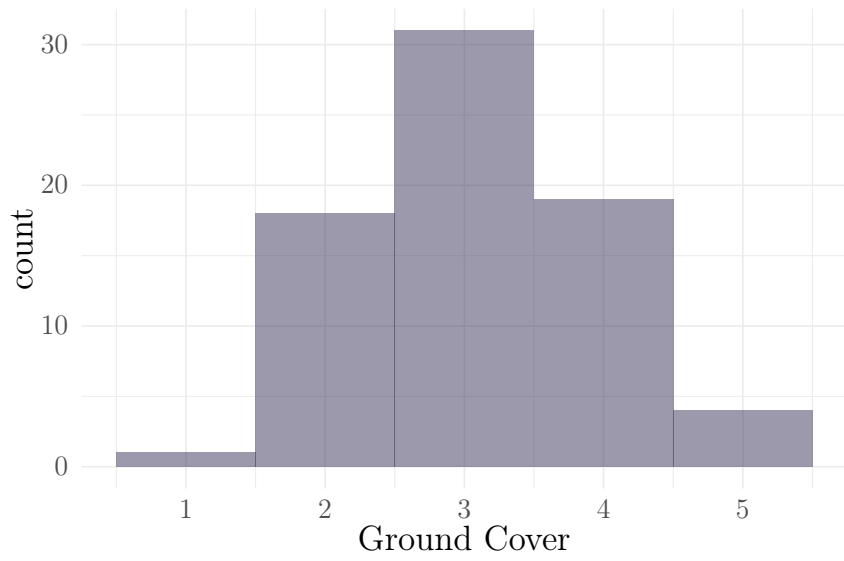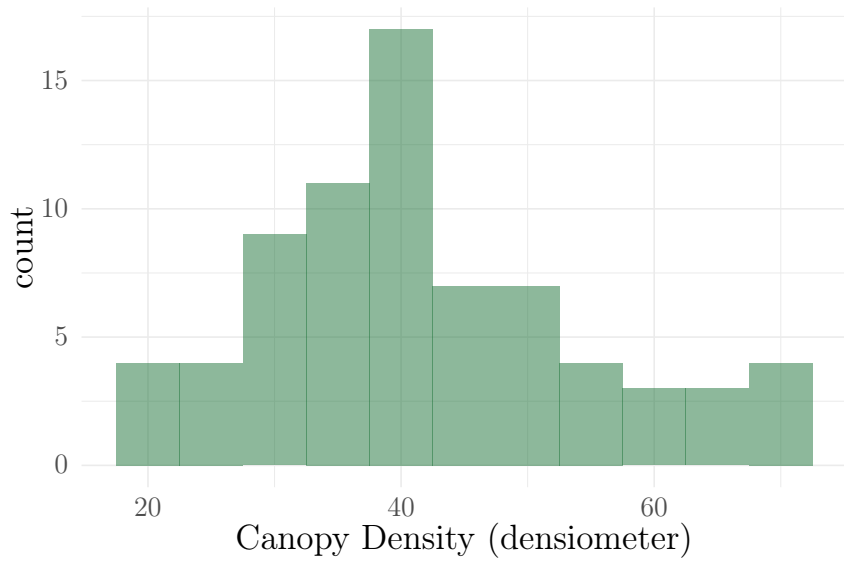

Figure A.2.1: Caption

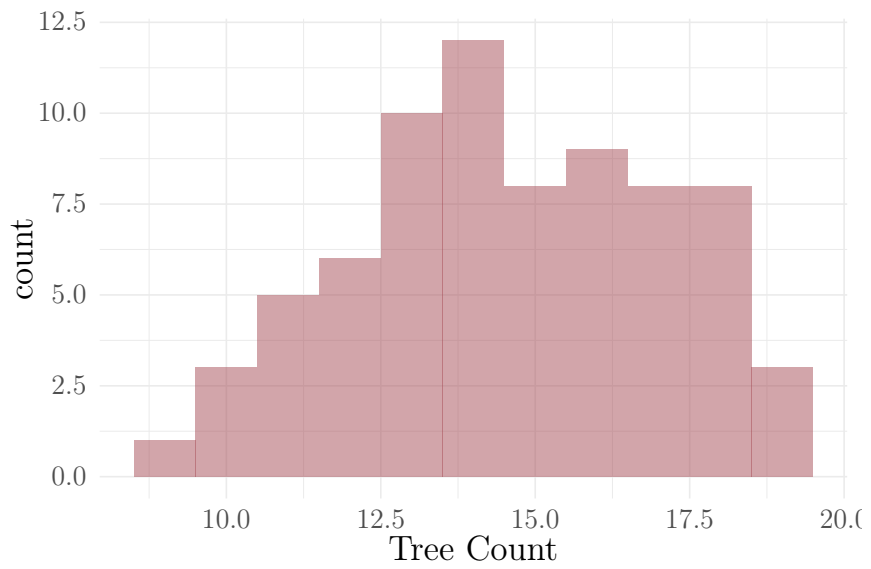Figure A.2.3: Caption

Figure A.2.2: Caption

Figure A.2.4: Caption

A.3   Scatterplots
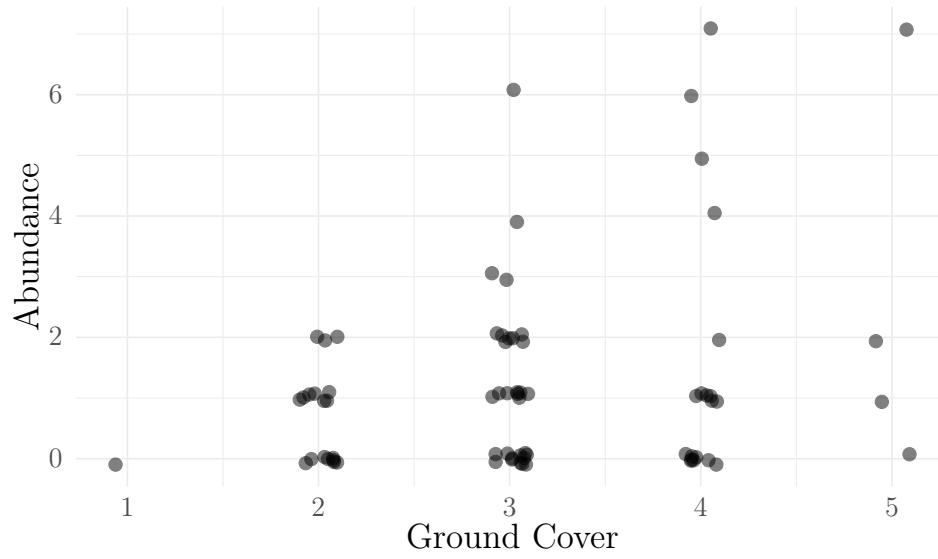

Figure A.3.1: Caption
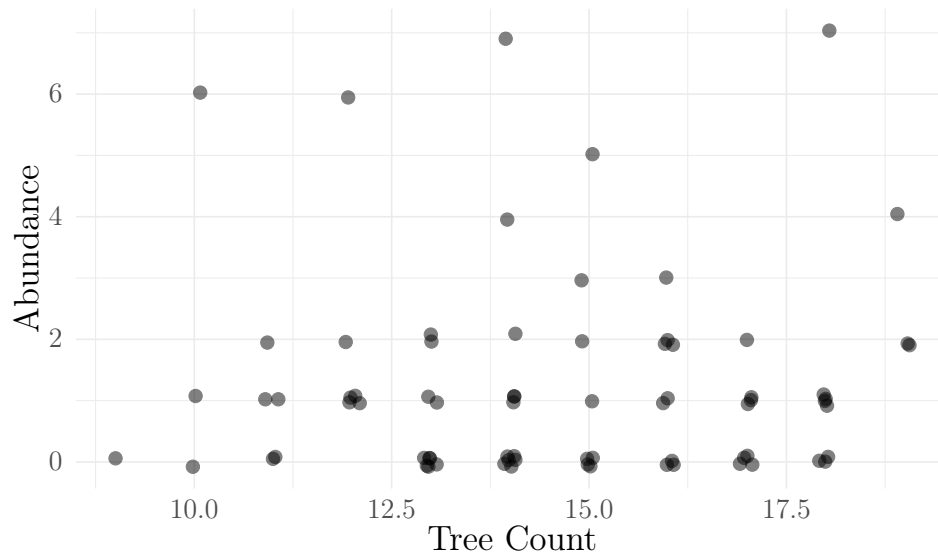

Figure A.3.3: Caption
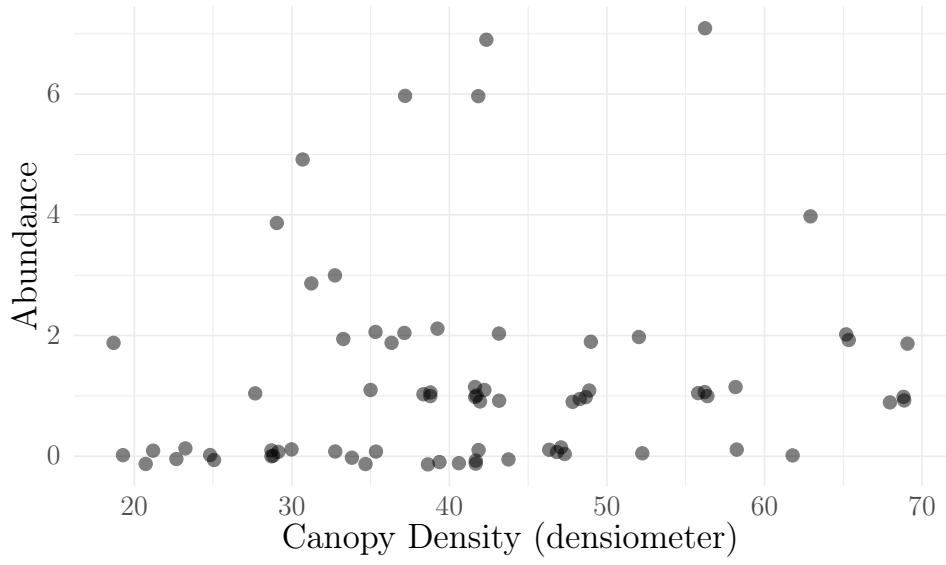
Figure A.3.2: Caption
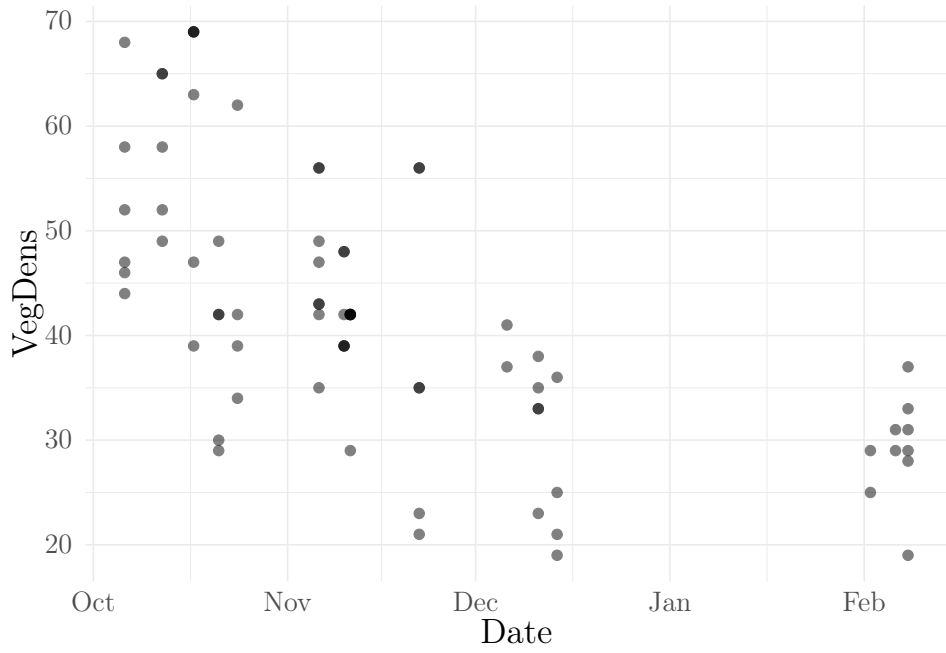
Figure A.3.4: Caption

B   Selected Code

B.1   Abundance GLM

```
> summary(global.model)

Call:
glm(formula = Abundance ~ VegGC + VegDens + VegTreeCount + Fall.Winter +
    AcerSacYes.No, family = poisson, data = dat)

Deviance Residuals:
    Min      1Q   Median       3Q      Max
-2.5272  -1.1670  -0.3830   0.3467   3.4467

Coefficients:
                Estimate Std. Error z value Pr(>|z|)
(Intercept)     -4.02624    1.04968  -3.836 0.000125 ***
VegGC            0.44936    0.11688   3.845 0.000121 ***
VegDens          0.04005    0.01138   3.519 0.000434 ***
VegTreeCount     0.02174    0.04629   0.470 0.638699
Fall.WinterW     0.94122    0.30969   3.039 0.002372 **
AcerSacYes.NoNM  0.60243    0.28007   2.151 0.031477 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 142.10  on 72  degrees of freedom
Residual deviance: 109.03  on 67  degrees of freedom
AIC: 227.32
```

```
Number of Fisher Scoring iterations: 6
> publish(global.model)    # Gerds and Ozenne (2018)
      Variable Units HazardRatio      CI.95    p-value
         VegGC              1.57 [1.25;1.97]  0.0001207
       VegDens              1.04 [1.02;1.06]  0.0004338
  VegTreeCount              1.02 [0.93;1.12]  0.6386987
   Fall.Winter    F           Ref
                  W           2.56 [1.40;4.70]  0.0023717
 AcerSacYes.No    M           Ref
                  NM          1.83 [1.05;3.16]  0.0314769
> Anova(global.model)       # Fox and Weisberg (2011)
Analysis of Deviance Table (Type II tests)

Response: Abundance
             LR Chisq Df Pr(>Chisq)
VegGC         14.9715  1  0.0001091 ***
VegDens       12.3514  1  0.0004407 ***
VegTreeCount   0.2204  1  0.6387334
Fall.Winter    9.3756  1  0.0021990 **
AcerSacYes.No  5.1027  1  0.0238886 *
> pchisq(global.model$deviance, df=global.model$df.residual, lower.tail=F)
[1] 0.0008979055
```

B.2   Logit GLM

```
> summary(logitMod)

Call:
glm(formula = Bird.NoBird ~ VegDens + VegGC + AcerSacYes.No +
    VegTreeCount, family = binomial(link = "logit"), data = dat)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-2.3940  -0.9606   0.4771   0.8667   1.9437

Coefficients:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)   -6.42701    2.64688  -2.428   0.0152 *
VegDens        0.07484    0.02504   2.989   0.0028 **
VegGC          0.52532    0.33706   1.559   0.1191
```

```
AcerSacYes.NoNM    1.23701    0.58220   2.125    0.0336 *
VegTreeCount       0.08969    0.11541   0.777    0.4371
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

    Null deviance: 98.872  on 72  degrees of freedom
Residual deviance: 80.307  on 68  degrees of freedom
AIC: 90.307

Number of Fisher Scoring iterations: 4
> publish(logitMod)
      Variable Units OddsRatio        CI.95    p-value
       VegDens            1.08   [1.03;1.13]   0.002801
         VegGC            1.69   [0.87;3.27]   0.119103
 AcerSacYes.No     M        Ref
                  NM       3.45  [1.10;10.78]   0.033610
  VegTreeCount            1.09   [0.87;1.37]   0.437105
> Anova(logitMod)
Analysis of Deviance Table (Type II tests)

Response: Bird.NoBird
            LR Chisq Df Pr(>Chisq)
VegDens       11.0033  1  0.0009095 ***
VegGC          2.6274  1  0.1050342
AcerSacYes.No  4.6816  1  0.0304876 *
VegTreeCount   0.6119  1  0.4340803
# per R Data Analysis Examples: Logit Regression (n.d.)
> pchisq(logitMod$null.deviance-logitMod$deviance,
+ logitMod$df.null-logitMod$df.residual, lower.tail=F)
[1] 0.0009564603
```

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