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Assessment of Factors Influencing Migratory Landbird Use of Forested Stopover Sites Along the Delmarva Peninsula During Autumn Migration

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ASSESSMENT OF FACTORS INFLUENCING MIGRATORY LANDBIRD USE OF FORESTED STOPOVER SITES ALONG THE DELMARVA PENINSULA DURING AUTUMN MIGRATION

by

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ABSTRACT

ASSESSMENT OF FACTORS INFLUENCING MIGRATORY LANDBIRD USE OF FORESTED STOPOVER SITES ALONG THE DELMARVA PENINSULA DURING AUTUMN MIGRATION

J. Andrew Arnold
Old Dominion University, 2020
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Autumn migration is a time when billions of birds move from breeding grounds in North America to wintering grounds in Central and South America, with many individuals relying on stopover habitats en route for resting and refueling purposes. These stopover sites are critical to the survival of the hundreds of species of migratory landbirds that migrate annually, and thus identifying important stopover sites is a high priority for conserving such taxa. The Delmarva Peninsula; a coastal region of Delaware, Maryland, and Virginia along the mid-Atlantic flyway; consists of forested habitats with ample food and shelter that likely serves as quality stopover sites for many species during autumn migration. Determining both extrinsic and intrinsic factors that most influence migrant use of forested stopover sites during this period is a necessary step towards providing adequate protection for vulnerable species, and one requiring a multi-scale analytical approach. I assessed the influence of variables at the regional- (i.e. proximity to the coast, location latitudinally), landscape- (i.e. proportions of surrounding land cover types), and patch-scales (i.e. habitat structure and vegetative characteristics) on migratory landbird use of forested stopover sites at 48 forested areas located across Delaware, Maryland, and Virginia during autumn migration in 2013 and 2014. Using boosted regression tree modelling techniques, I conducted analyses to determine variable influence on forested site use for 13 migratory species, as well as season-wide and early- vs. mid-season analyses using all nocturnal migratory landbird species. For season-wide analyses, autumn migration was separated into four 21-day

sampling periods (period 1 = 15 Aug – 4 Sep, period 2 = 5 Sep – 15 Oct, period 3 = 26 Sep – 16 Oct, period 4 = 17 Oct – 7 Nov).

Predictor variables were not consistent in influence across multiple spatial and temporal scales during the migratory season. For all season-wide analyses, including the grouped model and thirteen individual species models, time of sampling (sampling period) was the most influential predictor variable in explaining migrant density. At the regional-scale, latitude was the most consistently influential predictor variable in explaining migrant density, generally showing higher densities at sites located further north. At the landscape-scale, proportion of hardwood forest, shrubland, impervious surface, and permanent water surrounding stopover sites were all influential at predicting migrant bird density, although their degrees of influence and relationship to migrant density (positive or negative) varied greatly across models. At the patch-scale, densities of invertebrate food resources and understory vegetation were influential predictor variables across migrant models. Early in the migratory season (15 Aug – 4 Sep), proportion of surrounding land cover (low impervious surface and high shrubland and hardwood forest) and metrics associated with patch-scale habitat structure (high ground vegetation and shrub counts) were the most influential predictor variables of migrant density. Alternatively, during the middle of the migratory season (26 Sep – 16 Oct), latitude and food availability were far more influential in predicting migrant use. These results demonstrate how spatially and temporally variable migrant use of forested stopover sites can be. Using a multi-scale approach, while logistically difficult, is necessary to understand the complexity of migrant use of stopover sites.

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CHAPTER 1

INTRODUCTION

Avian migration, the movement between breeding and wintering grounds in the pursuit of favorable conditions and resources, is undertaken biannually by approximately two-thirds of all landbirds that breed in North America (Keast and Morton 1980, Rappole 1995, Newton 2010). Nearctic-Neotropical migrant landbirds, those species that breed across North America’s temperate zone as far north as the boreal forests and winter throughout the Tropics, possess complex and diverse migratory strategies (Faaborg et al. 2010a, Newton 2010). Blackpoll Warblers (*Setophaga striata*), for example, have developed the physiological ability to undergo a non-stop transoceanic flight while traveling to their wintering grounds in South America, a journey lasting up to three days and spanning over 2,200 km (DeLuca et al. 2015). Many North American passerine families such as flycatchers (*Tyrannidae*), kinglets (*Regulidae*), thrushes (*Turdidae*), vireos (*Vireonidae*), and warblers (*Parulidae*) migrate primarily at night (Newton 2010). Migrants presumably choose to move at night to leave more time to feed during the day, thus reducing the duration of their overall migratory journey. Nighttime can also provide more favorable conditions for travel such as lower temperatures with higher humidity, reducing water loss and metabolic stress, as well as generally experiencing lower wind speeds, which could potentially reduce energy expenditure if faced with a headwind. Additionally, moving at night likely reduces risk from aerial predators and overall risk of depredation (Moore and Kerlinger 1989, Newton 2010).

Many migratory landbirds stop numerous times as they travel between breeding and wintering grounds (Newton 2010). During the migratory period, landbirds can spend upwards of

85% of their total time resting and obtaining necessary resources at stopover sites instead of flying (Hedenstrom and Alerstam 1997, Matthews and Rodewald 2010). The migration phase can be a time of vulnerability, exemplified by Black-throated Blue Warblers (*Setophaga caerulescens*), a Neotropical migratory landbird species shown to sustain up to 85% of their total adult mortality during just the 13 to 17 weeks of their annual migration (Sillett and Holmes 2002). The inherent risk during this period is further amplified by anthropogenic sources, as demonstrated in a long-term tower strike study that found over 94% of casualties were Neartic-Neotropical migrants, consisting mainly of Red-eyed Vireos (*Vireo olivaceus*) but also including migrants such as Ovenbird (*Seiurus aurocapillus*), and various species of warbler (*Dendroica spp.*) (Crawford and Engstrom 2001). For many vulnerable species exposed to the stress and demands of migration, the effects of which influence future performance and overall survival (Alerstam et al. 2003), this period may significantly limit populations (Newton 2006). Given the evident need for quality stopover sites and the inherent risk associated with migration, identifying important stopover sites, as well as the influence of habitat and landscape variables, is a critical step towards adequate conservation planning (Petit 2000, Mehlman et al. 2005, Moore et al. 2005, Faaborg et al. 2010b, Sheehy et al. 2011).

Particular details such as route(s) taken, time spent traveling, and distance covered during migration can vary greatly across taxa and even within species (Dingle 2014). Fox Sparrows (*Passerella iliaca*), for example, migrate in a “leapfrog” pattern, with those northernmost breeding individuals moving over intermediate migrants to the southernmost wintering sites (Swarth 1920). Alternatively, subspecies of Rosy Finches (*Leucosticte spp.*) that breed in isolated populations will travel to the same wintering destinations, meaning that those breeding farther north will make substantially longer overall journeys (King and Wales 1964). Migrants appear to consider both extrinsic (e.g., weather) and intrinsic (e.g., current body condition and fat reserves) factors when making individual decisions about route choice. For example, a migrant may depart over an oceanic barrier early if winds are favorable but may otherwise continue along a longer land route and thus increasing migration time while decreasing the amount of ocean crossing (Alerstam 2001, Bulte et al. 2014), ultimately determining where migrants land to refuel (Buler and Moore 2011). Some individuals, upon landing at an initial stopover site after first light, may decide to instead leave in search of better habitat offering more resources, a process known as “morning flight” (Moore et al. 1995). One study, wherein Red-eyed Vireos were captured and weighed prior to crossing the Gulf of Mexico during autumn migration, found that those birds with more body fat exhibited far more migratory restlessness when caged and left the area faster upon release than their leaner counterparts (Sandberg and Moore 1996). Other studies have demonstrated that leaner migrants with less fat reserves are more active at stopover sites (Moore and Aborn 2000, Matthews and Rodewald 2010), and that some delay foraging to adjust their weight to help reduce the risk of predation (Van der Veen and Sivars 2000). This variability in migration strategies within and among taxa, coupled with movement over different spatial scales, makes the study of migration behavior difficult quantify and interpret (Dingle 2014).

The majority of previous research on migratory landbird use of stopover habitat has focused on limited, patch-scale approaches (Moore and Aborn 2000), determining that migrants partition themselves relative to food availability, predicting observed patterns in stopover habitat use (Hutto 1985). The supply of food, while considered a local patch-scale resource, can be influenced by larger-scale events such as climatic oscillations. Black-throated Blue Warblers, for example, experience reduced food availability during periods of El Niño, which consequently leads to reduced reproductive output and overwinter survival, and may even affect survivorship during migration (Sillett et al. 2000).

The diversity and abundance of potential food resources needs to be considered when assessing habitat quality (Parrish 1997, Buler et al. 2007, Greenberg et al. 2012), especially given the variability in life-history strategies of different species. Yellow-rumped Warbler (*Setophaga coronata*), for example, transition from foraging mostly higher up in trees when breeding to foraging primarily on the ground post-breeding (Askins et al. 1990), and the latter portion of their migratory phase is strongly driven by localized environmental conditions such as food availability (Terrill and Crawford 1988). This species also has the ability to digest fruits extremely high in saturated fats, a property not found in other closely related warblers (Place and Stiles 1992).

Fruit is known to be an important factor for many migratory bird species, providing antioxidants that help combat the high oxidative stress encountered during migration (Alan et al. 2013, Bolser et al. 2013). The presence of fruiting plants has even been suggested to be more important than habitat structure in determining habitat use (Suthers et al. 2000). Many otherwise insectivorous species substantially increase the amount of fruit in their diet during migration (Parrish 1997, Smith et al. 2007b), while some taxa (e.g. Aquatic Warblers [*Acrocephalus paludicola*]) specialize on a few select orders of insects during stopover (Provost et al. 2010). In captive studies, a mixed diet consisting of both fruits and invertebrates increased the rate of weight gain of migratory species such as Red-eyed Vireo (Parrish 2000) and Hermit Thrush (*Catharus guttatus*, Long and Stouffer 2003). Although occurring during spring migration, one study found that midges (flying invertebrates in the order Diptera) and spiders (of multiple orders in the class Arachnida) are important to the diet of American Redstarts (*Setophaga ruticilla*) during stopover, and that the abundance of this food resource helped determine habit quality (Smith et al. 2007a). Given an individual migrant's unfamiliarity with the distribution of resources across a landscape during a stopover bout, however, lower-quality sites with fewer available resources may inadvertently be selected and used over those thought to be more suitable (Shochat et al. 2002), and migrants may stop at near-coastal sites as a result of juvenile inexperience and misdirection (Ralph 1978). Competitive interactions may also force birds into low-quality habitat with few food resources (Woodrey 2000). While stopover habitat use may be somewhat unpredictable, enough prior studies on stopover site fidelity have been conducted that demonstrate that migrants can purposefully select areas in which to stop over (Somershoe and Chandler 2000, Somershoe et al. 2009, Vogt et al. 2012).

At the patch-scale, habitat structure can also greatly influence site quality and thus potential migrant use. Pine (*Pinus* spp.) forests, for example, generally have a lower abundance and diversity of fruiting species than hardwood (Greenberg et al. 2012). Furthermore, bottomland hardwood forests support a higher arthropod abundance (Buler et al. 2007). Preference for structurally diverse habitat such as forest edges, with high food availability and ample cover, has also been demonstrated (Moore et al. 1995, Rodewald and Brittingham 2004). At least in the context of overall food availability, hardwood forests generally provide high quality stopover habitat for migrants. This influence of hardwood can also extend across multiple scales, potentially influencing site use at both the localized patch-scale and larger landscape-scale (Buler et al. 2007).

Studies that have examined migrant stopover habitat at broader scales have found that both geographic location (e.g. proximity to the coast) and landscape composition (e.g. hardwood forest cover) are both important factors in determining overall migrant densities at the regional and landscape scales, respectively (Buler et al. 2007, Lafleur et al. 2016). More recent landscape-scale approaches have confirmed high migrant densities in areas of high hardwood forest cover (Buler and Dawson 2014). These findings suggest that many migrants are attracted to hardwood forests when selecting a stopover site (Buler et al. 2007). Broader, landscape-scale factors can also influence the quality of nearby stopover sites. Urbanized forest patches, for example, typically exhibit a lower abundance and diversity of arthropods than contiguously forested areas (Matthews and Rodewald 2010), the former often of lesser quality because of the effects of fragmentation (Moore et al. 1995, Faaborg et al. 2010a, Matthews and Rodewald 2010). Loss of habitat to urbanization also typically results in a reduction in food resources, which consequently increases competition and has implications for survivorship (Askins and Askins 2002). Uncertainty regarding habitat and resource availability and distribution while en route necessitates the ability of individuals to efficiently identify high quality stopover sites (Cohen et al. 2014).

Numerous factors may influence stopover duration and location, including but not limited to weather conditions (Schaub et al. 2004), body condition (Moore and Aborn 2000, Matthews and Rodewald 2010), resource availability (Suthers et al. 2000), competition for limited resources (Moore and Wang 1991), risk of predation (Aborn 1994), and preference for a particular habitat structure (Rodewald and Brittingham 2007). These factors all function at different spatial scales, and may potentially interact with each other, thus resulting in scale-dependent habitat use patterns (Hutto 1985, Petit 2000, Moore et al. 2005, Buler at al. 2007, Buler and Moore 2011).

Given the extreme variability in the spatial scale of factors that may influence migrant habitat use, a multi-scale analysis approach is needed. Multi-scale analyses are a way of incorporating variables across multiple spatial scales (i.e. patch, landscape, regional), while accounting for the spatial unevenness of those factors, to determine their influence on a variable of interest (Kotliar and Weins 1990, Cushman and McGarigal 2002, Buler et al. 2007, Buler and Moore 2011). Despite the appeal of this approach, there are many difficulties such as obtaining adequate funds or having access to enough skilled observers to successfully conduct such studies. It follows that few studies of stopover habitat use by migratory landbirds have been conducted (Cushman and McGarigal 2002, Buler et al. 2007).

My objective in this study was to assess the relative importance of various habitat features; including those at the patch- (e.g. food abundance, habitat composition, and vegetative structure), landscape- (e.g. proportion of habitat types within surrounding buffers), and regional-scales (e.g. proximity to an oceanic barrier, latitude); to determine their role in explaining migratory landbird use of forested stopover habitats along the mid-Atlantic Flyway during autumn migration, as well as determine how the relative importance of those habitat features changes over the course of a migratory season.

CHAPTER 2

METHODS

2.1 Methods – Data Collection

Field work was carried out under the following permit: Old Dominion University Institutional Animal Care Use Committee Protocol (16-025).

Study Area and Site Selection

To examine the influence of multi-scale variables on landbird migrant density at stopover sites, I established transects (500 m long) within 48 hardwood forests along the mid-Atlantic region of North America’s Delmarva Peninsula and just below, an area including the coastal states of Delaware, Maryland, and Virginia. Thirty-six sites covered the entire Delmarva Peninsula, with 12 located in Delaware, 12 in Maryland, 12 along Virginia’s Eastern Shore. The remaining 12 sites were on the mainland in coastal Eastern Virginia south of the Chesapeake Bay (Fig. 1). This research endeavor was part of a larger project aimed at assessing migratory stopover sites along the northeastern United States using radar and predictive modeling data (see Buler and Dawson 2014). Established methodologies used in previous studies of migrant stopover sites were used for comparative purposes (see Buler et al. 2007).

All forested sites were at least 4 ha in size and, with the exception of those located at the southern tip of Virginia’s Eastern Shore, separated from other sites by a minimum of 10-km. I used hardwood forest sites because this habitat represents a dominant vegetative community type available in the region. Sites were similar in their habitat characteristics, consisting of mostly-flat topography and with strong representations of hardwood species such as oaks (*Quercus sp.*),

Source: Esri, DigitalGlobe, GeoEye, i-cubed, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Fig. 1. Stopover habitat survey locations across the Delmarva Peninsula.

Sweetgum (*Liquidambar styraciflua*), Red Maple (*Acer rubra*), and pines – most notably Loblolly Pine (*Pinus. taeda*). Prior research has demonstrated that mature forested habitats can support large numbers of migrants, and this habitat type is likely of critical importance to many migratory taxa (Rodewald and Brittingham 2007). Using this prior knowledge, I attempted to select mature forest sites within the study area.

Transect Surveys

To examine the distribution of migrants among sites, transect surveys were conducted from 15 August through 7 November in 2013 and 2014. One 500- m transect was established in the interior forest at each site, at least 25 m from the forest's edge to ensure interior forest was sampled and to avoid edge effects, and marked using biodegradable flagging tape placed at 25-m intervals. While forest edge is an important habitat providing both food and cover for migrants (Rodewald and Brittingham 2004), it was avoided to maintain consistency in data collection location. Trimming of the survey path was minimized to avoid excessive habitat alteration, and primarily consisted of removing Greenbrier (*Smilax sp.*) vines impeding transect access.

Prior to every survey event, various atmospheric measurements were recorded using a Kestrel 2000 Pocket Meter (Kestrel Meters, USA), including temperature and wind speed, which was also measured via the observational Beaufort scale (0 = calm, smoke rises vertically (under 1.6 kph), 1 = smoke drift indicates wind direction (1.6-4.8 kph), 2 = leaves rustle (6.4-11.2 kph), 3 = leaves, small twigs in constant motion (12.8-19.3 kph), 4 = dust, loose paper raised up (20.9-28.9 kph), 5 = small trees sway (30.5-38.6 kph)), and sky condition codes (0 = clear skies, 1 = partly cloudy, 2 = cloudy or overcast, 3 = smoke or fog, 4 = drizzle, 5 = showers).

Birds were sampled along transects during a 30-min period (a pace of 1-km/h) from sunrise up to four hours post-sunrise, with order of transect surveys and field observers rotated regularly. This schedule allowed for each site to be sampled approximately twice per week, although surveying only occurred on days with favorable weather conditions (no rain and wind speeds < 24-km/h as determined at the site prior to surveys) as heavy winds and rain can limit one's ability to detect individuals, in addition to reducing the ability of migrants to move within and among stopover sites (Moore and Kerlinger 1989, Schaub et al. 2004). Species, number of individuals, method of detection (visual or aural), and sex / age metrics (when possible) were recorded. Any birds in aggregate were recorded as a “flock”. Distance measurements were also recorded for all detections, and included: 1) observer location along each transect, 2) distance of detection from the observer, 3) perpendicular distance of detection from transect, and 4) vertical height of detection. Height and distances were recorded in distance classes due to the difficulty in accurately measuring distances (Alldredge et al. 2007): 0-5 m, 5-10 m, 10-15 m, 15-20 m, 20-25 m, 25-50 m, and >50 m within habitat. Flyovers and flythroughs were also recorded, although not included in detection probability analyses. Methodology for detection probability analyses, which were used to quantify all migratory bird densities, is described under the “Methods – Data Analysis” section below.

Food Availability

To assess the amount of food available at each site across the season, I sampled fruit and insect abundance during each site visit. Six 20 m x 20 m plots were placed along the transect every 75 m. Sampling within the plots alternated each visit so that the 75 m, 225 m, and 375 m plots were sampled on one visit and the 150 m, 300 m, and 450 m plots on the following visit.

Fruit sampling consisted of recording all species of plants containing fleshy fruit within the 20 m x 20 m plots, including their abundance, ripeness, and relative height. Number of fruits was binned, for speed of counting, as follows: 1 (1-10), 2 (11-25), 3 (26-100), 4 (101-250), 5 (251-1000), 6 (1001- 3000), and 7 (3001-10000). The ripeness was recorded as the percentage of unripe, ripe, and overripe fruits for each species detected and relative height was recorded as the percentage found in the understory, midstory, and canopy for each species following Smith and

McWilliams (2009) for rapid fruit assessment. Fruit abundance was quantified as the density of ripe fruits detected per m^2 sampled for each survey effort.

Insect sampling was performed in two ways: 1) visual count of terrestrial arthropods, and 2) enumeration of arthropods from branch clippings, utilizing methodologies created and used in prior studies (see Cooper and Whitmore 1990, Strong 2000, Buler et al. 2007). Visual counts were conducted within 0.5 m x 0.5 m ground plots located within the larger 20 m x 20 m plot. Visual surveys were conducted by standing over the 0.5 m x 0.5 m plot for 3 min to record the size (mm) and order of arthropod taxa. Bagged branch clippings from within the 20 m x 20 m plot and all arthropods on or in the branch sample were collected. All arthropods were identified to order and size (mm) was recorded, and then stored in vials with isopropyl alcohol. Each branch clipping consisted of approximately 40 leaves from either the dominant site species, the woody species most common across all six sampling plots located at each site, or one of four common focal species (American holly [*Ilex opaca*], Red Maple, Sweetgum, or Blueberry [*Vaccinium angustifolium*]). Arthropod abundance within the understory was quantified as a mean density (per g) of branch for those clipped from trees, and a mean density (per m^2) for those detected during ground surveys. Clipped branches were weighed without drying.

Vegetation Sampling

Vegetation was sampled at each site once mid-season in 2013 using a modified protocol of James and Shugart (1970) at four 11.3-m radius circular plots along the transect centerline. See Fig. 2 for a visual representation of vegetation sampling plots methodology.

Using six distances along the transects (75, 150, 225, 300, 375, and 450 m), four of these six locations were randomly selected at each site to place the vegetative sampling plots.

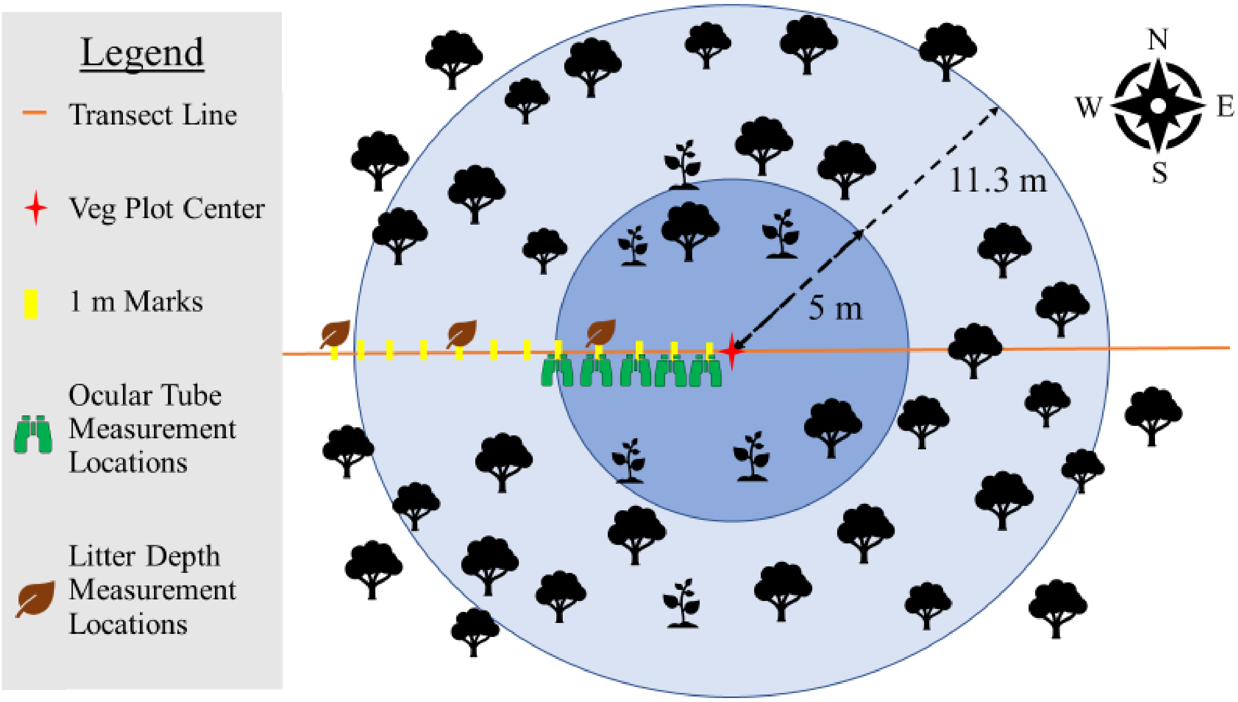


Fig. 2. Visual representation of vegetative sampling methodology utilized at four plot locations (one plot represented here) along every forested survey transect (orange line). Large 11.3-m radius (light blue circle) and smaller 5-m radius (dark blue circle) plots were established at each location using the transect as their center points (red star). See text for a detailed description of vegetative data collected within each circular plot. Note that locations for all ocular tube (green binoculars) and leaf litter (brown leaf) measurements occurred in each of the four cardinal directions for each plot, although only one direction is shown here.

Measurements of canopy cover were obtained using a crown densiometer based on the mean of four readings obtained by standing in the center of the plot and facing each cardinal direction; canopy height was determined by using a clinometer based on the mean of the four tallest trees within each plot. A measurement of crown density was also obtained for each of these four tallest trees, also using a clinometer, and subtracting the lowest point in the crown from the highest point (canopy height) recorded.

Using an ocular tube, vegetation cover estimates were obtained for the ground, shrub (<2 m tall), vine (in canopy), and midstory sections. These cover estimates were obtained at 1-, 2-, 3-, 4-, and 5-m locations in each of the four cardinal directions (for a total out of 20 measurements in each plot) and were simply a presence or absence measurement of vegetation obtained via an ocular tube reading.

Litter depth was recorded to the nearest millimeter at locations 4, 8, and 12 m from the plot's center in each of the four cardinal directions, for a total of 12 leaf litter depth measurements. Types of vegetation occurring on the forest floors within a 5-m radius of each plot's center were recorded, and included percent cover of forbs, ferns, mosses, greenbrier, vines, marsh, downed logs, and shrubs. Within each larger 11.3-m plots, a smaller 5-m radius circle was established and used for shrub density measurements. For the shrub measurement, stems less than 0.5 m in height and less than 3 cm diameter were counted and identified to species.

Tree density was measured within the 11.3 m-radius plot circle. Tree stems with a diameter at breast height (dbh) less than 2.5 cm and with a dbh between 2.5 cm and 8 cm were counted and arbitrarily binned according to their respective dbh classes for analysis purposes. Tree species and dbh were recorded for all trees with a dbh greater than 8 cm. Crown density was measured, described above for canopy height, for each of the four tallest trees.

Regional and Landscape Data

Landscape-level measures were quantified by creating buffers around each survey site, using each transects' starting coordinates as the center point, and generating measurements for all vegetative classes occurring in the surrounding landscapes. This was achieved using "extract by mask" in ArcGIS, a tool that provides an output of values from a defined spatial area using raster data. Spatially explicit landscape data were obtained from the Multi-Resolution Land Characteristics consortium's 2011 National Land Cover Database (NLCD 2011), a nationwide dataset categorizing all land cover types (Homer et al. 2015). The NLCD 2011 database separates all possible land cover types into 20 unique classes: open water, perennial ice/ snow, four levels of development, barren land, three forest types, two scrubland types, four herbaceous land cover classes, two types of agricultural land, and two wetland cover classes. Although all classes are listed here for completeness, not all these types occurred within the areas sampled for this study. Similar land cover groups, such as "low and medium urbanization / development" or "scrubland and shrubland", were combined to reduce the number of overall buffer variables, and subsequent analyses used four buffer categories: hardwood forest, shrubland / scrubland, impervious surface, and permanent water (Table 1). Area of water was excluded from total area for all terrestrial buffers.

Buffers were placed around each survey site location, using a distance of 1-km radius to quantify habitat variation at a landscape scale, and the cell values (proportion of each land cover type within an individual buffer, denoted by differing colors) for each land class were extracted for analysis. Buffers were chosen at the 1-km scale based on recent work from a similar study in which the authors titrated out landscape cover and confirmed 1 km as suitable for capturing landscape-scale influence (McLaren et al. 2018).

Table 1. All potential variables available for the BRT ensemble models. Table includes variable name, spatial scale of measurement, whether variable was log transformed (Y= yes, N= no), and whether the variable was included in the ensemble models used for BRT analysis (Y= yes, N= no). Note * = dependent variables of interest within dataset; ** = not included as a predictor variable in period-specific analyses.

Variable Name	Scale	Variable Description	Transformed Data (Y/N)	Used In Final Models (Y/N)
Date	-	Dates of patch-scale data collection	N	N
Transect	Patch	Survey sites; random effect in ALL models	N	N
Region	Regional	a = AKQ , b = ESVA , c = MD , d = DE	N	N
Year	-	a = 2013 , b = 2014	N	Y
Period**	-	21 days each; a = 15Aug-4Sep , b = 5Sep-25Sep , c = 26Sep-16Oct , d = 17Oct-7Nov	N	Y
AllMigPerHa*	Patch	Density corrected migrants per ha, all nocturnal migrant species	Y	Y
ACFL*	Patch	Density corrected Acadian Flycatcher per ha	Y	Y
AMRE*	Patch	Density corrected American Redstart per ha	Y	Y
BTBW*	Patch	Density corrected Black-throated Blue Warbler per ha	Y	Y
GCFL*	Patch	Density corrected Great Crested Flycatcher per ha	Y	Y
GCKI*	Patch	Density corrected Golden-crowned Kinglet per ha	Y	Y
GRCA*	Patch	Density corrected Gray Catbird per ha	Y	Y
HETH*	Patch	Density corrected Hermit Thrush per ha	Y	Y
NOPA*	Patch	Density corrected Northern Parula per ha	Y	Y
OVEN*	Patch	Density corrected Ovenbird per ha	Y	Y
REVI*	Patch	Density corrected Red-eyed Vireo per ha	Y	Y
YBCU*	Patch	Density corrected Yellow-billed Cuckoo per ha	Y	Y
YRWA*	Patch	Density corrected Yellow-rumped Warbler per ha	Y	Y
YSFL*	Patch	Density corrected Northern Flicker per ha	Y	Y
InvPerGrBr	Patch	Invertebrates per g of branch, all species	Y	N
InvVism2	Patch	Invertebrate density (per m2 ground surveyed), all species	Y	N
InvBrAR	Patch	Arachnids per g of branch	Y	Y
InvVisAR	Patch	Arachnids per m2 ground surveyed	Y	Y
InvBrLep	Patch	Lepidoptera per g of branch	Y	Y
InvVisLep	Patch	Lepidoptera per m2 ground surveyed	Y	Y
InvBrDI	Patch	Diptera per g of branch	Y	Y
InvVisDI	Patch	Diptera per m2 ground surveyed	Y	Y
InvBrOR	Patch	Orthoptera per g of branch	Y	Y

Table 1. Continued.

Variable Name	Scale	Variable Description	Transformed Data (Y/N)	Used In Final Models (Y/N)
InvVisOR	Patch	Orthoptera per m2 ground surveyed	Y	Y
FrtAllm2	Patch	Ripe fruit per m2 for all species	Y	N
FrtBGum	Patch	Ripe Black Gum per m2	Y	Y
FrtHolly	Patch	Ripe American Holly per m2	Y	Y
FrtBlueB	Patch	Ripe Blueberry per m2	Y	Y
FrtDogw	Patch	Ripe Flowering Dogwood per m2	Y	Y
FrtGrape	Patch	Ripe Grape per m2	Y	Y
FrtParB	Patch	Ripe Partridge Berry per m2	Y	Y
FrtSmilax	Patch	Ripe Greenbrier per m2	Y	Y
Latitude	Regional	Latitude (decimal)	N	Y
CanopyC	Patch	Mean canopy cover (%)	N	Y
CanopyHt	Patch	Mean canopy height (m)	N	N
LitterDep	Patch	Mean litter depth (mm)	N	Y
CtGrLeaf	Patch	Ocular tube litter count (out of 20)	N	Y
CtGrVeg	Patch	Ocular tube ground vegetation count (out of 20)	N	Y
CtMidstory	Patch	Ocular tube midstory count (out of 20)	N	N
CtVine	Patch	Ocular tube vine count (out of 20)	N	Y
CtGrShrub	Patch	Ocular tube shrub count (out of 20)	N	Y
ShrubStemCt	Patch	Count of total shrub stems	N	Y
ShrubDiv	Patch	Number of shrub species	N	N
BlueBShrub	Patch	Blueberry shrubs present (Y/N)	N	N
PrivetShrub	Patch	Privet shrubs present (Y/N)	N	N
WaxShrub	Patch	Wax Myrtle shrubs present (Y/N)	N	N
LgTreeDiv	Patch	Number of tree species (>8cm DBH)	N	N
LgTreeSp	Patch	Most abundant tree; a = Holly , b = Pine , c = Gum , d = Maple , e = Sweetgum , f = Oak , g = Poplar	N	N
basalarea	Patch	Total basal area for each site	N	Y
distcoast	Regional	Distance to nearest coast	N	N
distatl	Regional	Distance to Atlantic Ocean	N	Y
impurban1km	Landscape	Impervious urbanization within buffer	N	Y
water1km	Landscape	Permanent water within buffer	N	Y
ag1km	Landscape	Agriculture / pasture within buffer	N	N
hrdwood1km	Landscape	Deciduous forest within buffer	N	Y
pine1km	Landscape	Evergreen forest within buffer	N	N
shrub1km	Landscape	Scrub / shrubland within buffer	N	Y
wetlnd1km	Landscape	Marsh / wetland within buffer	N	N
grassurb1km	Landscape	Grassland / urban lawns within buffer	N	N

Survey sites were blocked into one of four geographic regions (Delaware, Maryland, Coastal Virginia (Eastern Shore), and Southeast Virginia (South of Chesapeake Bay)) based on their location, referred to as "Region" in the dataset, with each region containing 12 sites. Measurements of both distance to the nearest coast and distance to the Atlantic Ocean were obtained for each transect location in ArcGIS via the "measure" tool. Latitude, collected manually with a GPS while conducting transect sampling, was also included in the analysis dataset (Table 1).

2.2 Methods – Data Analysis

I estimated detection probabilities and migrant densities within R (R Development Core Team 2016) using package "unmarked" (Fiske and Chandler 2011). Temperature, wind, sky code, and observer were incorporated as covariates, and to ensure adequate sample size, all nocturnal migrant landbirds were lumped together (Appendix A). Detections of these nocturnal migrant landbirds, and their respective distances within the forested site, were then used to fit a detection function and create detection-adjusted densities (Buckland et al. 2004, Buckland 2006). I used Akaike's Information Criterion adjusted for small sample sizes (Hurvich and Tsai 1989) and, using the top-ranked detection function model, computed a mean visit density (birds per hectare per visit) for each transect. Subsequent analyses were run using these detection-probability adjusted migrant densities.

Patch, landscape, and regional habitat variables for each survey site were assessed to determine which factors were most influential in determining the use of a stopover site by a migrant. For all analyses, surveys without all covariates recorded (e.g. survey efforts missing fruit and invertebrate sampling data) and any predictor variables with unusual or inconsistent data (e.g. clear discrepancies in canopy height by observer) were not considered.

A Pearson correlation analysis was run on all covariates to avoid including highly correlated variables (Table 2), and those exhibiting high multicollinearity were selectively excluded from analyses. Prior to analyses in R (see below), raw data such as food measurements that did not meet Gaussian assumptions were log-transformed (Table 1). Preliminary tests to examine for temporal autocorrelation in the data were run in R using the “acf” package and function for temporal data (Venables and Ripley 2002), and the Moran.I function in the “ape” package for spatial data (Gittleman and Kot 1990). To account for seasonal phenology of migrants, I included sampling periods (each 21-days long [period 1 = 15 Aug – 4 Sep, period 2 = 5 Sep – 15 Oct, period 3 = 26 Sep – 16 Oct, period 4 = 17 Oct – 7 Nov]). Sampling periods of this length allowed multiple visits to each site to occur. Variables exhibiting high autocorrelation (r>0.7) were removed from future consideration when building models.

Analyses were conducted in R using boosted regression tree (BRT) models developed using the packages “gbm” and “dismo”, and the “gbm.step” function (Ridgeway 2006, Elith et al. 2008). Boosted regression trees allow for the modeling of complex functions, as well as quantifying variable interactions, without the need to worry about otherwise common analytical issues such as handling different variable types (i.e. – categorical, continuous), including additional uninformative variables in models that lead to a reduction in model power, and considering *a priori* assumptions regarding variable relationships (Ridgeway 2006, De’ath 2007, Elith et al. 2008, Buston and Elith 2011).

Table 2. Correlation matrix of explanatory variables used in modeling bird densities.

Variable	A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	F1	F2	F3	F4	F5	F6	F7	F8	R1	H1	H2	H3	H4	H5	H6	H7	H8	R2	L1	L2
A 2	0.06																													
A 3	0.05	0.89																												
A 4	0.72	0.05	0.06																											
A 5	0.03	0.28	0.03	0.02																										
A 6	0.04	0.08	0.05	-0.02	0.14																									
A 7	-0.02	0.39	0.18	0.00	0.02	0.01																								
A 8	0.39	0.09	0.07	0.03	0.01	0.05	0.05																							
A 9	0.01	0.07	0.00	-0.01	0.06	0.02	-0.01	0.02																						
A10	0.22	0.02	0.00	0.02	0.05	-0.01	-0.02	0.07	0.02																					
F 1	0.07	0.00	0.01	-0.01	-0.05	0.04	-0.04	0.09	-0.02	0.04																				
F 2	-0.03	0.09	0.09	-0.01	-0.02	-0.01	0.03	0.04	0.02	0.05	0.25																			
F 3	0.02	-0.02	0.00	0.00	-0.05	-0.01	-0.04	0.04	-0.04	-0.07	0.45	0.07																		
F 4	-0.01	-0.01	-0.01	-0.02	0.00	-0.01	-0.03	0.00	0.00	0.09	-0.02	0.00	-0.02																	
F 5	0.03	-0.01	-0.01	-0.01	0.01	-0.01	-0.03	-0.02	-0.02	0.02	0.05	-0.02	-0.01	0.01																
F 6	0.11	-0.01	0.00	-0.02	-0.03	0.05	-0.04	0.05	0.02	0.08	0.47	-0.01	0.02	-0.01	0.07															
F 7	0.04	-0.02	-0.02	0.03	0.00	-0.03	0.00	0.05	-0.02	0.00	-0.05	-0.02	-0.03	-0.03	0.03	-0.04														
F 8	-0.02	0.02	0.03	-0.01	-0.02	0.00	-0.01	0.03	0.01	0.00	0.17	0.18	0.05	-0.01	0.07	0.05	-0.05													
R 1	-0.24	-0.11	-0.12	-0.13	0.01	-0.04	0.02	-0.06	-0.02	-0.15	-0.22	-0.07	-0.07	0.08	-0.01	-0.13	0.02	-0.07												
H 1	-0.11	0.00	-0.01	-0.05	0.01	-0.03	0.04	0.03	-0.02	-0.10	-0.17	0.02	-0.11	0.04	-0.10	-0.09	0.03	0.01	0.38											

Table 2. Continued.

Variable	A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	F1	F2	F3	F4	F5	F6	F7	F8	R1	H1	H2	H3	H4	H5	H6	H7	H8	R2	L1	L2
H 2	-0.09	-0.11	-0.13	-0.02	0.03	0.01	-0.05	-0.11	-0.02	-0.11	-0.13	-0.21	-0.03	0.03	0.00	0.02	0.04	-0.10	0.38	0.09										
H 3	0.02	0.01	0.00	-0.01	0.01	0.04	0.00	0.05	0.01	0.09	0.14	0.04	0.01	-0.05	0.00	0.07	0.02	0.01	-0.06	-0.32	0.08									
H 4	-0.06	-0.05	-0.04	-0.06	-0.03	-0.04	0.01	0.03	-0.03	-0.09	-0.17	-0.02	-0.10	0.03	-0.07	-0.08	-0.04	0.01	0.40	0.70	0.12	-0.23								
H 5	0.14	0.02	0.02	0.00	-0.05	0.00	0.02	0.09	0.01	0.06	0.27	0.02	0.01	-0.05	-0.04	0.25	-0.11	0.07	-0.41	-0.02	-0.19	0.09	0.04							
H 6	-0.08	-0.06	-0.06	-0.09	0.02	-0.01	0.01	-0.05	0.00	-0.07	-0.18	-0.17	-0.04	-0.01	0.00	-0.03	0.18	-0.04	0.34	0.16	0.39	-0.01	0.23	-0.11						
H 7	-0.12	-0.05	-0.04	-0.10	-0.01	0.00	-0.01	0.04	-0.03	-0.04	-0.10	0.04	-0.02	0.03	0.02	-0.09	0.00	0.00	0.43	0.14	0.03	0.29	0.06	-0.05	0.20					
H 8	0.03	0.06	0.05	-0.06	-0.02	-0.03	0.09	0.03	-0.04	0.00	0.07	-0.01	0.01	-0.02	0.01	0.10	0.05	0.03	-0.06	0.23	-0.12	-0.26	0.25	0.31	0.21	-0.02				
H 9	-0.04	0.12	0.09	-0.02	0.00	-0.01	0.10	0.05	0.00	0.02	0.04	0.25	0.01	-0.03	-0.04	-0.04	-0.01	0.05	0.05	0.21	-0.24	0.12	0.04	-0.14	-0.38	-0.10				
R 2	0.02	0.12	0.09	0.04	0.06	0.07	0.05	-0.05	-0.03	0.08	-0.04	0.04	0.00	-0.04	0.06	-0.07	-0.02	0.09	-0.40	-0.39	-0.24	0.03	-0.48	-0.03	-0.10	-0.06	-0.01			
L 1	0.13	-0.05	-0.05	-0.04	-0.03	0.02	0.00	0.09	0.01	0.04	0.16	-0.06	-0.04	-0.01	-0.04	0.11	-0.12	-0.05	-0.17	0.05	-0.12	-0.04	0.13	0.41	-0.11	-0.12	-0.16	-0.17		
L 2	0.13	-0.01	0.01	-0.03	-0.06	-0.01	-0.04	0.04	0.04	0.02	0.26	-0.08	0.10	-0.05	0.02	0.31	-0.02	0.03	-0.34	-0.03	0.10	-0.02	0.00	0.48	-0.04	-0.30	-0.01	-0.26	0.21	
L 3	-0.14	0.04	0.04	0.00	0.00	-0.03	0.07	-0.02	-0.01	-0.03	-0.20	0.13	-0.09	0.07	0.04	-0.18	-0.01	0.08	0.23	0.12	-0.26	-0.15	0.17	-0.31	-0.13	0.27	0.11	0.10	-0.37	-0.52

Notes: Values presented in the table are Pearson correlation coefficients. Variables are: patch-scale invertebrate variables A1 – A10, representing (in ascending order) all invertebrates per m2 of ground surveyed, all invertebrates per g of branch sampled, Arachnids per g of branch, Arachnids per m2 of ground surveyed, Lepidoptera per g of branch, Lepidoptera per m2 of ground surveyed , Diptera per g of branch, Diptera per m2 of ground surveyed , Orthoptera per g of branch, and Orthoptera per m2 of ground surveyed, respectively; patch-scale ripe fruit variables F1 – F8, representing all ripe fruit per m2 surveyed, ripe Black Gum per m2 surveyed, ripe American holly per m2 surveyed, ripe Blueberry per m2 surveyed, ripe Flowering Dogwood per m2 surveyed, ripe Grape per m2 surveyed, ripe Partridge Berry per m2 surveyed, and ripe Greenbrier per m2 surveyed in ascending order, respectively; R1, latitude, and R2, the shortest measured distance in kilometers to the Atlantic Ocean (regional scale); patch-scale variables H1 – H8, habitat structure measurements representing (in ascending order) canopy cover, mean of leaf litter count, mean of ground vegetation, mean of midstory count, mean of vine count, mean of ground shrubs, shrub stem count, and basal area, respectively; landscape-scale variables representing (in order) the proportion of impervious surface, permanent water, and hardwood forest cover within 1-km (L1 – L3).

Boosted regression tree model development requires the adjustment of specific parameters to determine the best-fitting model with the greatest predictive performance given the dataset being analyzed. These parameters included “learning rate” (*lr*; i.e. shrinkage parameter indicating amount each tree is contributing to the overall final model) and “tree complexity” (*tc*; interaction depth determining the level of independent variable interactions allowed at each split) to identify the optimal “number of trees” (*nt;* number of iterations) required to obtain the greatest model accuracy. Model performance can additionally be improved by introducing stochasticity, which in the case of “gbm” is accomplished by denoting a portion of data to randomly select each step via “bag fraction” (Elith et al. 2008, Buston and Elith 2011).

For all models and analyses, I used a bag fraction of 0.5 (i.e., half the data is randomly selected each step) and a tree complexity of 5 (up to 5-way variable interactions), constituting an adequate level of randomized subset selection as well as a sufficient number of splits for variable interactions (Elith et al. 2008, Buston and Elith 2011, Müller et al. 2013). Learning rates were adjusted following general guidelines for model parameters established *a priori* (De’ath 2007, Elith et al. 2008), and models built using the gbm.step function with learning rates ranging from 0.01 to 0.0001 were tested to determine the optimal rate for each analysis, which produced around 1,000 trees in the final model (Table 3). A 10-fold cross-validation (CV) was implemented within each developing gbm.step model, using a new subset of the entire dataset each iteration to progressively test for and ensure that the final model’s fit was still general enough for use on independent data, and thus reducing the chance of overfitting (Elith et al. 2008, Buston and Elith 2011).

Table 3. Parameters and predictive performance metrics for all BRT models used in analysis, obtained from 10-fold cross-validation and using the 31 predictor variables detailed in Table 1. Table values indicate: the response variable for each model, each model's optimal learning rate, number of trees fitted for the final ensemble model, proportion of total deviance explained of the training data, and cross validation correlation. For all models, bag fraction was left at 0.5 and tree complexity at 5. See Table 1 for species codes.

Response Variable (Model)	Learning Rate	No. of Trees	Proportion Deviance Explained	CV Correlation
AllMigPerHa	0.0075	1100	0.42	0.47
ACFL	0.0075	1200	0.60	0.61
AMRE	0.0025	1400	0.31	0.35
BTBW	0.0025	1400	0.34	0.39
GCFL	0.001	1600	0.23	0.32
GCKI	0.0025	1500	0.67	0.75
GRCA	0.0025	1300	0.38	0.46
HETH	0.0025	1100	0.53	0.59
NOPA	0.001	800	0.10	0.15
OVEN	0.001	800	0.08	0.10
REVI	0.005	800	0.54	0.65
YBCU	0.001	1500	0.19	0.23
YRWA	0.0025	1300	0.48	0.56
YSFL	0.0025	1400	0.38	0.46

The final ensemble of models developed and used in all analyses included 31 predictor variables, with the exception of sampling-period-specific models, which had sampling period removed as a predictor variable (Table 1). Sixteen separate analyses were conducted using these predictor variables, with one model fit for "grouped nocturnal migrant species" across the entire migratory season, two models fit for "grouped nocturnal migrant species" during specific sampling periods (period 1 = 15 Aug – 4 Sep, period 3 = 26 Sep – 16 Oct), and 13 models fit for individual migratory species of interest, those occurring at different time during the migratory season and with an adequate number of detections (>50) to allow for density adjustments (Hurvich and Tsai 1989, Buckland et al. 2004). For each analysis conducted, a ranked list of the relative influence of each predictor variable was produced, along with partial-dependence plots that depicted visually the effect of a particular predictor variable on the response variable while controlling for the effects of all remaining predictor variables in the models. The sum of these relative influence measurements equaled 100% for each model, and I arbitrarily considered those variables with 5% or more relative influence in explaining migrant density to be important predictor variables, as each model had an adequate number of highly influential variables rank well above this cutoff. Interactions between all predictor variables were also calculated automatically within the program for each model, allowing me to identify potentially important interactions occurring along with predictor variables, and the highest ranked (i.e. more important) interactions, which are discussed, below.

The goal of these analyses were to use boosted regression tree modelling techniques to assess which ecological variables of interest, including temporal trends in localized factors such as food availability as well as spatially-explicit metrics such as shrub density at the local scale and proportional buffers at the landscape scale, showed the greatest influence on determining the density of select migratory species at mid-Atlantic forested stopover sites, and how their influence varied within the season.

CHAPTER 3

RESULTS

I conducted 1,593 (836 in 2013 and 757 in 2014) avian transect surveys during the two autumn migratory seasons. On average, I visited each survey site 17 times (range 13-20) in 2013 and 15 times (range 13-18) in 2014 (Table 4). In total, 16,632 useable bird detections from 128 species were recorded, with 5,002 (30%) of these detections of nocturnal migratory landbirds (Appendix A). Migratory landbird densities were fairly consistent over both survey seasons (Fig. 3) and among sites (Fig. 4). Densities peaked during the latter portion of the migratory season and were notably higher at the northernmost sites located in the Delaware region (Figs. 5-6). Branch invertebrates were consistently available throughout the entire survey season and across multiple years (Figs. 7-8). The southernmost sites located in inland coastal Virginia had the greatest densities of branch invertebrates detected (Fig. 9). Arachnids were the most abundant invertebrate group detected via branch clippings (Fig. 10), and accounted for 60% of all branch invertebrates in both 2013 and 2014. Diptera was the second most abundant branch invertebrate group, accounting for 10% and 11% of all branch invertebrates in 2013 and 2014, respectively. Ground invertebrate detections decreased slightly as the season progressed in both years (Fig. 11), and were generally lower overall at sites located further north (Figs. 12-13). Arachnids were the most abundant invertebrate group detected in ground visual surveys (Fig. 14), and accounted for 38% and 32% of all ground invertebrates in 2013 and 2014, respectively. Dipterans were the second most abundant ground invertebrate group, accounting for 20% and 23% of all branch invertebrates in 2013 and 2014, respectively. Ripe fruit became more abundant as the migratory season progressed (Fig. 15), with more ripe fruit detected on average in 2014 (0.83 ripe fruit per

Table 4. List of survey sites and which, if any, radar (AKQ = Wakefield, VA; DOX = Dover, DE) the transect falls within range of, the number of surveys conducted at each transect in 2013 and 2014, and general transect location (DE = Delaware, ES = Eastern Shore of Virginia, MD = Maryland, VA = Inland SE Virginia).

Transect	Radar	Surveys (2013/2014)	Location of Site
CBSN	AKQ	19 / 18	VA
CPSP	AKQ	20 / 17	VA
CSNA	AKQ	19 / 18	VA
GDNW	AKQ	14 / 16	VA
GDSE	AKQ	19 / 17	VA
GDSW	AKQ	13 / -	VA
HCWP	AKQ	19 / 17	VA
MSBT	AKQ	20 / 17	VA
PACP	AKQ	19 / 17	VA
RACP	AKQ	19 / 18	VA
SOQU	AKQ	15 / 17	VA
WADI	AKQ	- / 13	VA
ZUNI	AKQ	16 / 17	VA
BFLP	DOX	17 / 15	DE
BHNW	DOX	14 / 15	DE
BLWA	DOX	17 / 15	DE
CHSP	DOX	18 / 15	DE
FBNP	DOX	17 / 15	DE
KPSP	DOX	17 / 15	DE
MAHO	DOX	18 / 16	MD
MASP	DOX	18 / 16	MD
MCWS	DOX	16 / 16	DE
MNWA	DOX	16 / 15	DE
NWWA	DOX	17 / 15	DE
PHWA	DOX	17 / 15	DE
THWO	DOX	16 / 15	DE
TUSP	DOX	17 / 15	DE
BROW	Outside	17 / 16	ES
CACH	Outside	18 / 16	ES
EAVA	Outside	17 / 16	MD
ESSW	Outside	18 / 16	ES
FOES	Outside	17 / 16	MD
IDYL	Outside	18 / 16	MD
KIPT	Outside	16 / 16	ES
MAFA	Outside	15 / 15	ES
MARU	Outside	17 / 16	MD
MILA	Outside	17 / 16	MD
MUHU	Outside	18 / 16	ES
NAMI	Outside	19 / 16	MD
NASS	Outside	18 / 16	MD
OAGR	Outside	18 / 16	ES
PHFA	Outside	17 / 15	ES
PIHA	Outside	18 / 16	ES
POSF	Outside	18 / 15	MD

Table 4. Continued.

Transect	Radar	Surveys (2013/2014)	Location of Site
PRAN	Outside	18 / 15	MD
QUIN	Outside	16 / 14	ES
SANE	Outside	18 / 16	ES
WAIS	Outside	14 / 14	ES
WICO	Outside	19 / 16	MD

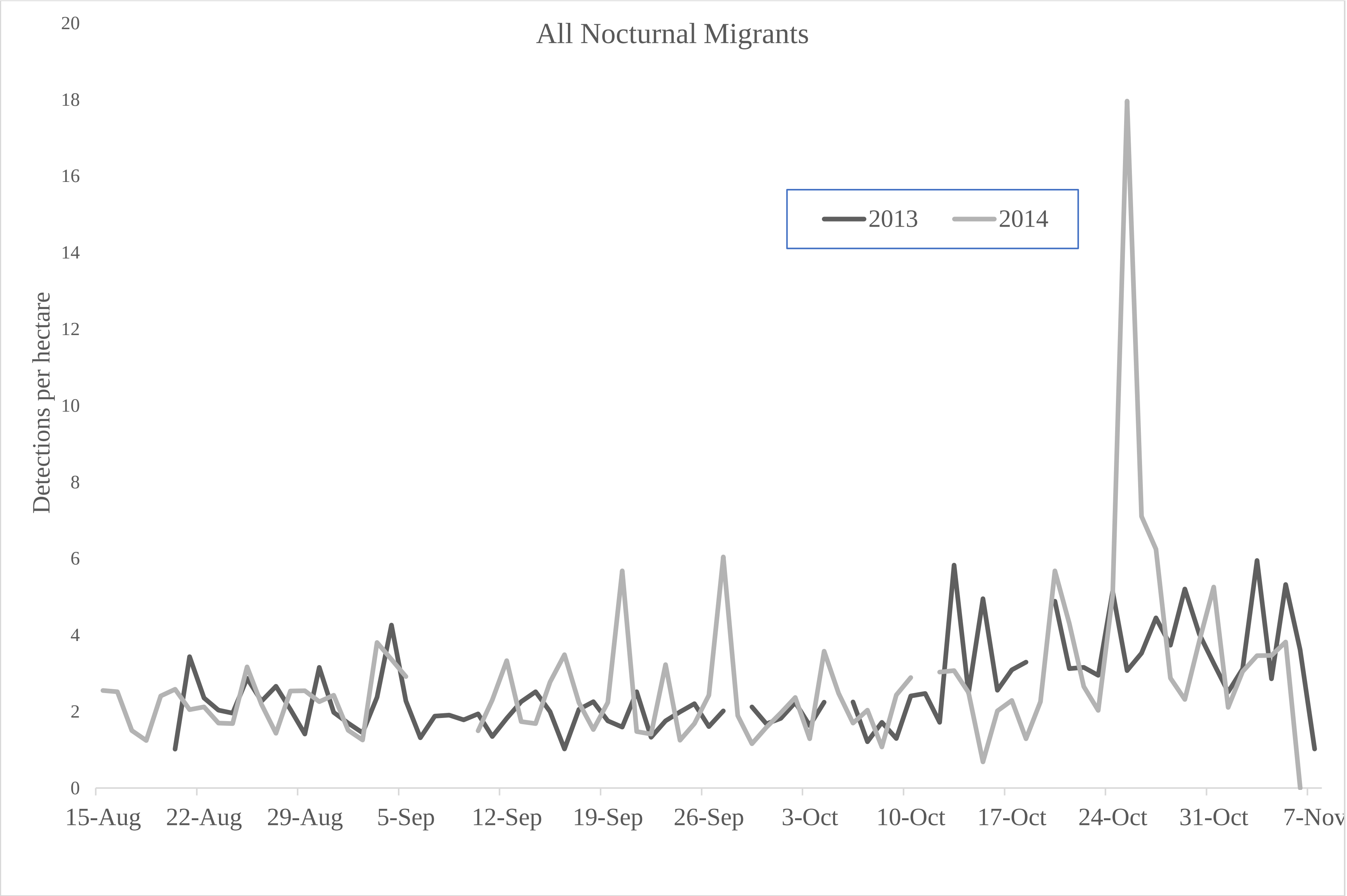


Fig. 3. Temporal trend for all nocturnal landbird migrant detections, averaged across all transect surveys conducted in 2013 and 2014.

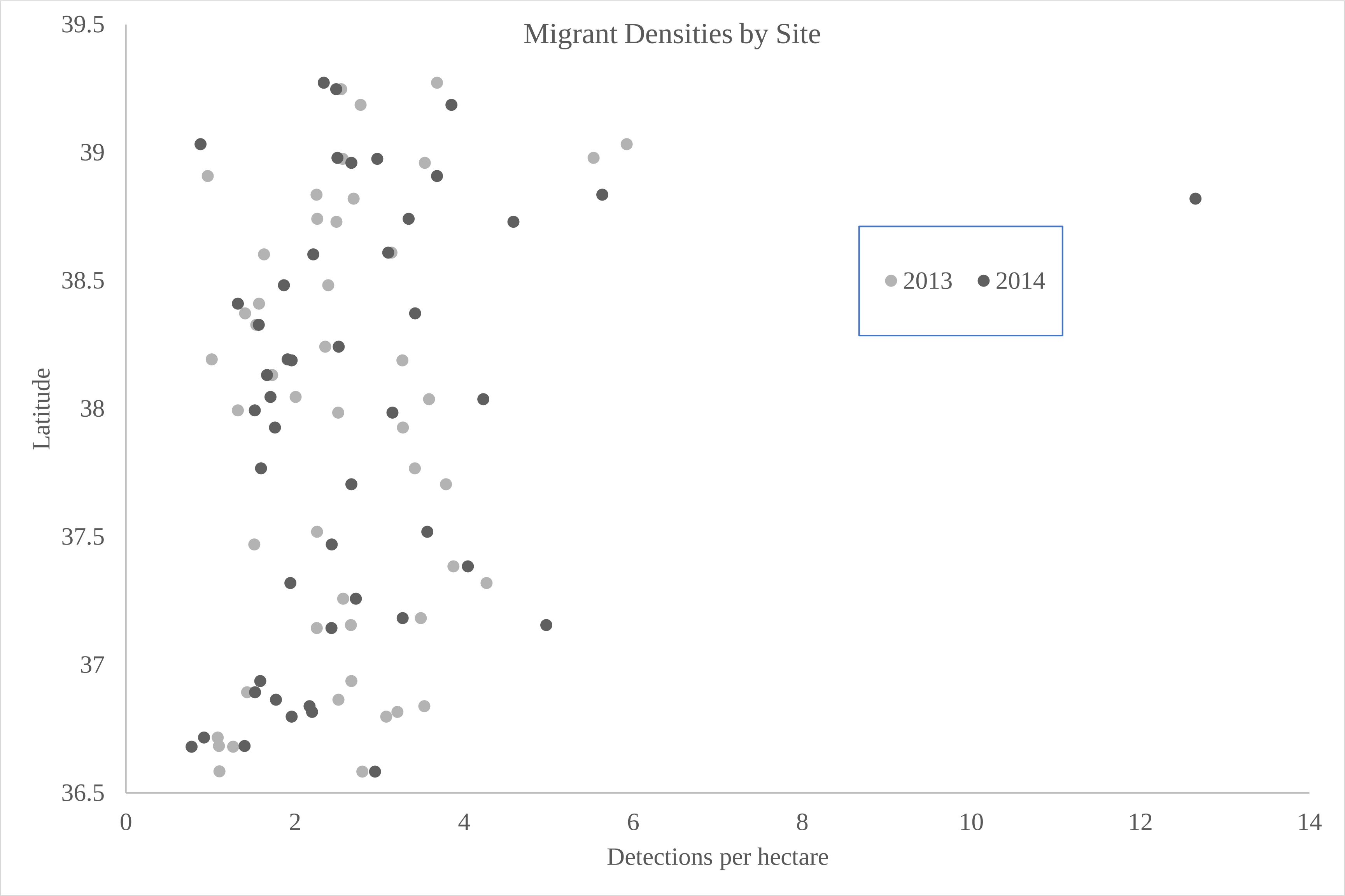


Fig. 4. Seasonal mean of all nocturnal migrant detections for each survey site in 2013 and 2014. Sites, denoted by individual dots, are presented in decreasing latitude (north to south).

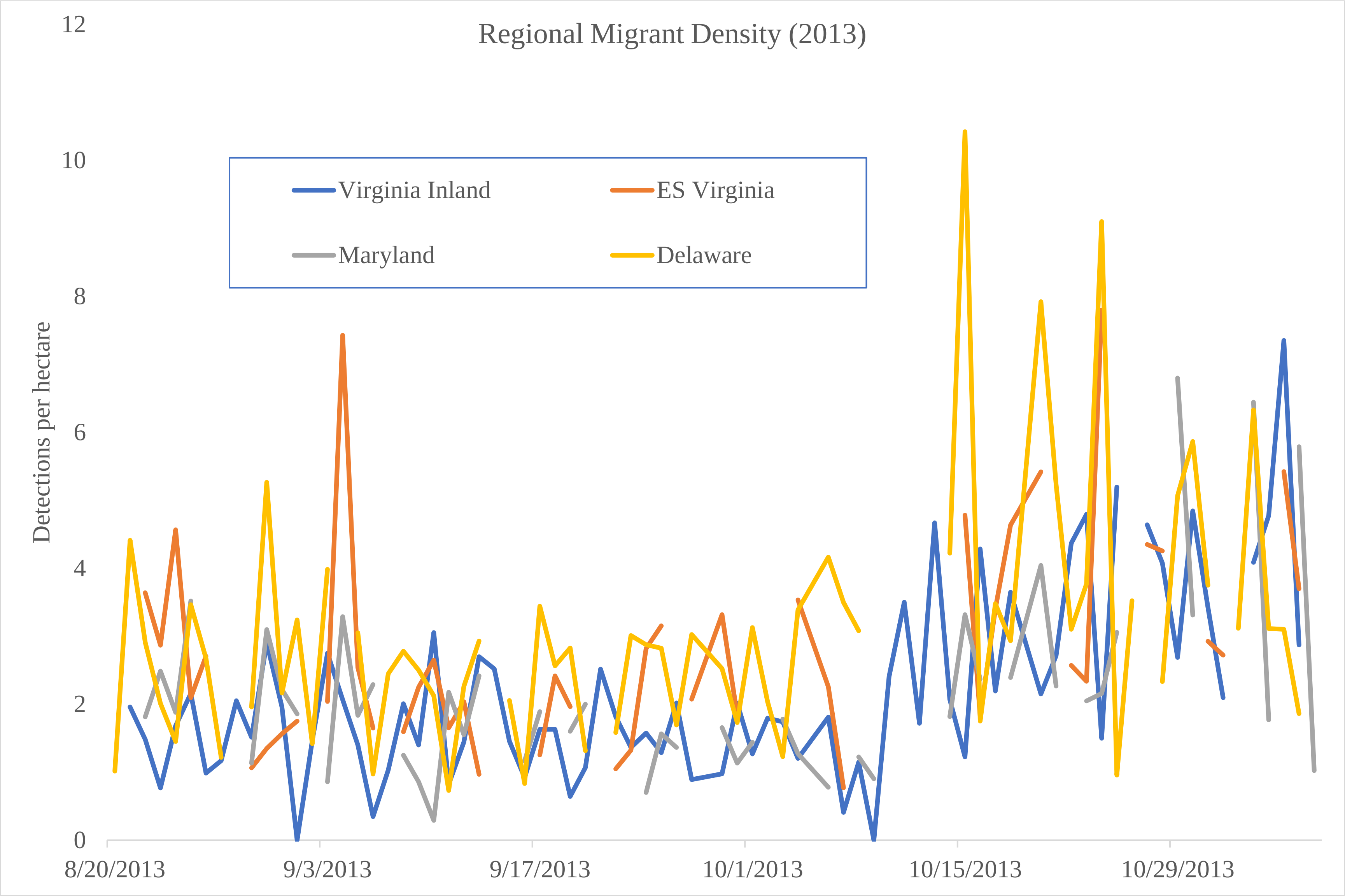


Fig. 5. Temporal trend in nocturnal migrant detections in 2013, with transect survey sites grouped by region (four regions with 12 sites each).

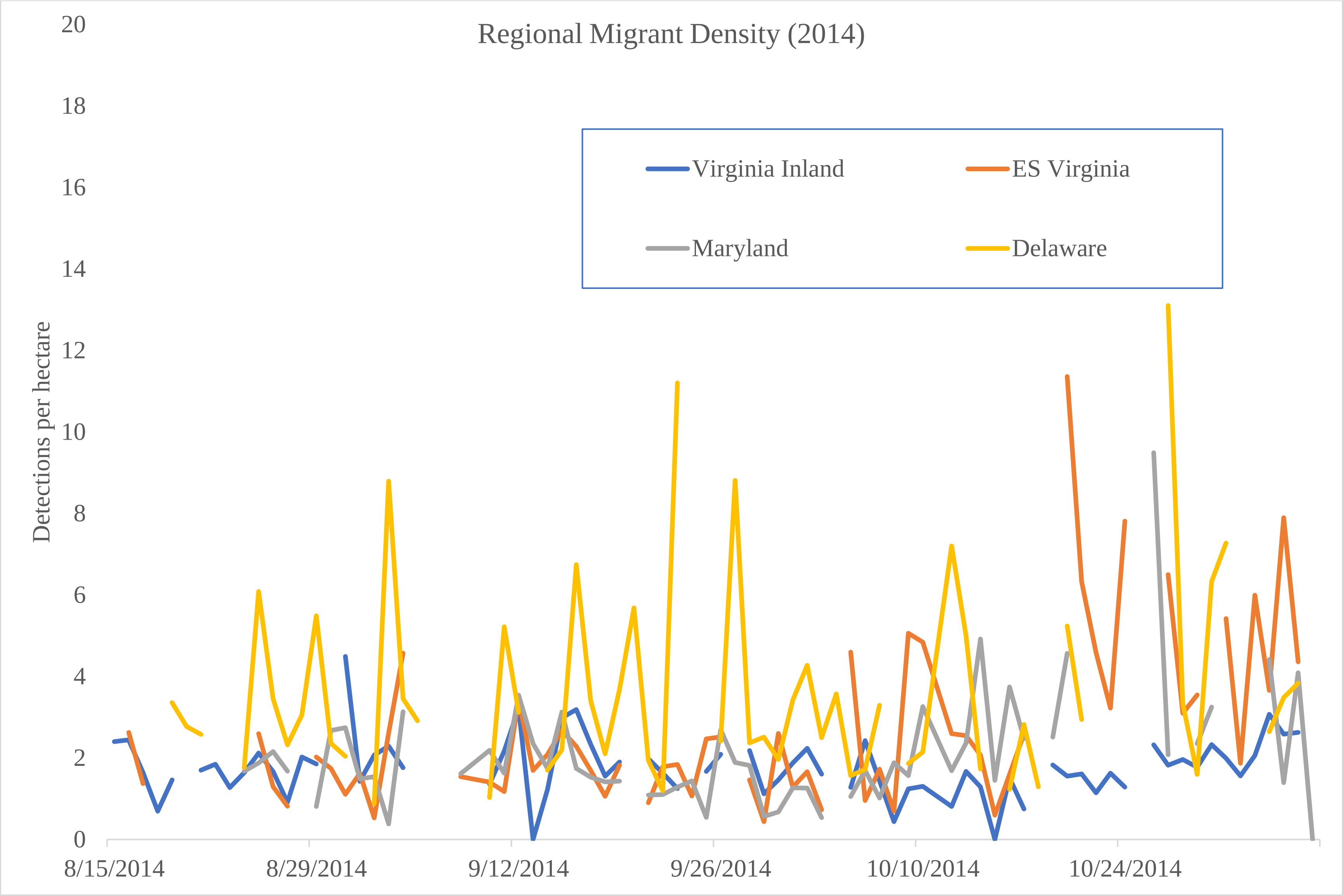


Fig. 6. Temporal trend in nocturnal migrant detections in 2014, with transect survey sites grouped by region (four regions with 12 sites each).

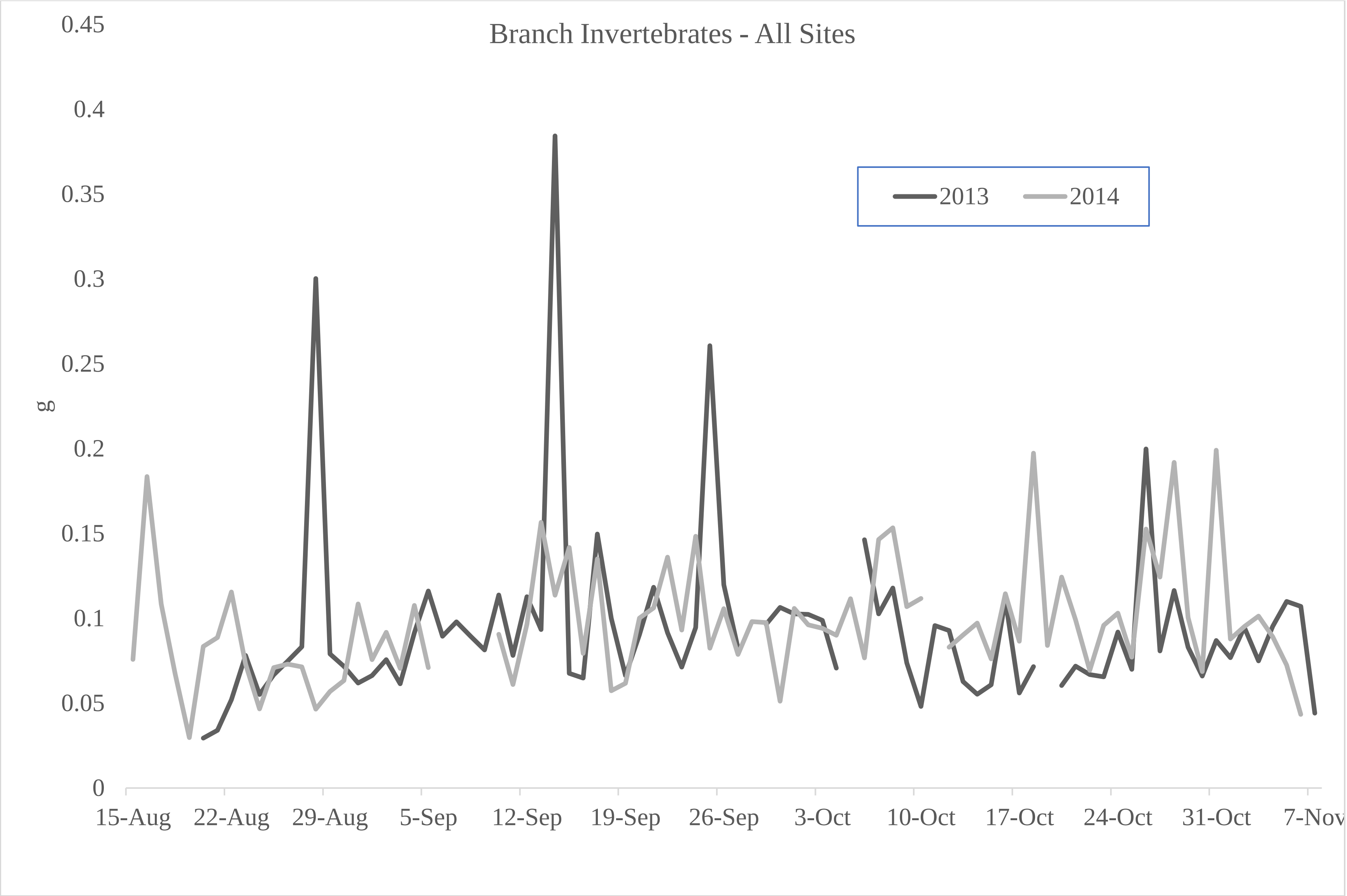


Fig. 7. Temporal trend in invertebrate detections, obtained from branch clippings, in 2013 and 2014.

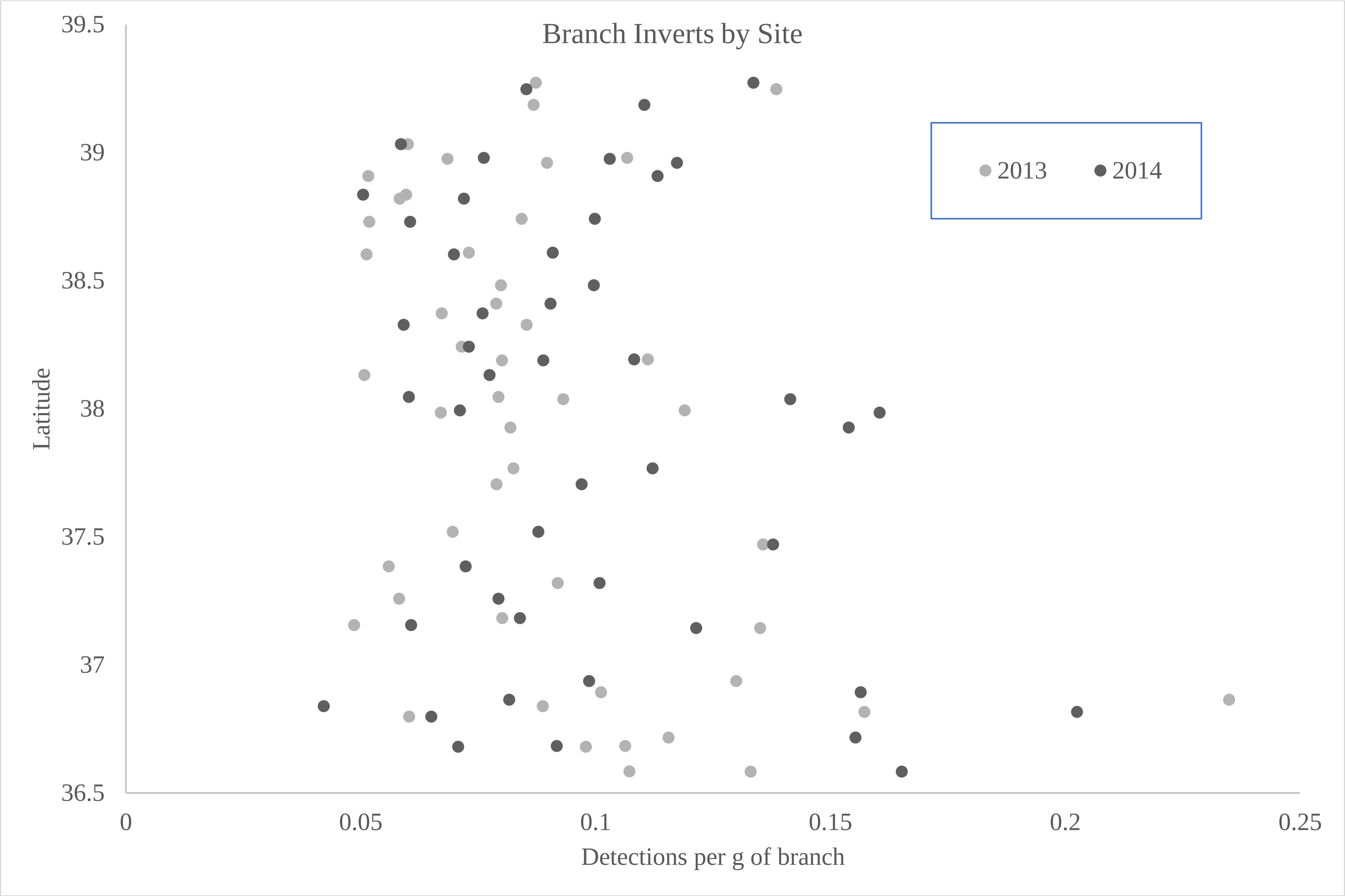


Fig. 8. Seasonal mean of invertebrates detected per g of branch for each survey site in 2013 and 2014. Sites, denoted by individual dots, are presented in decreasing latitude (north to south).

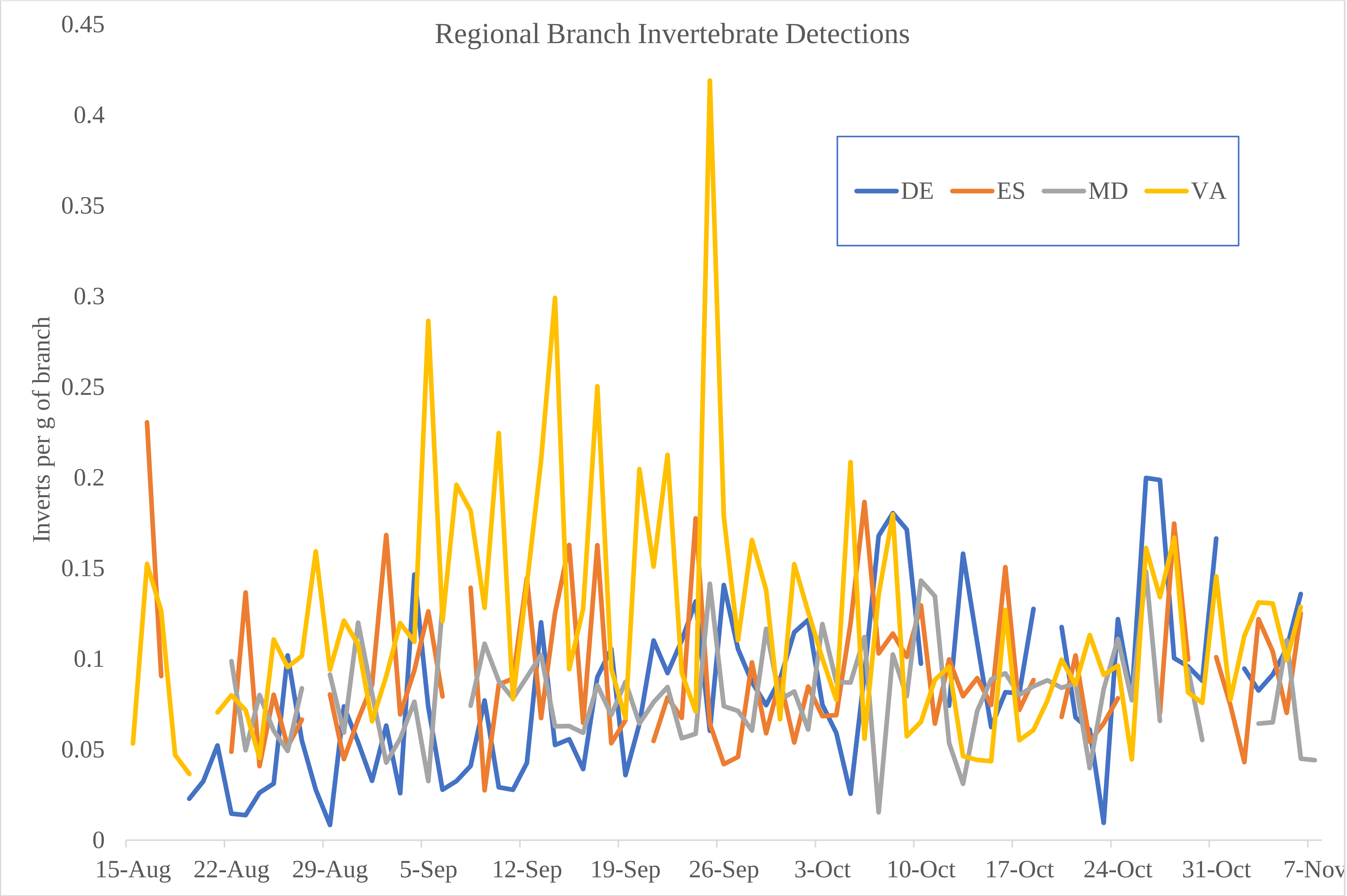


Fig. 9. Temporal trend in branch invertebrate detections, grouped by region (four regions with 12 sites each; DE = Delaware, ES = Eastern Shore of Virginia, MD = Maryland, VA = Coastal Virginia) and averaged across sampling years.

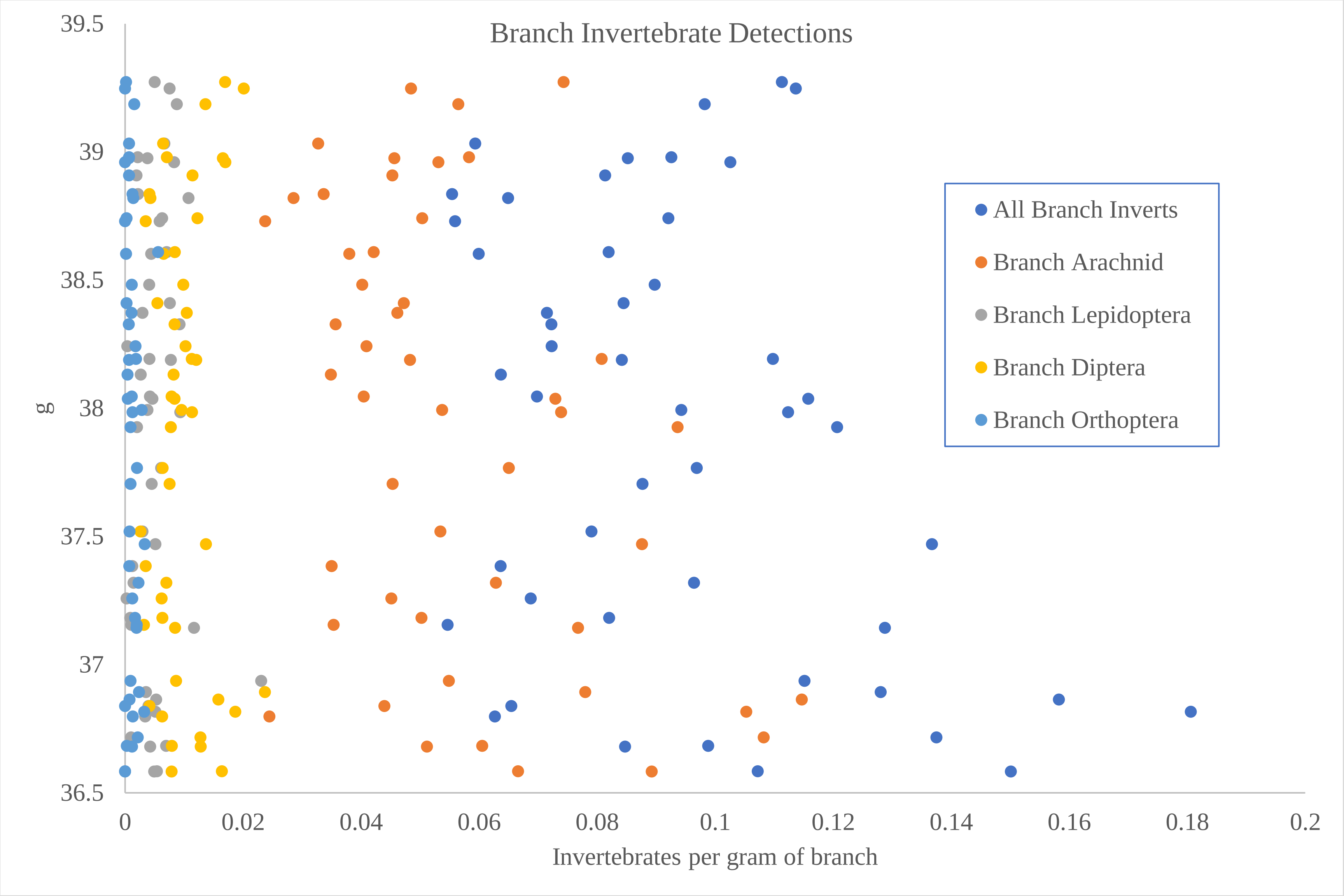


Fig. 10. Detections per g of branch of common invertebrate groups as well as all combined detections, averaged across both sampling years, for each survey site. Sites, denoted by individual dots, are presented in decreasing latitude (north to south).

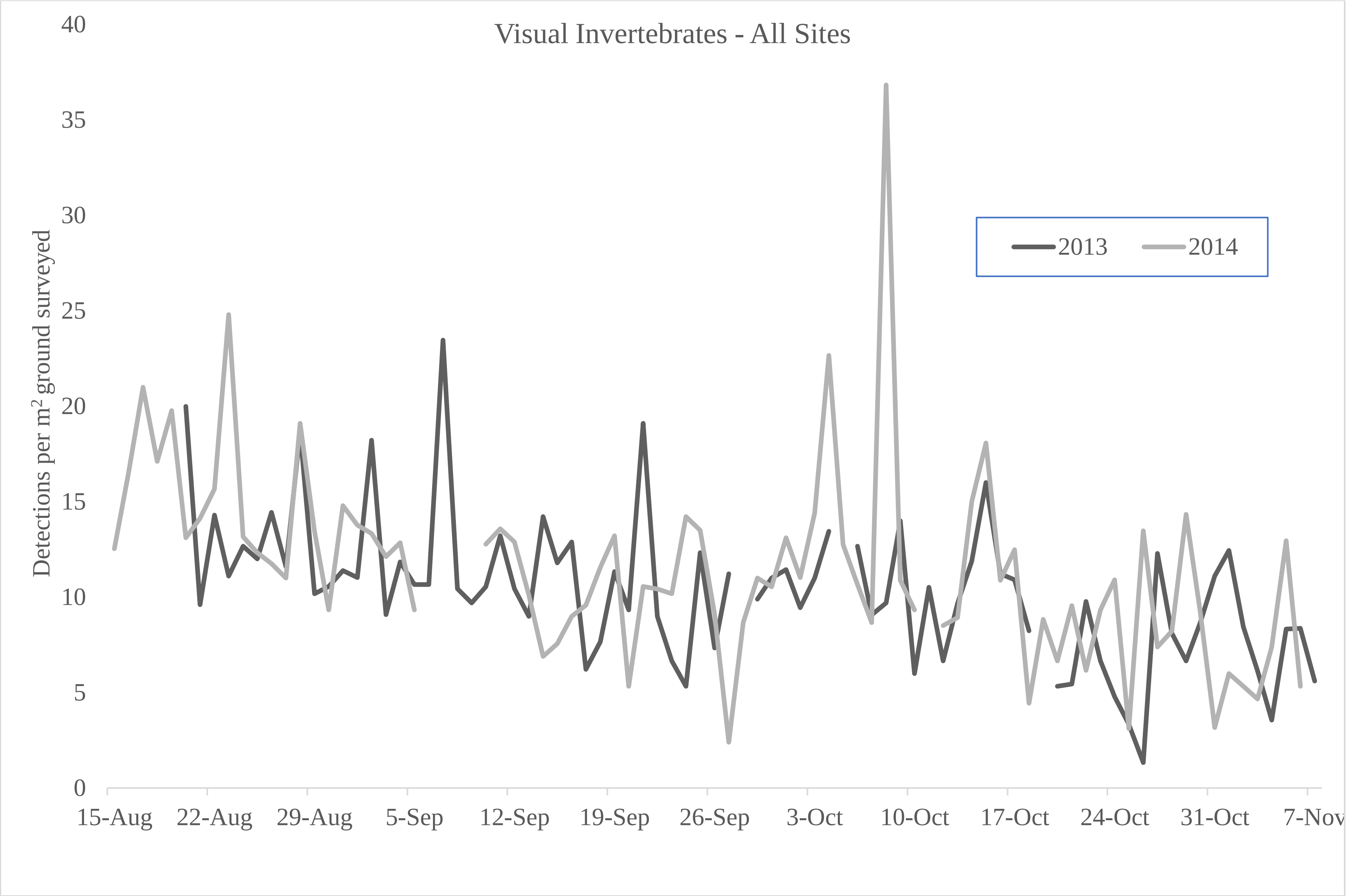


Fig. 11. Temporal trend in invertebrate detections, obtained from visual ground count surveys, in 2013 and 2014.

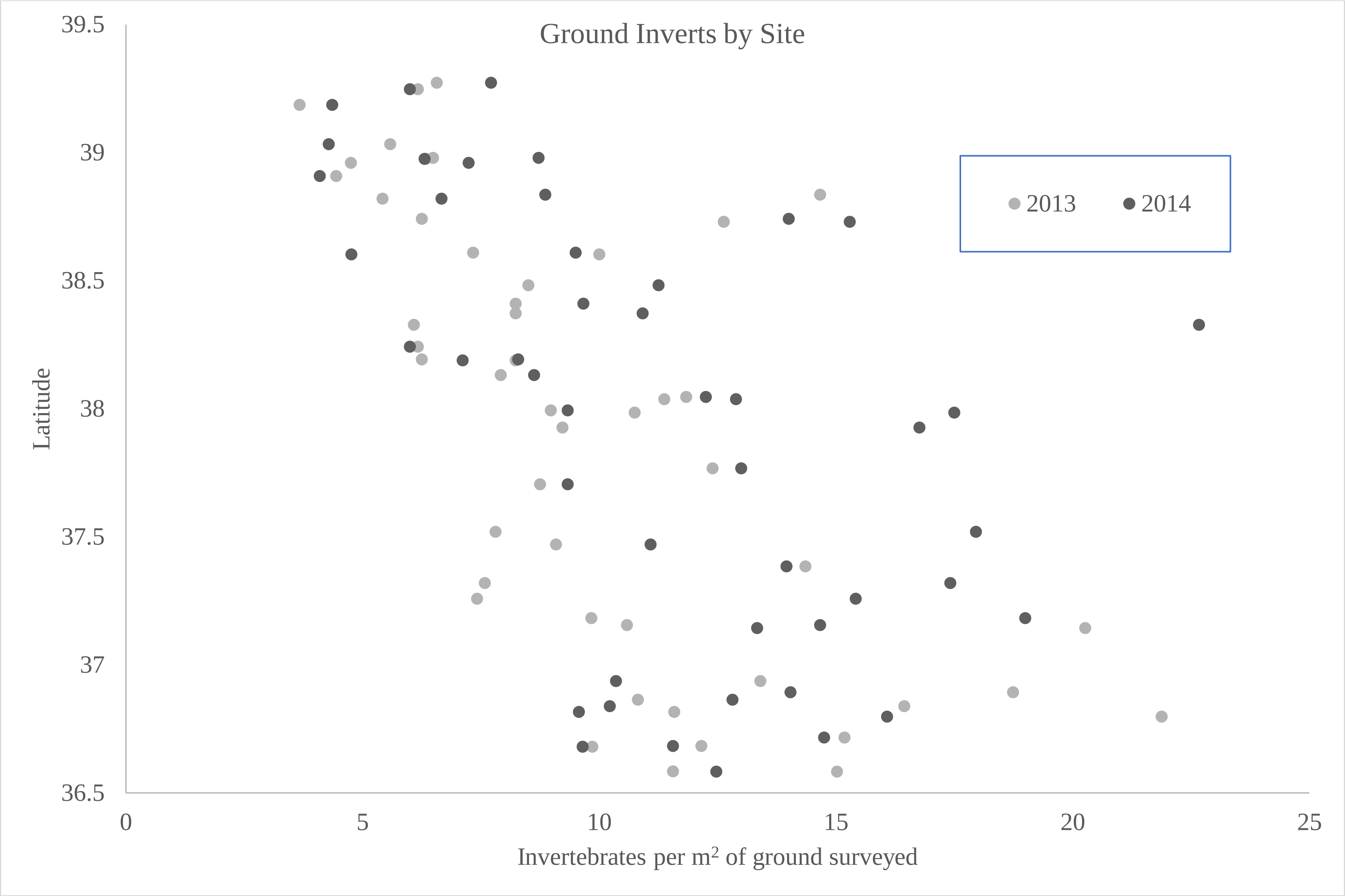


Fig. 12. Seasonal mean of invertebrates detected per m^2 of ground surveyed for each survey site in 2013 and 2014. Sites, denoted by individual dots, are presented in decreasing latitude (north to south).

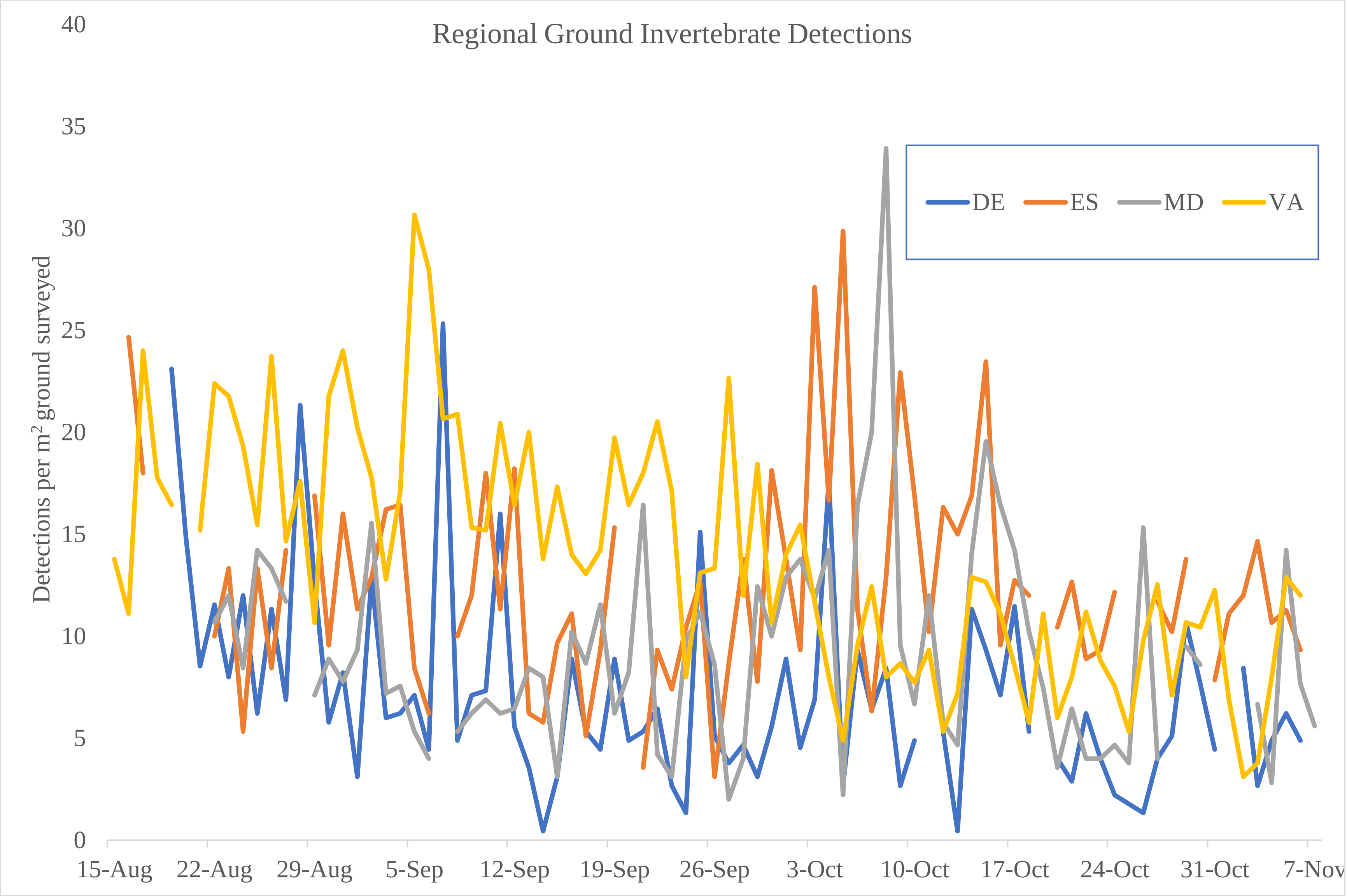


Fig. 13. Temporal trend in ground invertebrate detections, grouped by region (four regions with 12 sites each; DE = Delaware, ES = Eastern Shore of Virginia, MD = Maryland, VA = Coastal Virginia) and averaged across sampling years.

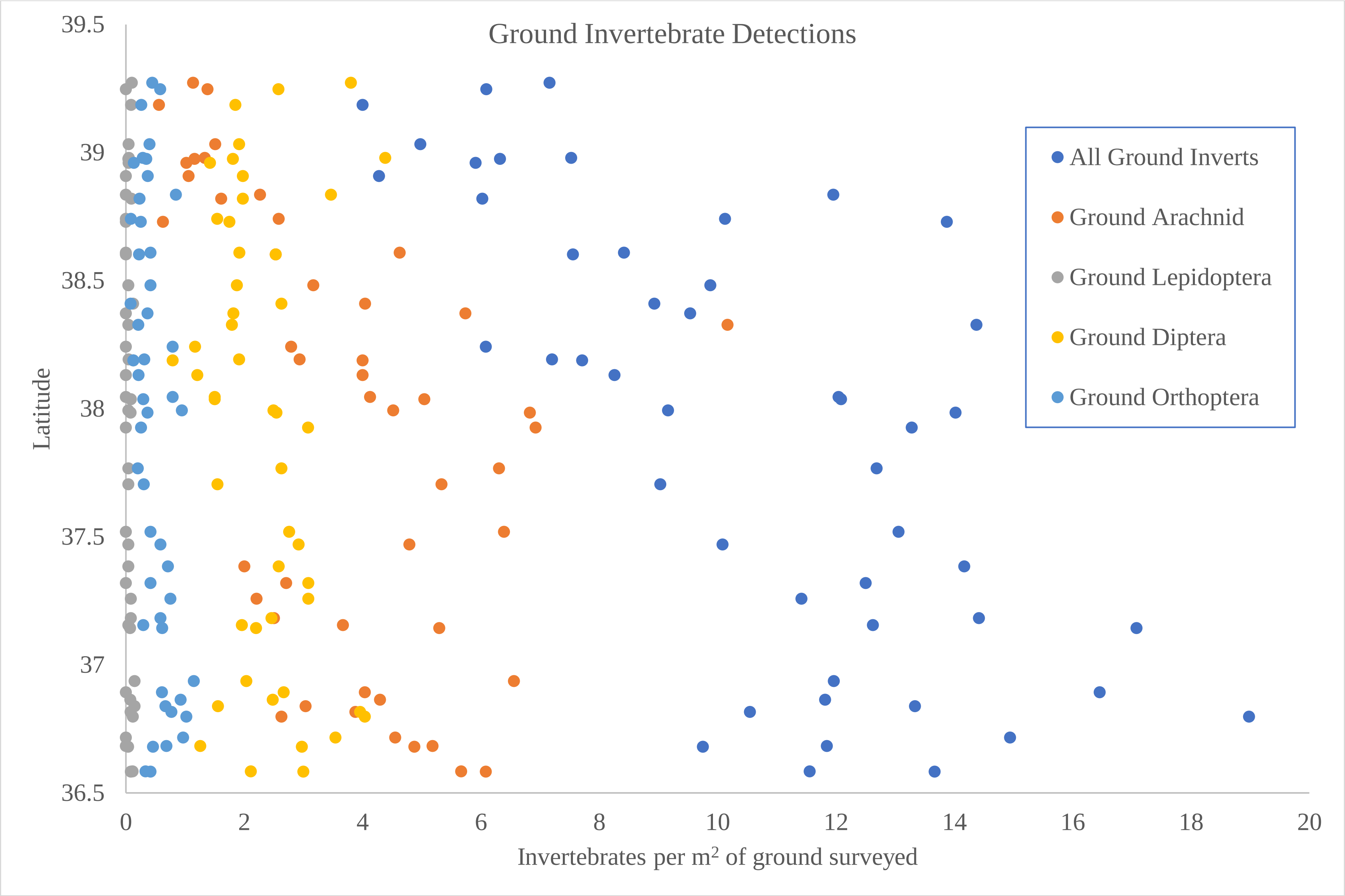


Fig. 14. Detections per m^2 of ground surveyed of common invertebrate groups as well as all combined detections, averaged across both sampling years, for each survey site. Sites, denoted by individual dots, are presented in decreasing latitude (north to south).

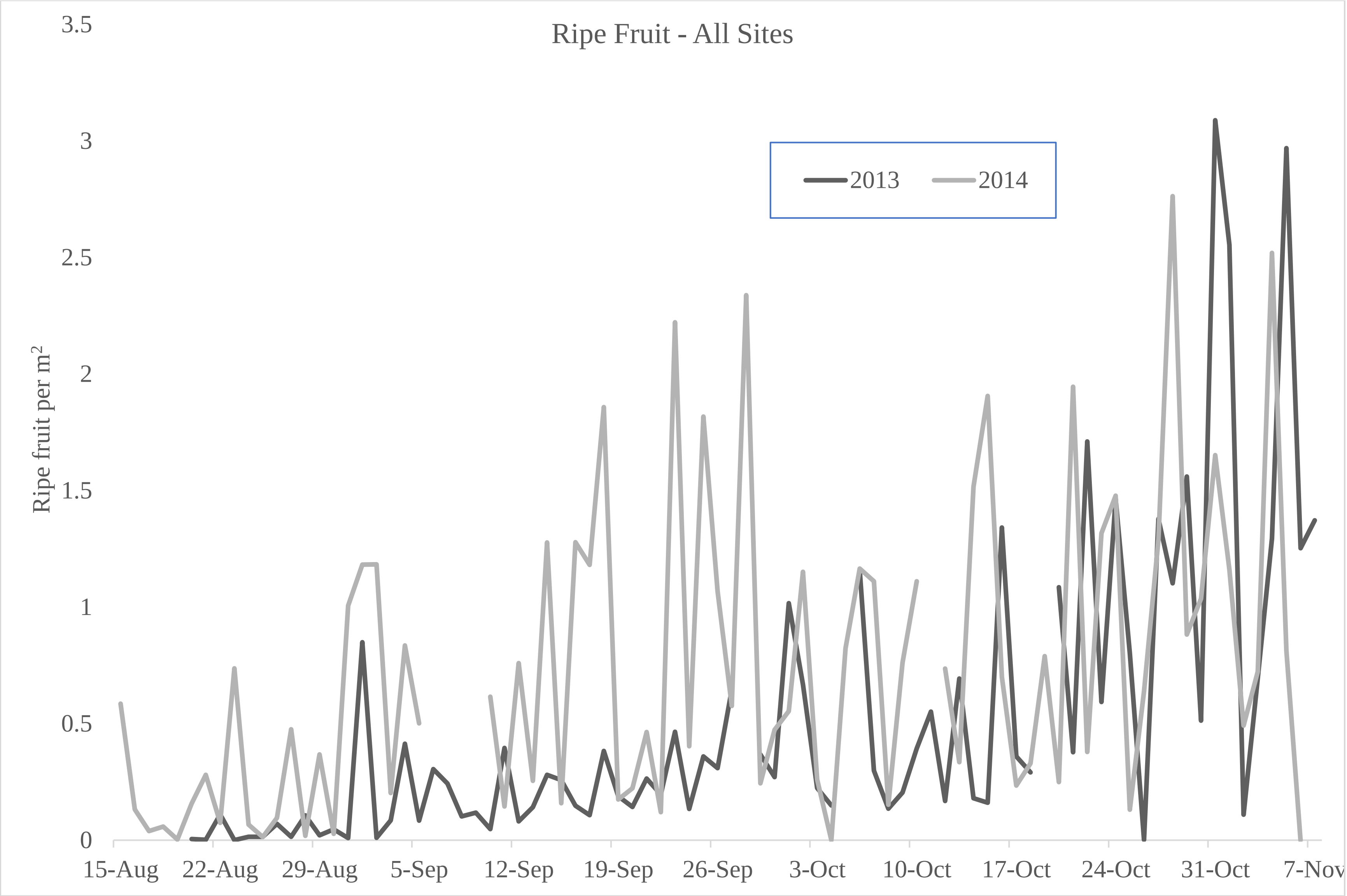


Fig. 15. Temporal trend in ripe fruit detections for all fruiting species and survey sites in 2013 and 2014.

m^2) than 2013 (0.55 ripe fruit per m^2). Ripe fruit was more abundant at sites further south, and highly variable between years (Fig. 16). Mid-season fruit availability was highest along Virginia's Eastern Shore, while late season availability was generally higher at the southernmost inland coastal Virginia sites (Fig. 17). American holly, Black Gum (*Nyssa sylvatica*), Grape (*Vitus* spp.), and Greenbrier were among the most widespread and abundant ripe fruit species across all survey sites (Fig. 18). American holly was the most widespread fruiting species, yet ripe fruit production varied greatly between years, accounting for 38% of all ripe fruit in 2013 and only 14% in 2014. Black Gum and Grape ripe fruit production also varied greatly by year, accounting for only 5% of all ripe fruit in 2013, yet 13% and 18%, respectively, of all ripe fruit in 2014. Greenbrier ripe fruit production was more consistent, accounting for 4% and 6% of all ripe fruit in 2013 and 2014, respectively. American holly was also one of the latest fruits to ripen, doing so near the end of sampling efforts (Fig. 19).

Patch-scale habitat composition and structural features were extremely variable among sites (Figs. 20-23). Shrubs and midstory vegetation were common habitat features at each site, while vines and ground vegetation occurred less frequently (Fig. 20). Shrub density via stem count, as well as basal area at each site, were also highly variable across all sites; however, shrub density was generally the lowest at sites along Virginia's Eastern Shore and, to a lesser degree, coastal Maryland (Fig. 21). Canopy cover was generally high across all sites, with mean coverage of 93% (range 79.25% - 96%), although the northernmost sites were generally the highest (Fig. 22). At the landscape-scale, both type and proportion of surface surrounding each survey site were quite variable (Fig. 24). Hardwood forest was the most common land cover type within a 1-km buffer of each site, with a mean proportion of 0.41 (range 0.06 to 0.90). While low at most sites, permanent water (0.06 mean proportion within the surrounding 1-km landscape)

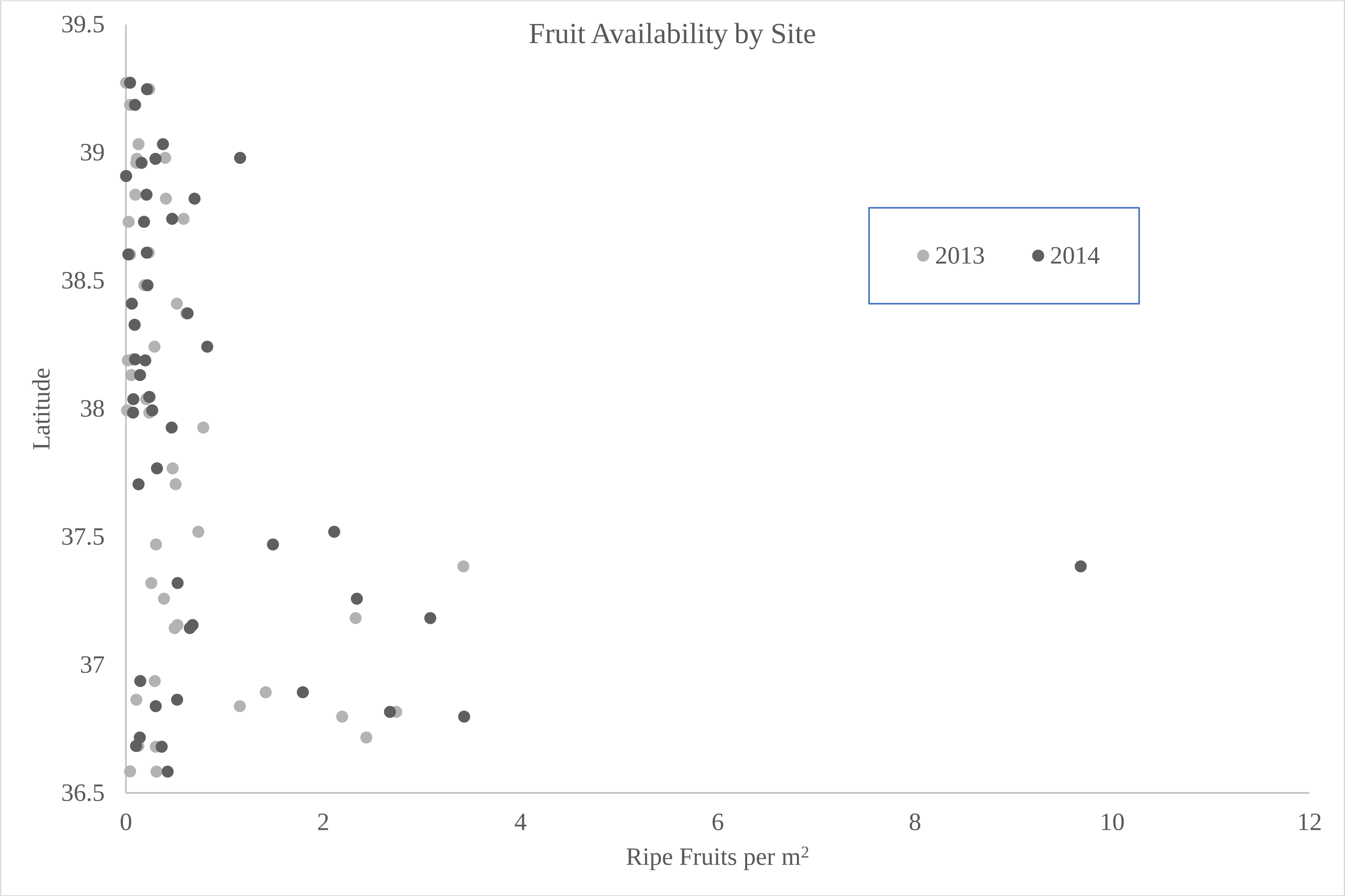


Fig. 16. Seasonal mean in ripe fruit availability for each survey site in 2013 and 2014. Sites, denoted by individual dots, are presented in decreasing latitude (north to south).

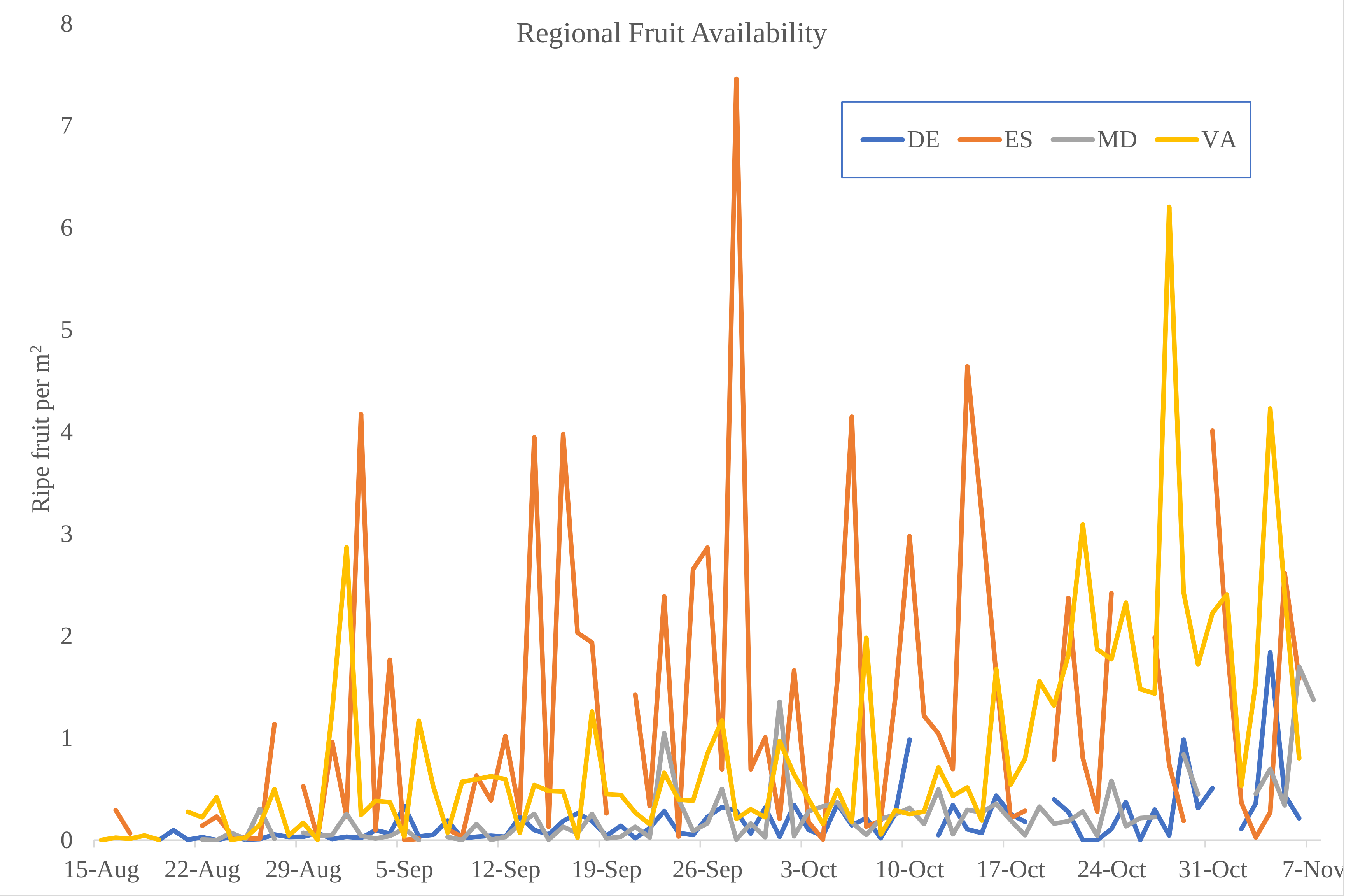


Fig. 17. Temporal trend in ripe fruit availability, grouped by region (four regions with 12 sites each; DE = Delaware, ES = Eastern Shore of Virginia, MD = Maryland, VA = Inland Southeast Virginia) and averaged for both sampling years.

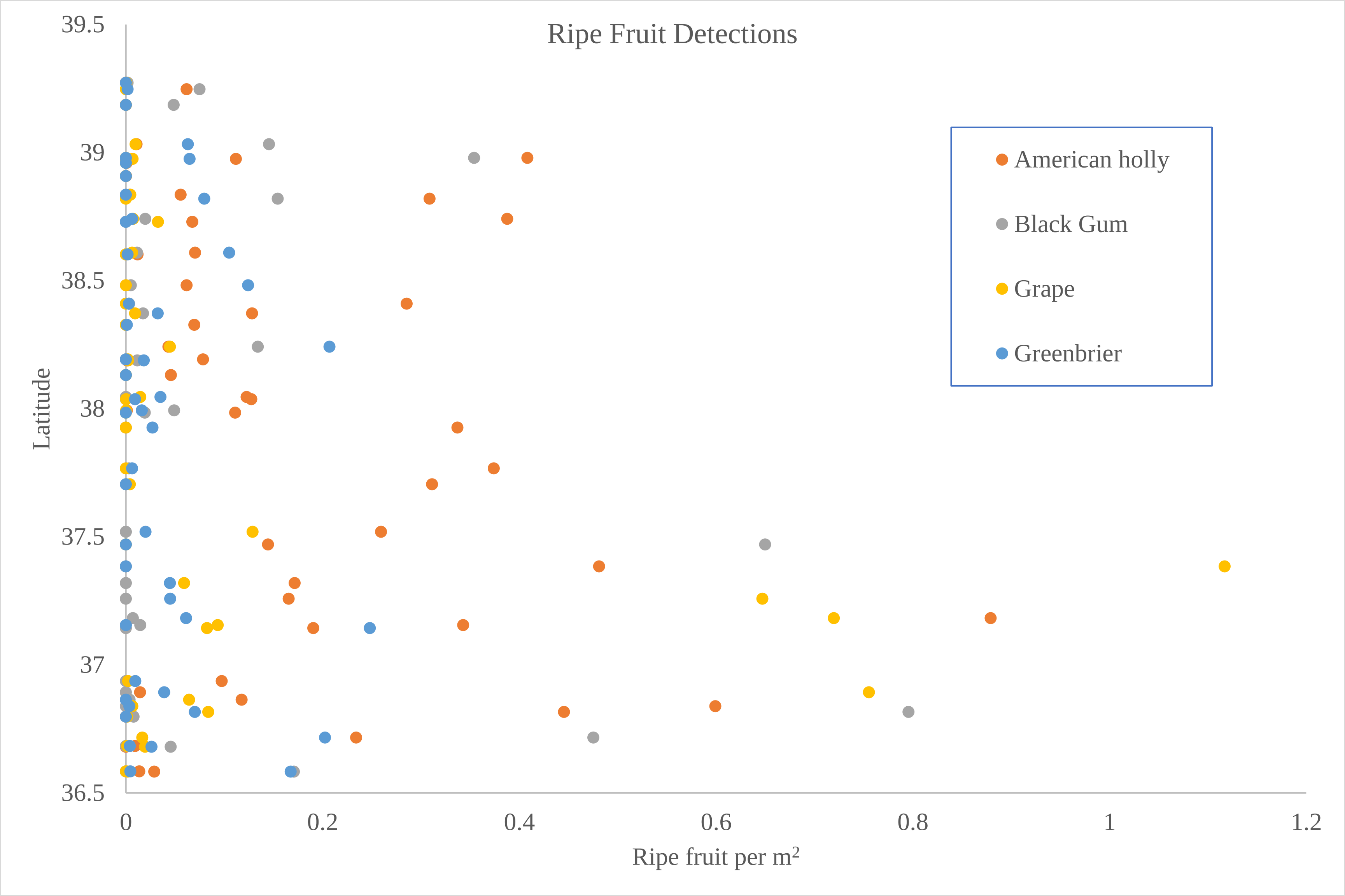


Fig. 18. Detections per m^2 of ripe fruits from some common species, averaged across both sampling years, for each survey site. Sites, denoted by individual dots, are presented in decreasing latitude (north to south).

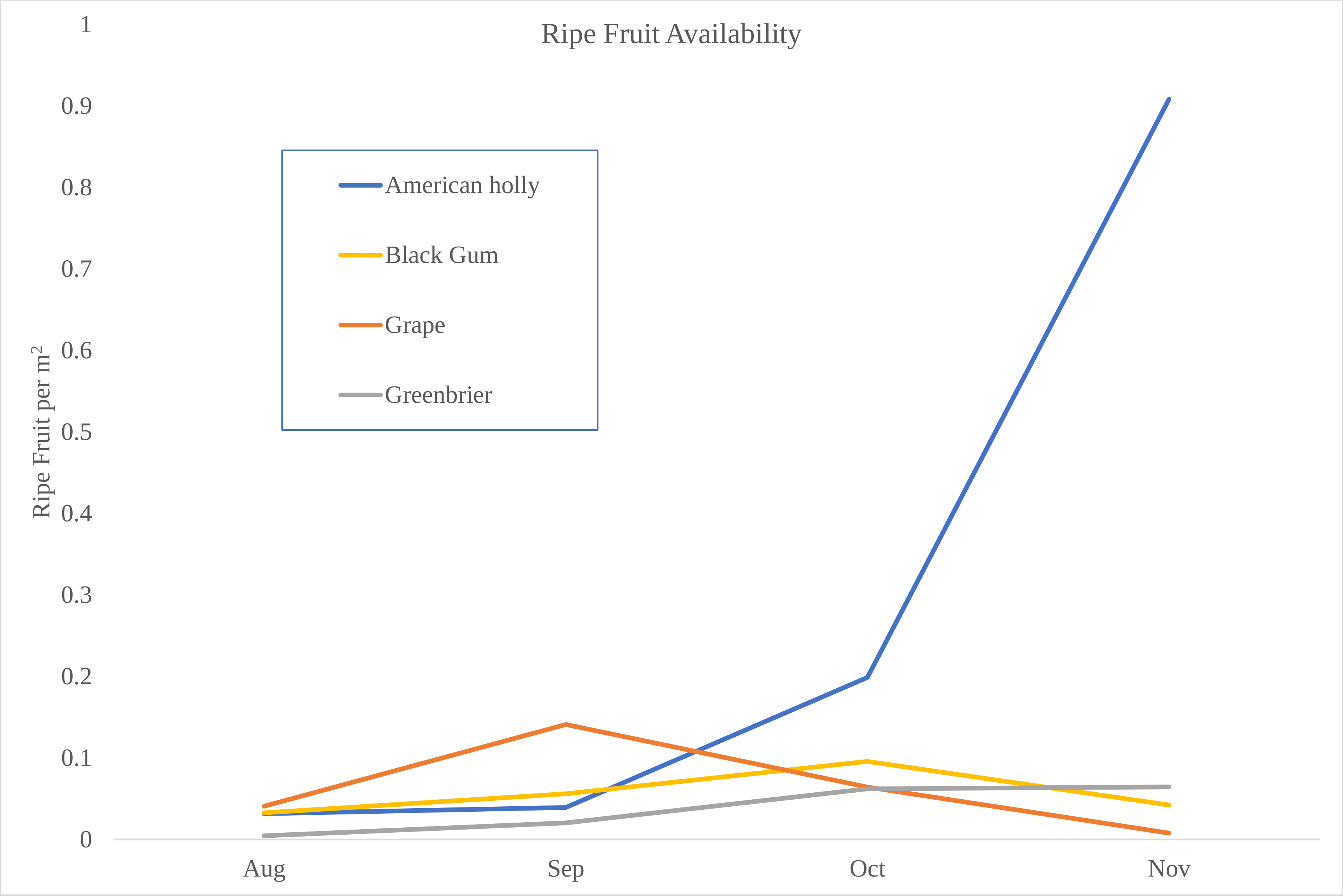


Fig. 19. Temporal trend in ripe fruit availability of some common species, averaged across both sampling years, for all survey sites.

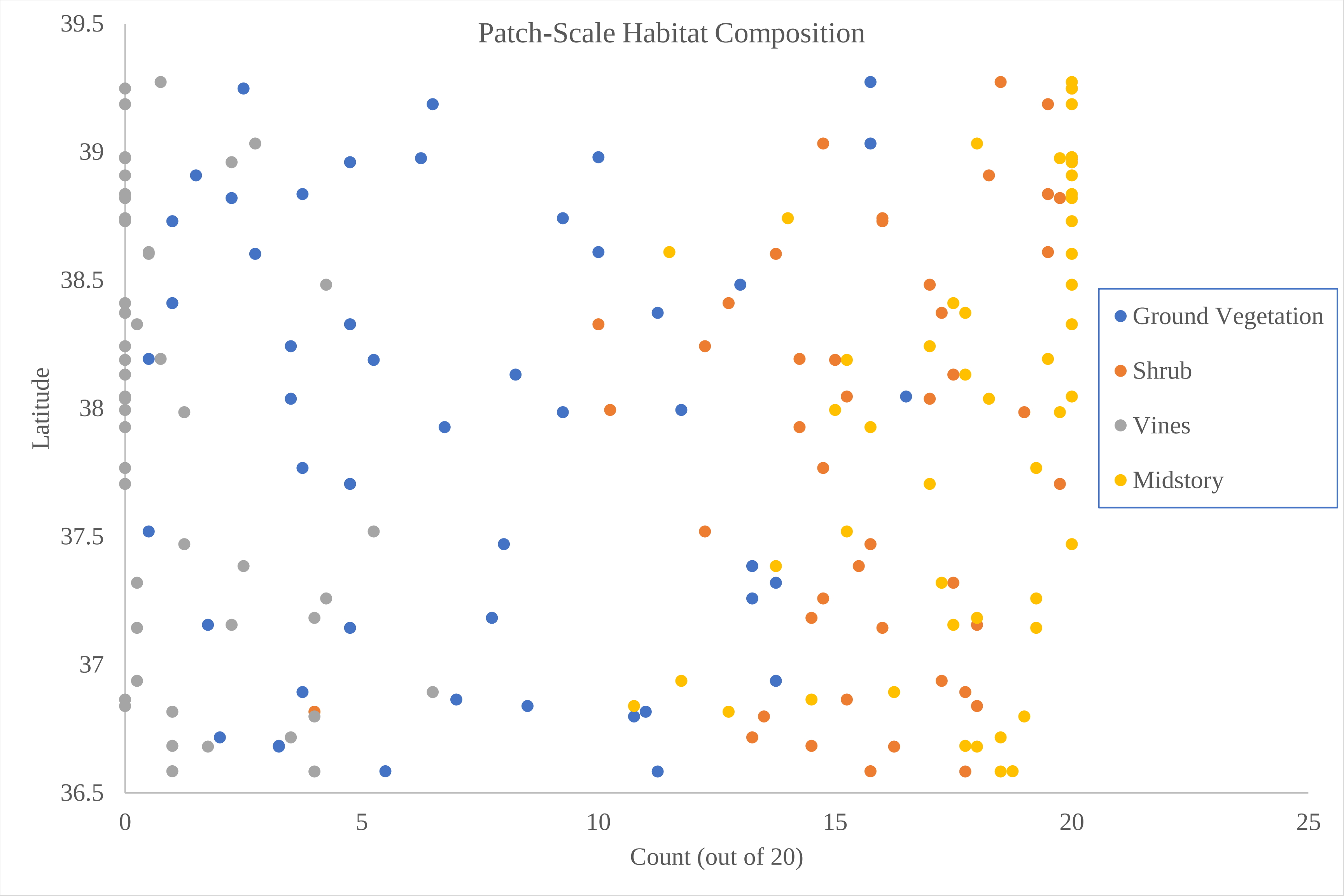


Fig. 20. Occurrence count (out of 20) of patch-scale habitat features recorded for each survey site. Sites, denoted by individual dots, are presented in decreasing latitude (north to south).

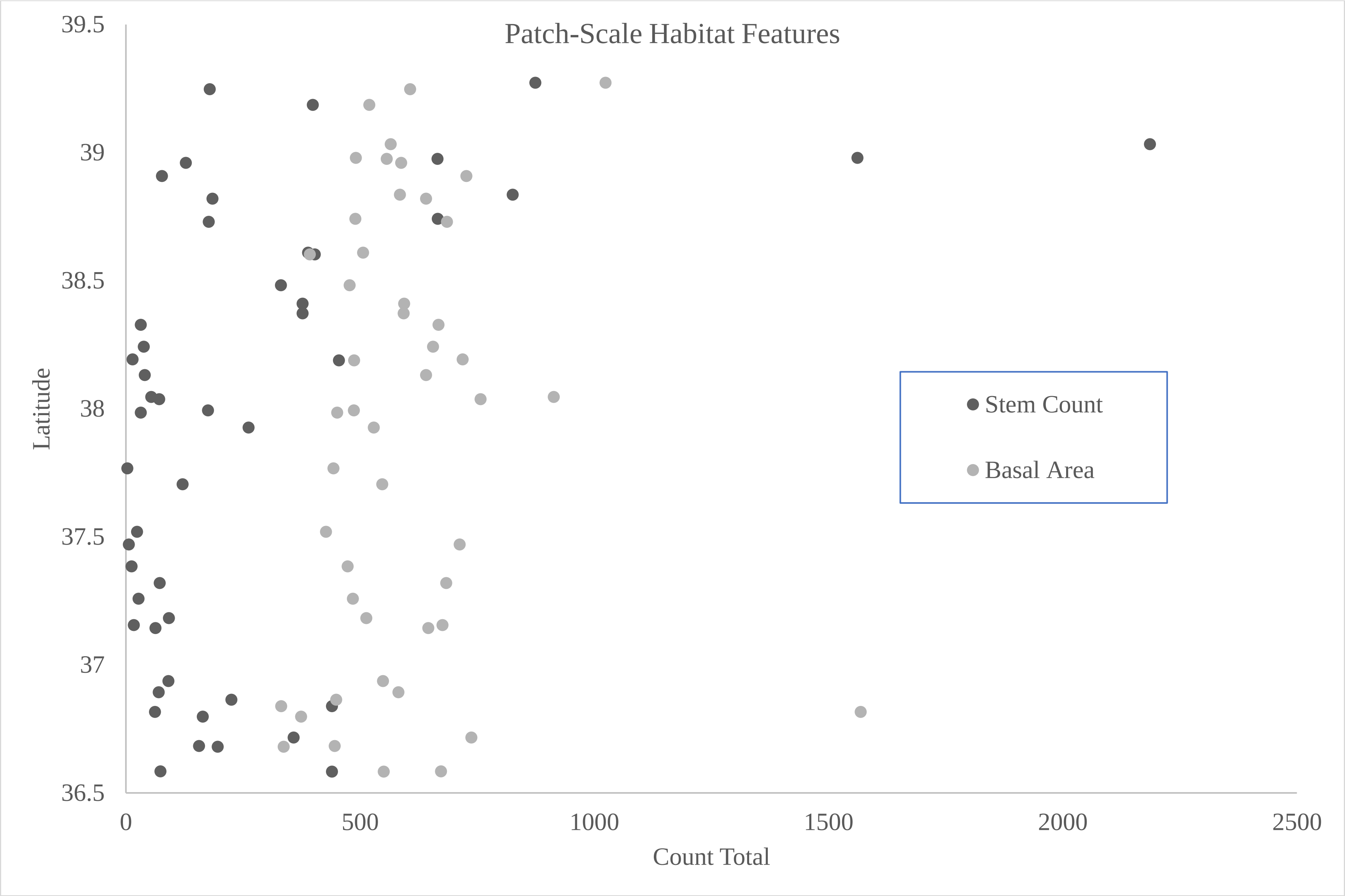


Fig. 21. Basal area and shrub density (via stem count) measurements for each survey site. Sites, denoted by individual dots, are presented in decreasing latitude (north to south).

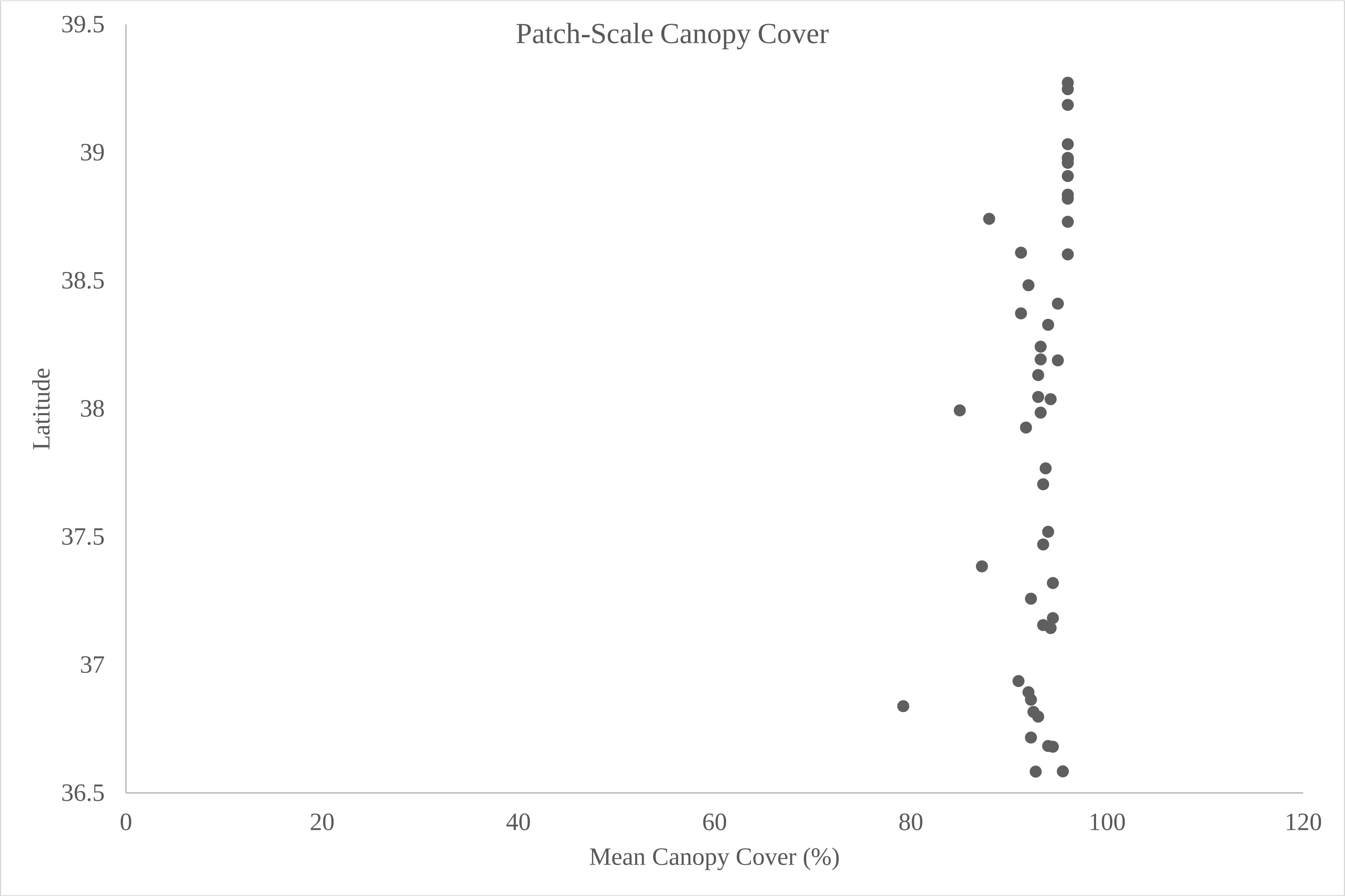


Fig. 22. Mean canopy cover (%) for each forested survey site. Sites, denoted by an individual dot, are presented in decreasing latitude (north to south).

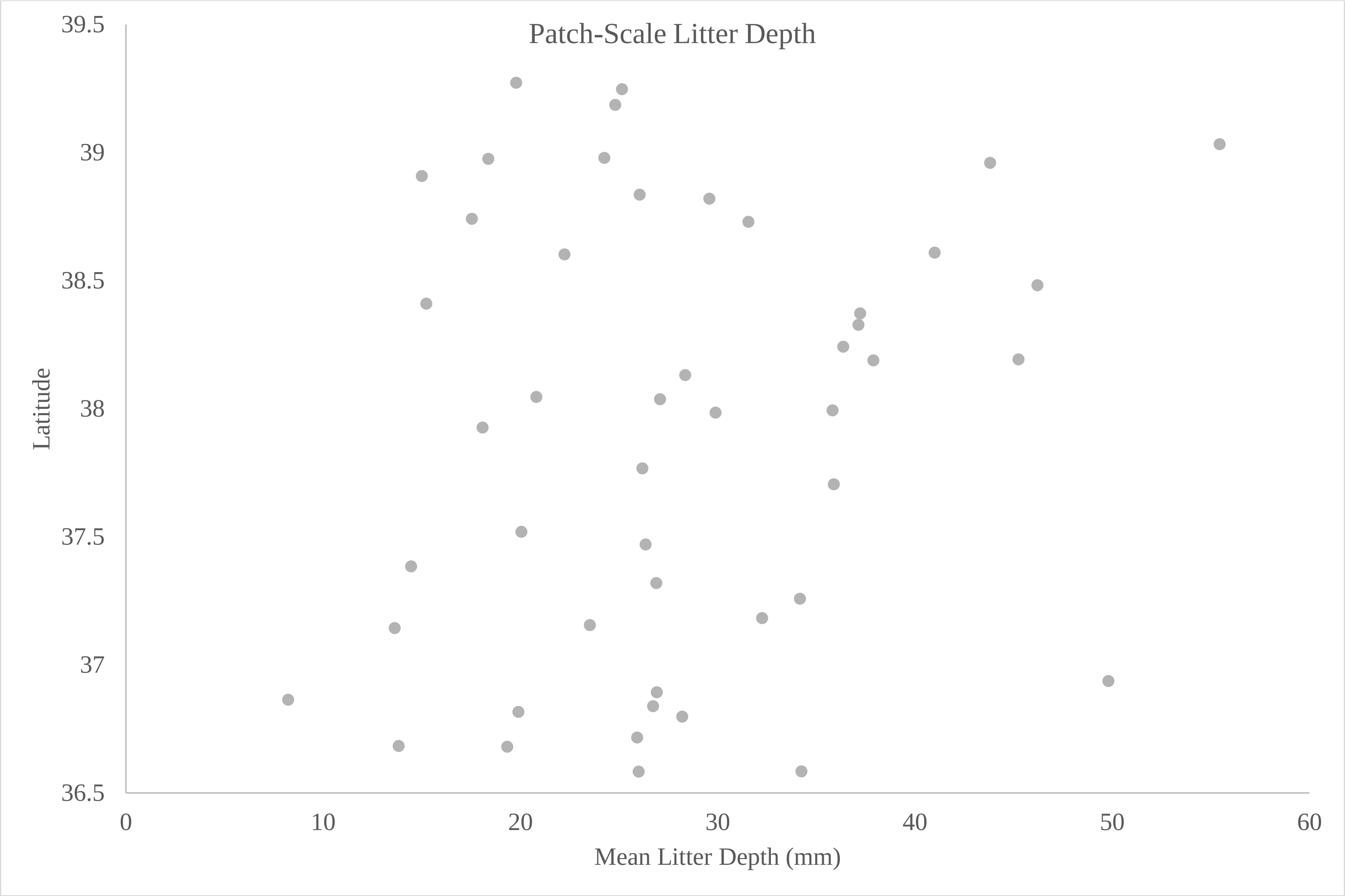


Fig. 23. Mean litter depth (mm) for each forested survey site. Sites, denoted by an individual dot, are presented in decreasing latitude (north to south).

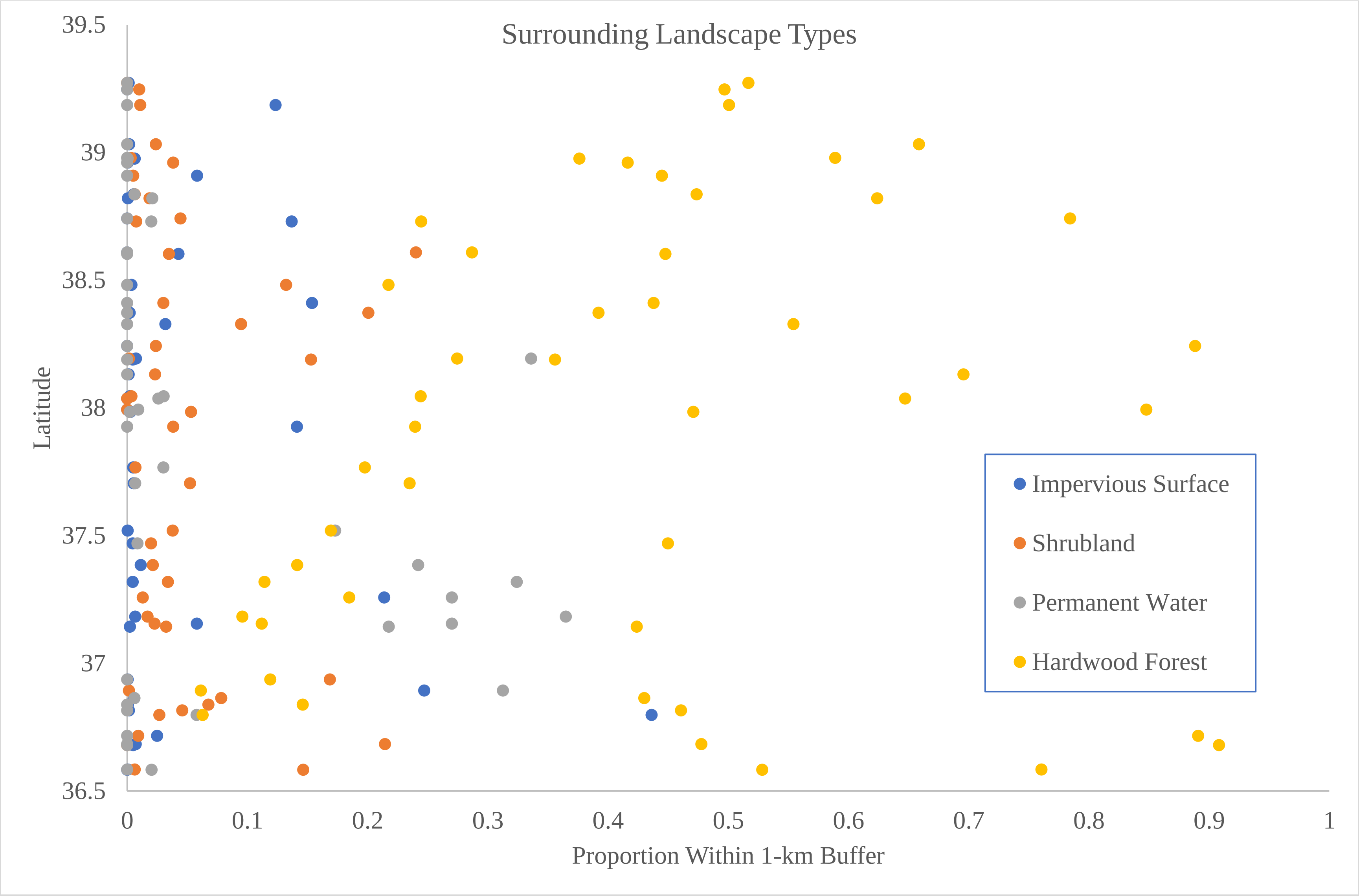


Fig. 24. Proportion of select landscape types surrounding each forested survey site within a 1-km radius. Sites, denoted by individual dots, are presented in decreasing latitude (north to south).

was relatively high at sites along Virginia’s Eastern Shore (up to 0.37 of total proportion). Although occasionally varying, proportions of impervious surface and scrub / shrubland within the surrounding 1-km landscape were also generally low among sites, averaging 0.04 and 0.05, respectively. Ground invertebrate detections exhibited a very slight decrease as the proportion of surrounding hardwood increased (Fig. 25). Branch invertebrate and ripe fruit detections, however, showed no noticeable influence from either surrounding hardwood or impervious surface (Figs. 26-27).

After omitting survey efforts with missing variable measurements, a finalized dataset containing 1,505 (772 in 2013, 733 in 2014) density-adjusted transect surveys and accompanying habitat and environmental metrics of interest, described above, was used in subsequent season-wide analyses. First, I explored the individual and interactive effects of 31 predictor variables, which collectively encompassed spatio-temporal and ecological data at the patch, landscape, and regional scales, and their influence on nocturnal migrant density (1 grouped migrant model set; 13 individual species’ model sets) using boosted regression tree techniques. See section 3.1 for detailed results. For these models, nocturnal migratory landbird use of hardwood-dominated forests located along the mid-Atlantic region was most strongly influenced by time of season (sampling period), exhibiting the greatest degree of influence on migrant densities for all season-wide models and species examined (Table 5).

To assess temporal changes on the influence of these predictor variables on nocturnal landbird migrant density across the autumn migratory season, I removed sampling period as a predictor variable and explored the individual and interactive effects of the remaining 30 predictor variables on nocturnal migrant density at different times during the migratory season. Period 1 (317 total surveys) and period 3 (398 total surveys) were used in period-specific

Table 5. Summary table for the relative contributions (%) of each predictor variable included in boosted regression tree models developed to identify which factors were most influential in determining migrant density, and includes modeling results for 13 individual species' analyses and one for all nocturnal migrants combined. Species and predictor variable codes defined in Table 1.

	Predictor	Response Variable (%)													
		AllMigPerHa	ACFL	AMRE	BTBW	GCFL	GCKI	GRCA	HETH	NOPA	OVEN	REVI	YBCU	YRWA	YSFL
Patch / Food Resources	InvBrAR	**6.42**	**6.20**	**6.56**	4.81	**8.47**	3.24	**7.29**	3.04	**8.10**	**12.99**	3.65	**6.15**	**8.74**	4.65
	InvVisAR	3.74	1.69	3.22	4.61	1.86	2.68	1.87	3.87	1.35	1.57	1.03	4.01	2.87	3.98
	InvBrLep	3.17	2.12	2.87	**9.22**	4.44	0.43	1.03	1.03	**5.82**	**6.50**	1.09	2.54	0.58	2.23
	InvVisLep	0.04	0.09	0.05	0.00	0.14	0.00	0.00	0.00	0.00	0.03	0.04	0.52	0.00	0.00
	InvBrDI	4.06	3.97	2.55	2.76	3.20	0.94	3.01	2.90	2.54	2.57	2.23	2.99	2.93	1.64
	InvVisDI	2.84	2.15	2.78	2.50	4.30	0.89	2.29	0.79	3.83	3.75	0.88	**5.41**	1.38	1.35
	InvBrOR	2.14	0.51	0.65	0.32	1.60	0.01	0.27	0.00	3.17	3.52	0.76	4.72	0.01	0.19
	InvVisOR	0.99	1.12	0.94	0.55	1.18	0.04	3.87	0.01	1.59	0.60	0.85	1.26	0.13	0.33
	FrtBGum	1.96	0.66	0.40	0.55	1.85	0.44	0.17	0.39	1.19	4.14	0.51	0.09	0.92	**7.02**
	FrtHolly	3.10	0.72	3.10	1.75	0.21	3.31	2.16	**14.18**	1.95	4.02	0.83	1.18	4.18	3.36
	FrtBlueB	0.37	1.12	0.00	0.00	0.70	0.00	0.00	0.00	0.23	0.54	0.73	0.00	0.00	0.04
	FrtDogw	0.38	0.17	0.12	0.00	0.00	0.02	0.01	0.00	1.77	0.01	0.00	0.00	0.00	0.11
	FrtGrape	3.08	0.21	**7.85**	4.52	0.14	0.31	**11.82**	0.05	1.03	4.83	0.50	0.68	0.96	2.42
	FrtParB	1.38	1.11	0.53	1.95	0.59	0.77	1.13	0.92	1.70	1.03	0.64	1.69	0.87	2.11
	FrtSmilax	2.18	0.04	3.16	2.09	0.08	1.38	3.47	2.44	4.16	0.23	0.31	0.29	3.24	2.87
Patch / Habitat Features	CanopyC	1.30	0.49	3.90	2.88	4.31	0.75	0.36	1.04	1.18	0.99	1.49	3.13	1.72	1.03
	LitterDep	2.27	**5.98**	4.65	2.22	1.84	1.25	2.18	1.60	**10.11**	3.83	0.89	4.07	1.19	**5.87**
	CtGrLeaf	0.80	2.28	1.32	0.36	0.35	0.87	0.33	0.20	2.02	1.38	0.41	0.37	0.72	1.33
	CtGrVeg	3.16	3.33	2.41	1.85	2.66	2.35	**5.81**	0.72	2.85	2.91	1.02	3.00	1.00	1.81
	CtVine	1.96	1.28	1.82	0.87	0.51	0.70	4.02	1.59	1.03	1.06	1.19	0.80	0.67	1.09
	CtGrShrub	**6.96**	4.42	2.47	**6.85**	2.37	0.91	0.71	4.22	1.49	**6.43**	**9.38**	1.71	1.29	2.71
	ShrubStemCt	2.14	3.52	2.73	1.74	**9.57**	1.03	0.75	3.43	2.40	3.72	2.87	**8.73**	**6.01**	1.40

Table 5. Continued.

	Predictor	Response Variable (%)													
		AllMigPerHa	ACFL	AMRE	BTBW	GCFL	GCKI	GRCA	HETH	NOPA	OVEN	REVI	YBCU	YRWA	YSFL
Patch / Habitat Features	basalarea	1.98	3.39	3.03	1.44	2.56	2.81	1.41	2.47	2.50	2.28	1.07	0.97	1.51	3.24
Landscape	impurban1km	3.80	**5.77**	4.01	**6.65**	1.66	1.28	**7.11**	1.59	2.26	1.07	2.23	4.22	0.99	0.98
	water1km	2.69	1.09	**10.35**	4.59	0.69	0.51	**13.23**	1.15	**6.41**	1.98	1.05	2.18	1.24	2.87
	hrdwood1km	**10.61**	**9.14**	1.64	1.45	**5.87**	1.02	3.81	0.99	2.31	1.24	2.45	**5.55**	1.32	1.41
	shrub1km	4.10	3.81	2.22	1.90	3.99	0.78	0.92	4.77	2.40	2.31	0.85	2.30	1.91	1.75
Regional	Latitude	4.13	**5.41**	1.74	4.67	4.46	3.12	2.75	1.87	3.54	3.26	**18.33**	**7.19**	2.89	2.52
	distatl	2.91	1.80	3.15	3.15	1.66	1.37	1.84	3.09	3.74	3.50	3.60	2.37	**6.63**	2.59
Temporal	Year	1.71	0.73	1.19	4.24	1.16	0.69	1.14	2.08	0.64	1.14	0.72	0.72	1.00	0.72
	Period	**13.48**	**25.52**	**18.45**	**19.33**	**27.41**	**65.98**	**15.12**	**39.43**	**16.55**	**16.42**	**38.24**	**21.00**	**42.97**	**36.24**

Note: All numbers in bold represent variables whose contributions accounted for at least 5% of the respective model's total, and were considered the most influential predictor variables for determining migrant density.

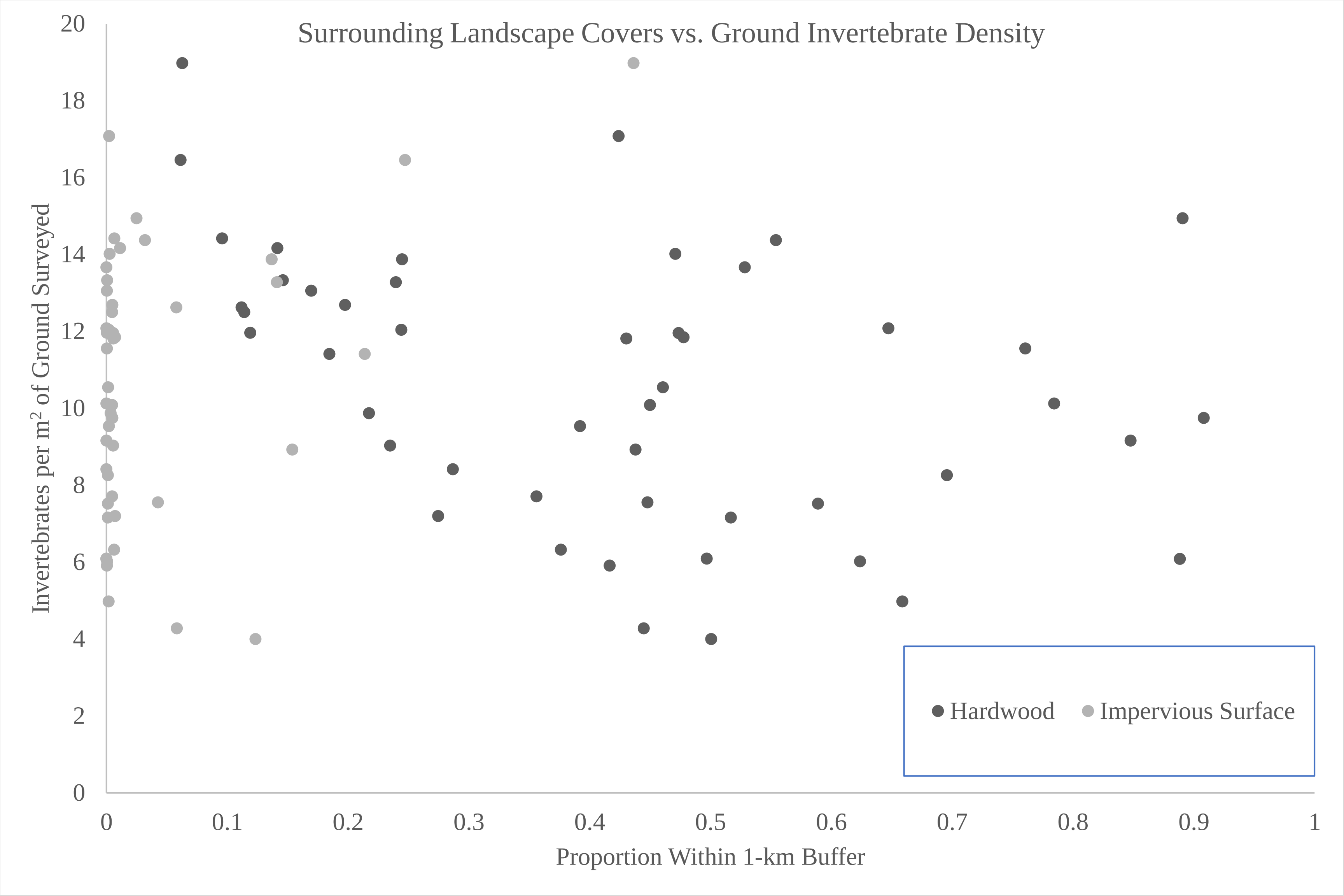


Fig. 25. Proportion of select land cover types within 1-km radius in relation to mean ground invertebrate density (averaged across both sampling years) for each forested survey site. Sites, denoted by individual dots, are presented in decreasing latitude (north to south).

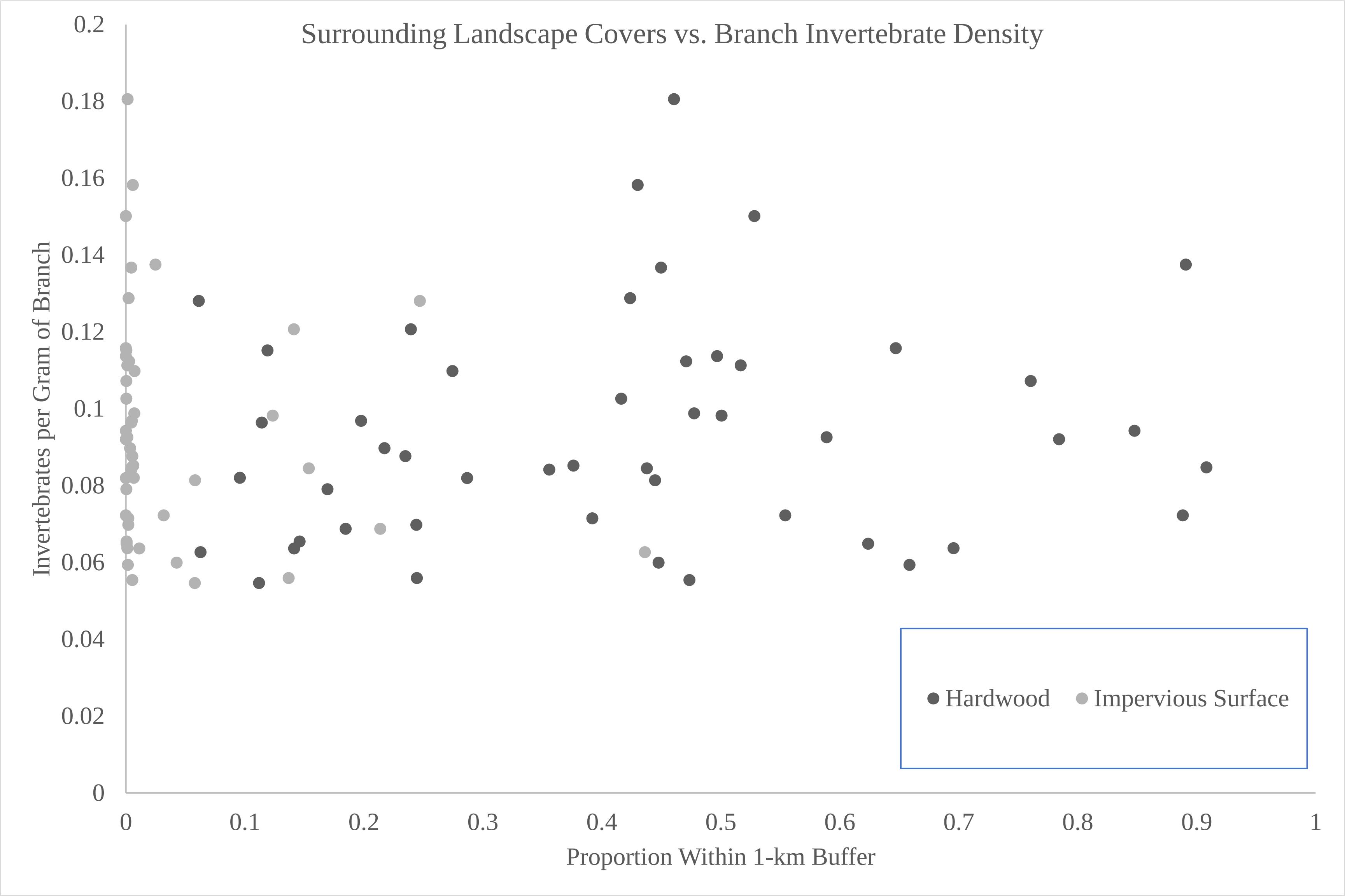


Fig. 26. Proportion of select land cover types within 1-km radius in relation to mean branch invertebrate density (averaged across both sampling years) for each forested survey site. Sites, denoted by individual dots, are presented in decreasing latitude (north to south).

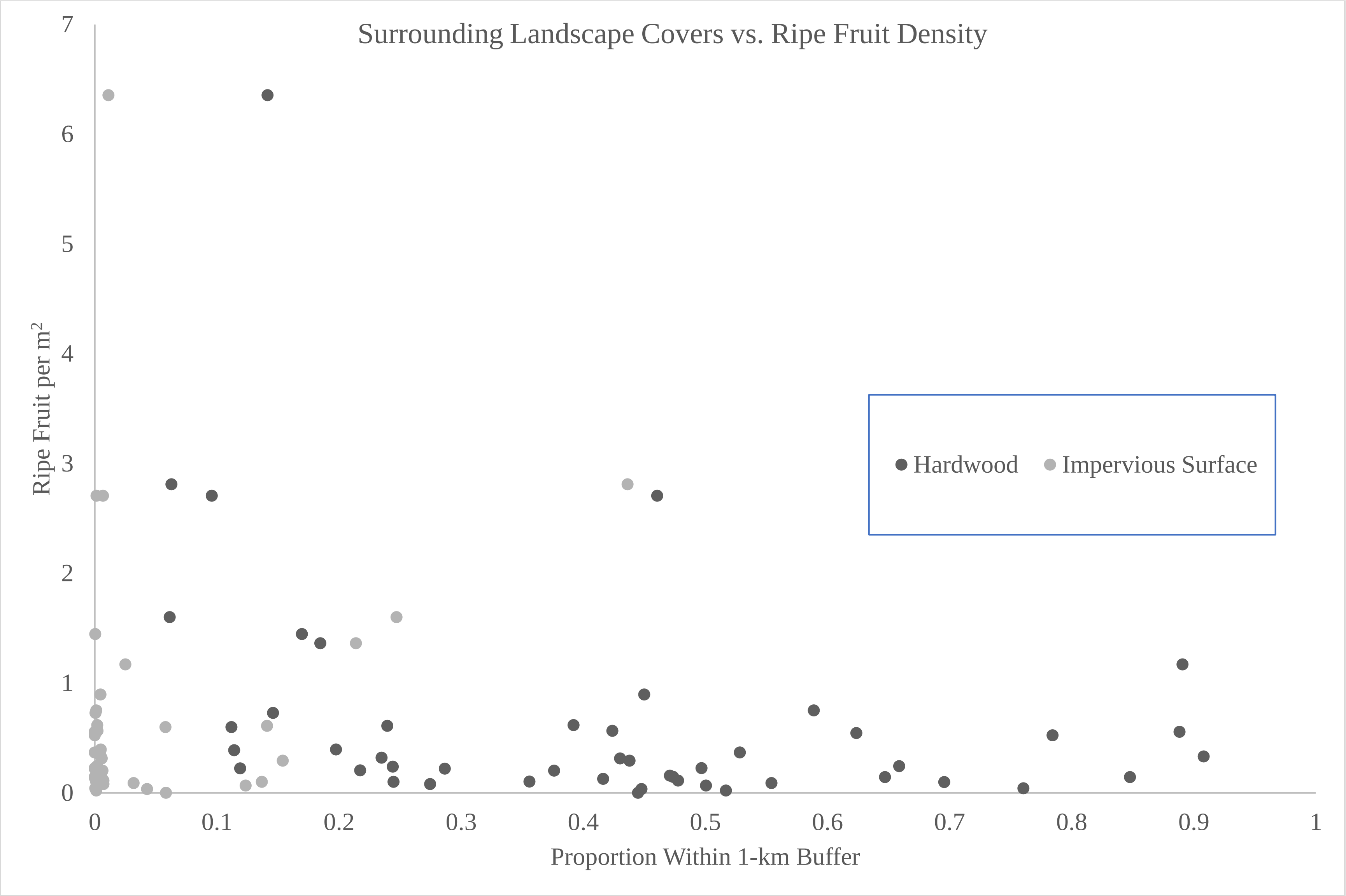


Fig. 27. Proportion of select land cover types within 1-km radius in relation to mean ripe fruit density (averaged across both sampling years) for each forested survey. Sites, denoted by individual dots, are presented in decreasing latitude (north to south).

analyses utilizing the same boosted regression tree techniques. See section 3.2 for detailed results.

3.1 Season-wide Analyses

Fourteen models of migrant density were developed, with one that included all nocturnal landbird migrants and 13 based on individual nocturnal migratory species. Adjustment of model parameters resulted in use of learning rates ranging from 0.0075 down to 0.001, and number of trees in each final optimized model ranging from 800 to 1,600 (Table 3). Out of the 31 total predictor variables that were included in each BRT model, 16 variables (added across all models) showed a relative contribution of 5% or greater, an arbitrary cutoff for signifying strongly influential predictor variables at explaining density (Table 5). Model fits were low to moderate based on proportion of deviance explained (0.08 to 0.67) and cross-validated correlation (0.10 to .75).

Sampling period was by far the most influential predictor of migrant density for all final season-wide optimized models (Figs. 28-41). Sampling period also showed strong interactions with other variables in each model (Tables 6-19), however, it should be noted that these observed interactions with "period" may be reflecting a relationship change with predictors when the migratory species of interest was generally absent.

At the patch-scale, both food resources as well as habitat characteristics showed strong influence in predicting migrant densities (Table 5). Arachnids per g of branch was the most influential food variable for explaining migrant density across the nocturnal migrant grouped model and eight individual species' models. All these models, apart from Northern Parula (*Setophaga americana*, see Fig. 36), showed a negative relationship between branch Arachnid

Table 6. Ranked interaction sizes for the ten most influential predictor variable interactions for the BRT analysis of all nocturnal migrant density. See Table 1 for predictor variable descriptions.

Rank	Variable 1	Variable 2	Interaction Size
1	hrdwood1km	Period	2.47
2	CtGrShrub	FrtGrape	2.24
3	CtGrShrub	Period	0.77
4	distatl	InvBrLep	0.76
5	CtGrVeg	Year	0.58
6	hrdwood1km	InvBrAR	0.36
7	InvVisOR	InvBrOR	0.36
8	Latitude	FrtSmilax	0.34
9	distatl	Period	0.33
10	impurban1km	Period	0.31

Note: Interactions presented that include the variable “Period” likely reflect changes in the relationships with predictors when nocturnal migratory landbirds were generally absent.

Table 7. Ranked interaction sizes for the ten most influential predictor variable interactions for the Acadian Flycatcher BRT analysis. See Table 1 for predictor variable descriptions.

Rank	Variable 1	Variable 2	Interaction Size
1	hrdwood1km	Period	7.95
2	LitterDep	Period	5.89
3	CtGrShrub	Period	3.63
4	basalarea	Period	2.72
5	ShrubStemCt	Period	0.93
6	Latitude	Period	0.89
7	impurban1km	Period	0.77
8	Latitude	InvBrAR	0.48
9	CtGrVeg	Period	0.35
10	shrub1km	Period	0.29

Note: Interactions presented that include the variable “Period” likely reflect changes in the relationships with predictors when Acadian Flycatchers were generally absent.

Table 8. Ranked interaction sizes for the ten most influential predictor variable interactions for the American Redstart BRT analysis. See Table 1 for predictor variable descriptions.

Rank	Variable 1	Variable 2	Interaction Size
1	water1km	Period	1.99
2	water1km	CanopyC	0.87
3	CanopyC	Period	0.76
4	FrtSmilax	Period	0.57
5	LitterDep	Period	0.40
6	InvBrAR	Period	0.28
7	water1km	LitterDep	0.26
8	InvBrDI	Period	0.24
9	impurban1km	Period	0.20
10	FrtSmilax	InvVisDI	0.16

Note: Interactions presented that include the variable “Period” likely reflect changes in the relationships with predictors when American Redstarts were generally absent.

Table 9. Ranked interaction sizes for the ten most influential predictor variable interactions for the Black-throated Blue Warbler BRT analysis. See Table 1 for predictor variable descriptions.

Rank	Variable 1	Variable 2	Interaction Size
1	Latitude	InvBrLep	1.50
2	Period	Year	1.32
3	CtGrShrub	Period	1.22
4	CtGrShrub	InvBrLep	0.87
5	FrtGrape	Period	0.34
6	water1km	Period	0.21
7	impurban1km	CtGrShrub	0.21
8	water1km	InvVisAR	0.20
9	InvVisAR	Period	0.17
10	CtGrShrub	FrtGrape	0.16

Note: Interactions presented that include the variable “Period” likely reflect changes in the relationships with predictors when Black-throated Blue Warblers were generally absent.

Table 10. Ranked interaction sizes for the ten most influential predictor variable interactions for the Great Crested Flycatcher BRT analysis. See Table 1 for predictor variable descriptions.

Rank	Variable 1	Variable 2	Interaction Size
1	ShrubStemCt	Period	0.97
2	hrdwood1km	Period	0.23
3	basalarea	Period	0.09
4	CtGrVeg	Period	0.09
5	FrtBGum	Period	0.09
6	InvBrDI	Period	0.09
7	InvBrLep	Period	0.06
8	Latitude	Period	0.05
9	CanopyC	Period	0.04
10	shrub1km	Period	0.03

Note: Interactions presented that include the variable "Period" likely reflect changes in the relationships with predictors when Great Crested Flycatchers were generally absent.

Table 11. Ranked interaction sizes for the ten most influential predictor variable interactions for the Golden-crowned Kinglet BRT analysis. See Table 1 for predictor variable descriptions.

Rank	Variable 1	Variable 2	Interaction Size
1	CtGrVeg	Period	3.08
2	Latitude	Period	2.68
3	basalarea	Period	1.63
4	InvVisAR	Period	1.10
5	FrtParB	Period	0.94
6	CtGrLeaf	Period	0.60
7	InvVisDI	Period	0.58
8	InvBrAR	Period	0.58
9	distatl	Period	0.52
10	LitterDep	Period	0.44

Note: Interactions presented that include the variable "Period" likely reflect changes in the relationships with predictors when Golden-crowned Kinglets were generally absent.

Table 12. Ranked interaction sizes for the ten most influential predictor variable interactions for the Gray Catbird BRT analysis. See Table 1 for predictor variable descriptions.

Rank	Variable 1	Variable 2	Interaction Size
1	FrtGrape	Period	1.54
2	water1km	Period	1.11
3	impurban1km	InvVisOR	1.06
4	impurban1km	InvBrAR	1.03
5	water1km	CtGrVeg	0.98
6	CtGrVeg	Period	0.84
7	CtVine	Period	0.62
8	LitterDep	FrtGrape	0.57
9	impurban1km	Period	0.33
10	water1km	FrtGrape	0.18

Note: Interactions presented that include the variable “Period” likely reflect changes in the relationships with predictors when Gray Catbirds were generally absent.

Table 13. Ranked interaction sizes for the ten most influential predictor variable interactions for the Hermit Thrush BRT analysis. See Table 1 for predictor variable descriptions.

Rank	Variable 1	Variable 2	Interaction Size
1	FrtHolly	Period	7.96
2	shrub1km	Period	1.26
3	Period	Year	0.64
4	InvVisAR	Period	0.63
5	CtGrShrub	Period	0.58
6	FrtSmilax	Period	0.41
7	InvBrDI	Period	0.40
8	InvBrLep	Period	0.28
9	distatl	Period	0.23
10	Latitude	FrtHolly	0.16

Note: Interactions presented that include the variable “Period” likely reflect changes in the relationships with predictors when Hermit Thrush were generally absent.

Table 14. Ranked interaction sizes for the ten most influential predictor variable interactions for the Northern Parula BRT analysis. See Table 1 for predictor variable descriptions.

Rank	Variable 1	Variable 2	Interaction Size
1	LitterDep	Period	0.25
2	InvBrLep	Period	0.09
3	FrtSmilax	Period	0.04
4	water1km	Period	0.02
5	InvBrAR	Period	0.02
6	impurban1km	InvVisOR	0.01
7	distatl	Period	0.01
8	ShrubStemCt	Period	0.01
9	CtGrVeg	Period	0.01
10	LitterDep	InvBrLep	0.01

Note: Interactions presented that include the variable "Period" likely reflect changes in the relationships with predictors when Northern Parula were generally absent.

Table 15. Ranked interaction sizes for the ten most influential predictor variable interactions for the Ovenbird BRT analysis. See Table 1 for predictor variable descriptions.

Rank	Variable 1	Variable 2	Interaction Size
1	FrtHolly	Period	0.10
2	FrtBGum	Period	0.07
3	InvBrLep	InvBrAR	0.04
4	distatl	InvBrOR	0.01
5	CtGrShrub	InvBrOR	0.01
6	CtGrShrub	InvBrLep	0.01
7	CtGrShrub	Period	0.01
8	LitterDep	InvBrAR	0.01
9	InvBrLep	Period	0.01
10	InvBrAR	Period	0.01

Note: Interactions presented that include the variable "Period" likely reflect changes in the relationships with predictors when Ovenbirds were generally absent.

Table 16. Ranked interaction sizes for the ten most influential predictor variable interactions for the Red-eyed Vireo BRT analysis. See Table 1 for predictor variable descriptions.

Rank	Variable 1	Variable 2	Interaction Size
1	Latitude	Period	17.92
2	CtGrShrub	Period	6.99
3	distatl	Period	1.44
4	ShrubStemCt	Period	0.89
5	InvBrDI	Period	0.52
6	CtVine	Period	0.36
7	FrtBGum	Period	0.35
8	FrtParB	Period	0.14
1	Latitude	Period	17.92
2	CtGrShrub	Period	6.99

Note: Interactions presented that include the variable “Period” likely reflect changes in the relationships with predictors when Red-eyed Vireos were generally absent.

Table 17. Ranked interaction sizes for the ten most influential predictor variable interactions for the Yellow-billed Cuckoo BRT analysis. See Table 1 for predictor variable descriptions.

Rank	Variable 1	Variable 2	Interaction Size
1	hrdwood1km	Period	0.18
2	ShrubStemCt	Period	0.15
3	CanopyC	Period	0.14
4	CtGrVeg	Period	0.08
5	InvVisDI	Period	0.08
6	LitterDep	Period	0.06
7	Latitude	Period	0.04
8	impurban1km	Period	0.03
9	water1km	Period	0.02
10	InvBrOR	Period	0.02

Note: Interactions presented that include the variable “Period” likely reflect changes in the relationships with predictors when Yellow-billed Cuckoos were generally absent.

Table 18. Ranked interaction sizes for the ten most influential predictor variable interactions for the Yellow-rumped Warbler BRT analysis. See Table 1 for predictor variable descriptions.

Rank	Variable 1	Variable 2	Interaction Size
1	InvBrAR	Period	22.28
2	distatl	Period	4.96
3	ShrubStemCt	Period	3.11
4	InvVisAR	Period	2.09
5	InvBrDI	Period	0.97
6	FrtBGum	Period	0.75
7	FrtSmilax	Period	0.74
8	Latitude	Period	0.73
9	FrtHolly	Period	0.64
10	hrdwood1km	Period	0.56

Note: Interactions presented that include the variable "Period" likely reflect changes in the relationships with predictors when Yellow-rumped Warblers were generally absent.

Table 19. Ranked interaction sizes for the ten most influential predictor variable interactions for the (Yellow-shafted) Northern Flicker BRT analysis. See Table 1 for predictor variable descriptions.

Rank	Variable 1	Variable 2	Interaction Size
1	FrtBGum	Period	2.98
2	LitterDep	Period	2.22
3	CtGrLeaf	Period	0.78
4	FrtGrape	Period	0.56
5	InvVisAR	Period	0.56
6	basalarea	Period	0.46
7	water1km	Period	0.43
8	CtGrShrub	Period	0.36
9	InvBrAR	Period	0.28
10	FrtSmilax	InvVisAR	0.25

Note: Interactions presented that include the variable "Period" likely reflect changes in the relationships with predictors when Northern Flickers were generally absent.

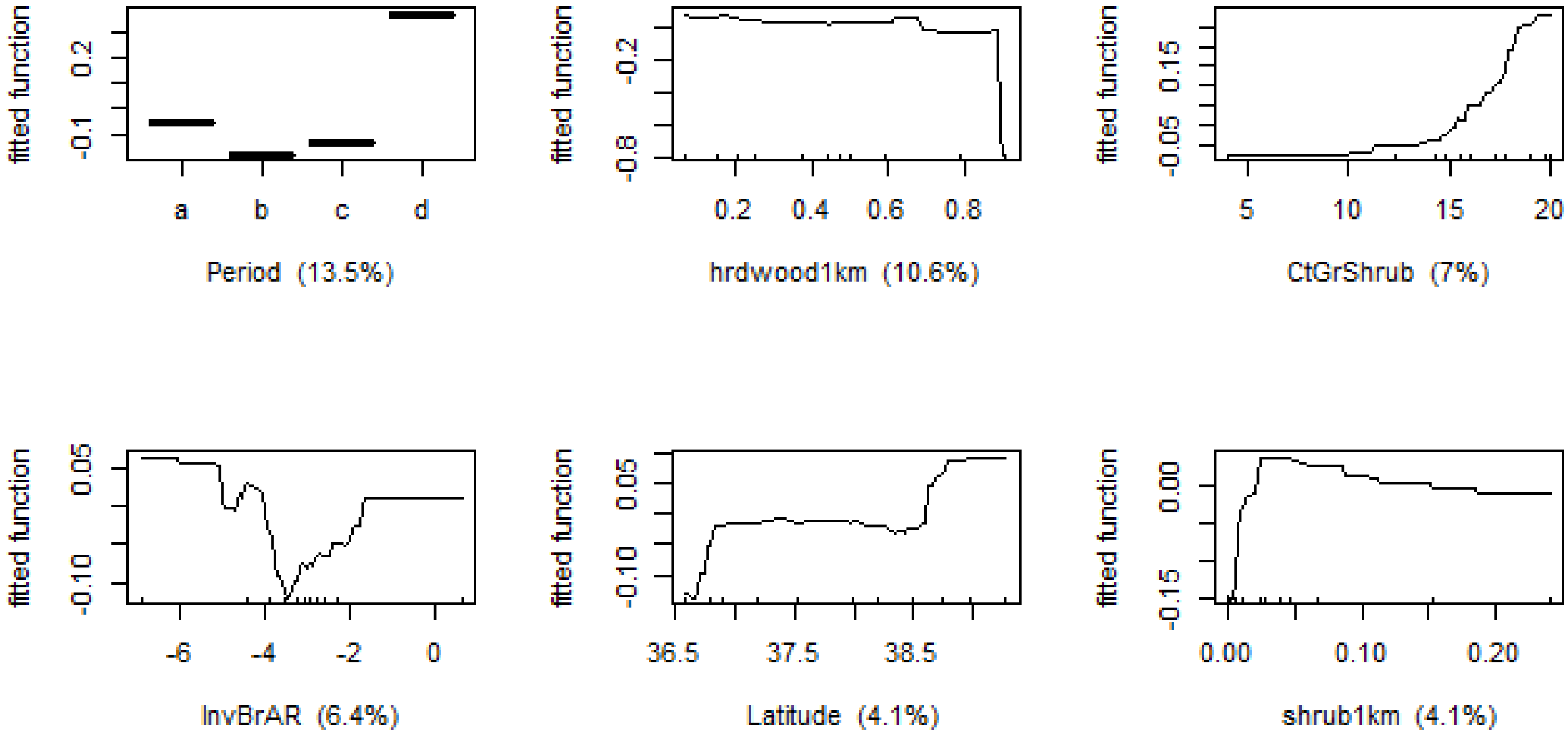


Fig. 28. Partial dependence plots for the six most influential variables that predict migrant density for all nocturnal landbird species included in the analysis. Rug plots located at the bottom of plots show the distribution of data, in deciles, for the *X*-axis variable. Relative influence is in parentheses. See Table 1 for predictor variable descriptions.

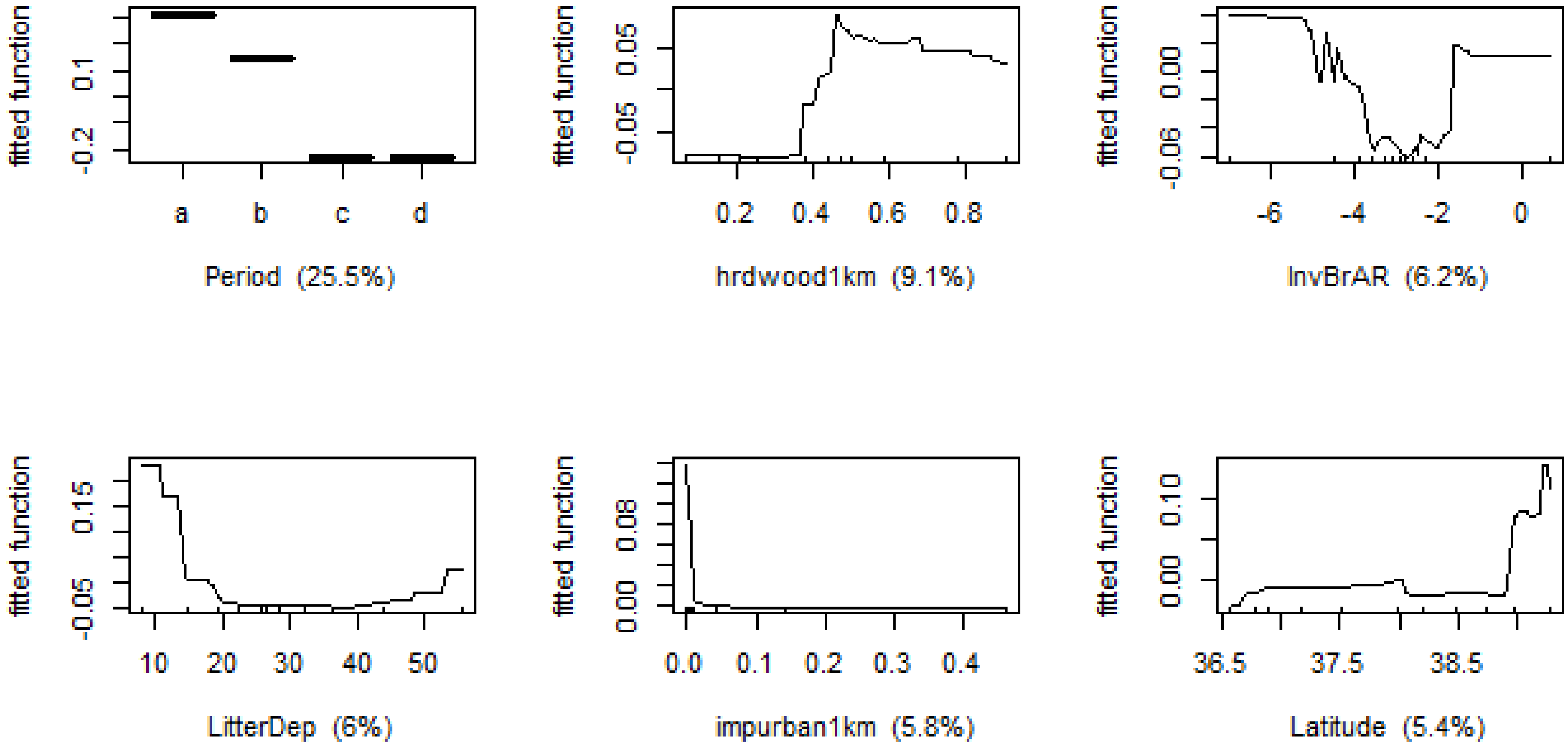


Fig. 29. Partial dependence plots for the six most influential variables that predict Acadian Flycatcher density. Rug plots located at the bottom of plots show the distribution of data, in deciles, for the *X*-axis variable. Relative influence is in parentheses. See Table 1 for predictor variable descriptions.

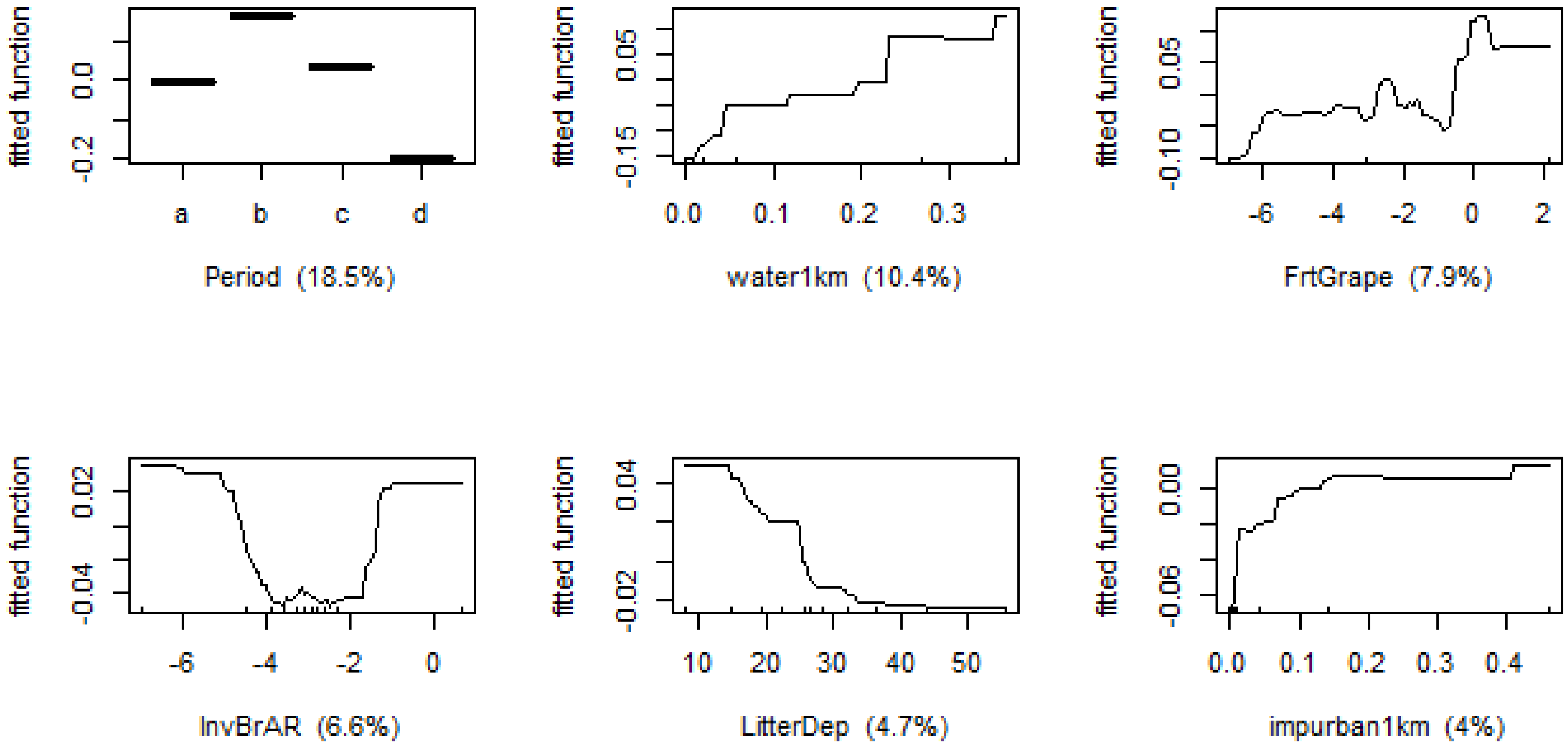


Fig. 30. Partial dependence plots for the six most influential variables that predict American Redstart density. Rug plots located at the bottom of plots show the distribution of data, in deciles, for the *X*-axis variable. Relative influence is in parentheses. See Table 1 for predictor variable descriptions.

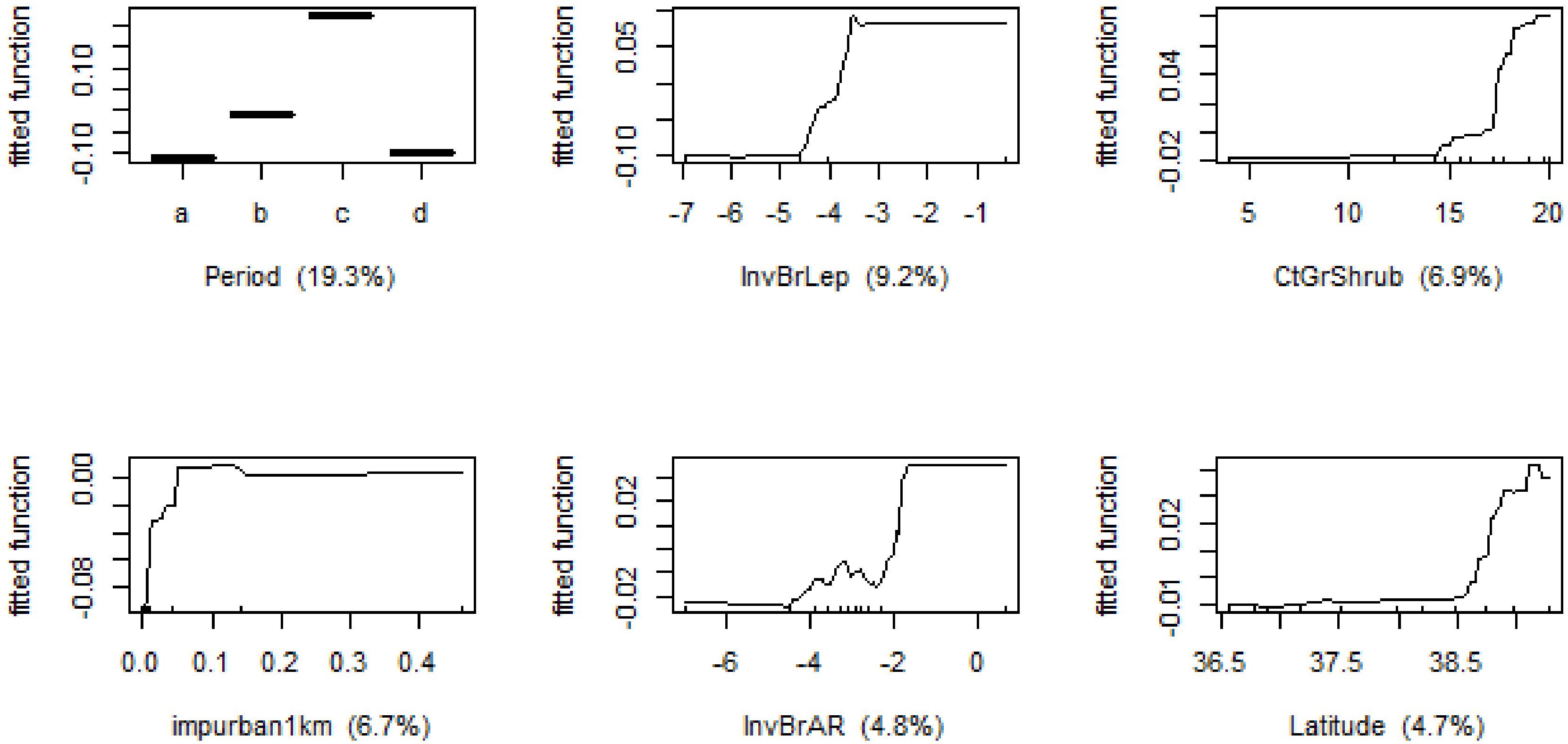


Fig. 31. Partial dependence plots for the six most influential variables that predict Black-throated Blue Warbler density. Rug plots located at the bottom of plots show the distribution of data, in deciles, for the *X*-axis variable. Relative influence is in parentheses. See Table 1 for predictor variable descriptions.

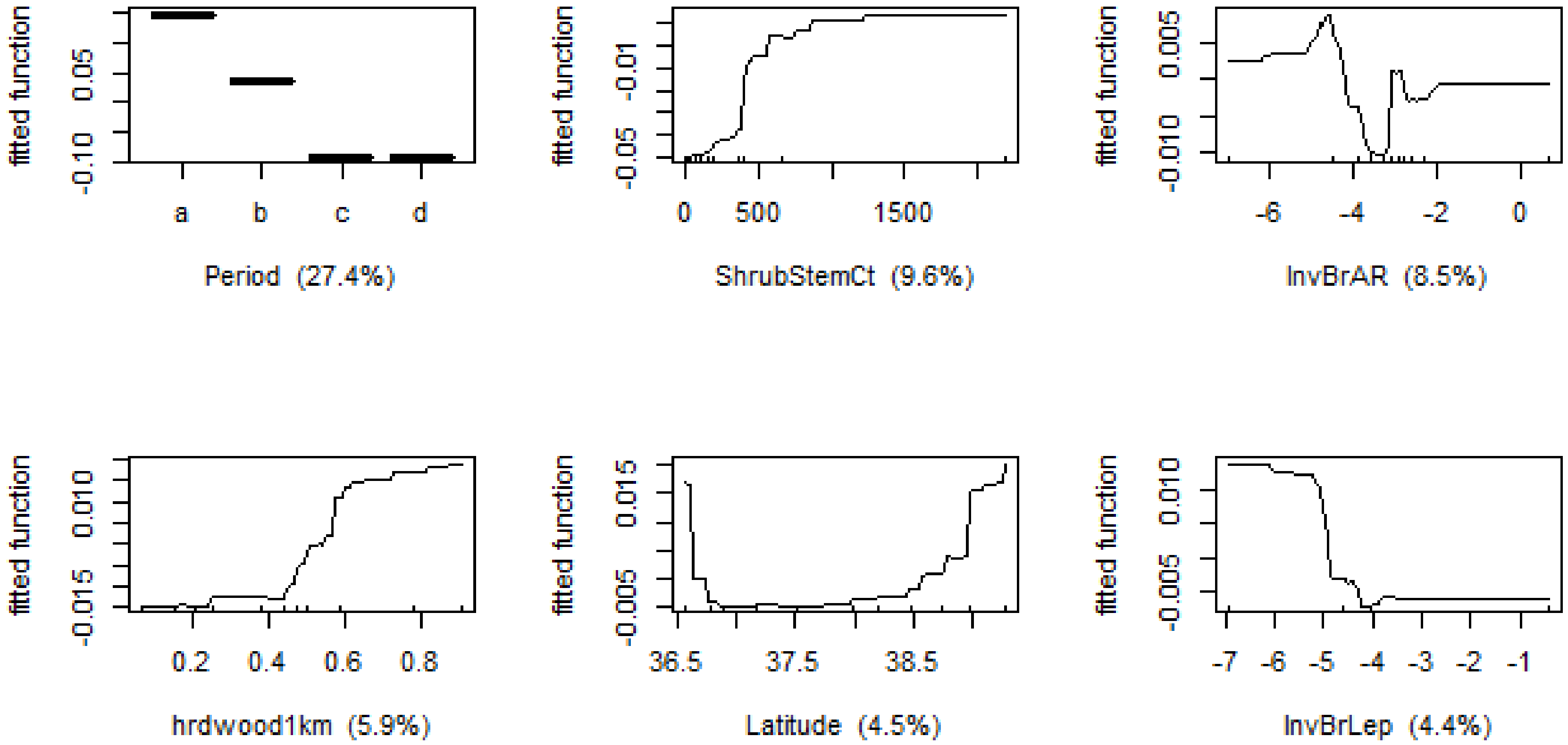


Fig. 32. Partial dependence plots for the six most influential variables that predict Great Crested Flycatcher density. Rug plots located at the bottom of plots show the distribution of data, in deciles, for the *X*-axis variable. Relative influence is in parentheses. See Table 1 for predictor variable descriptions.

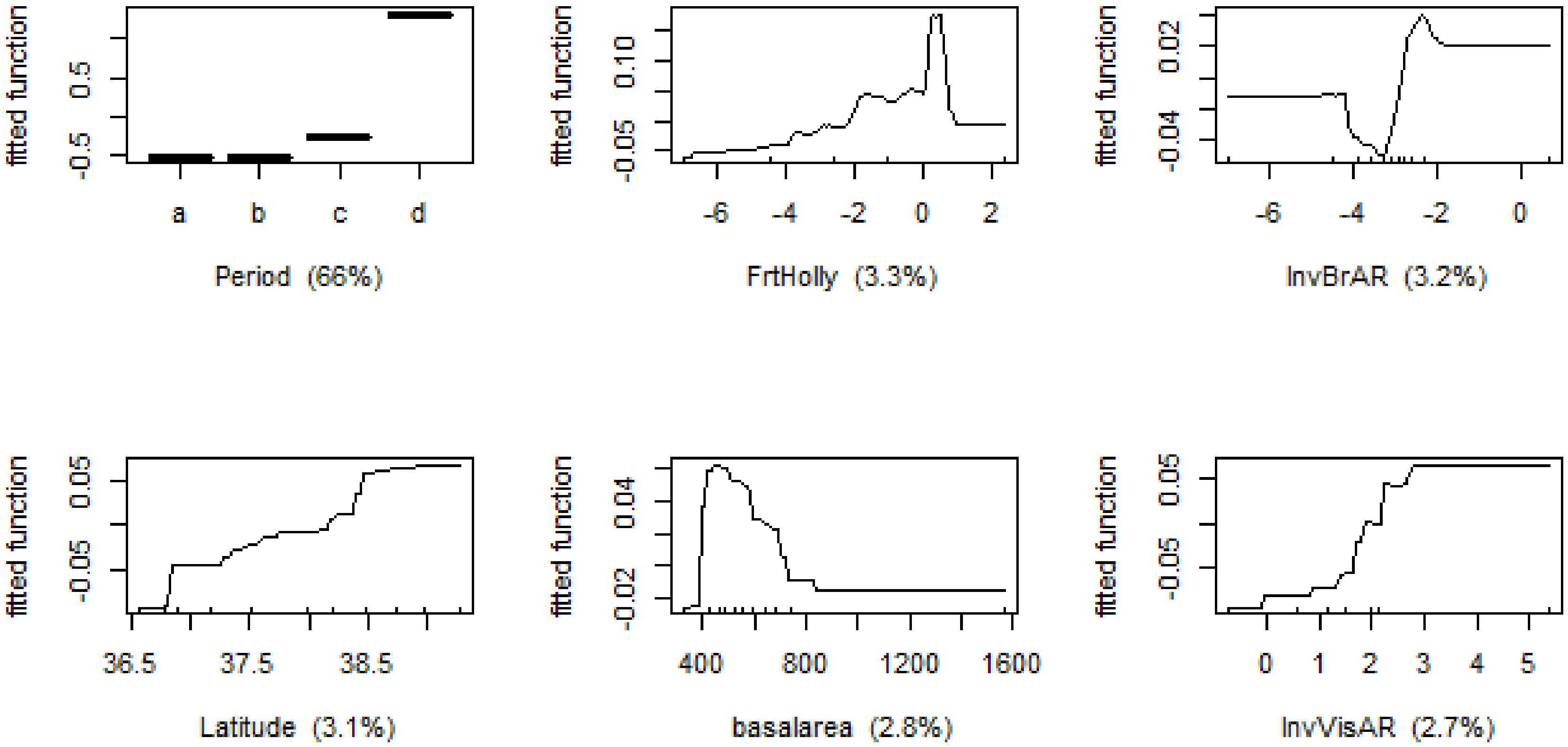


Fig. 33. Partial dependence plots for the six most influential variables that predict Golden-crowned Kinglet density. Rug plots located at the bottom of plots show the distribution of data, in deciles, for the *X*-axis variable. Relative influence is in parentheses. See Table 1 for predictor variable descriptions.

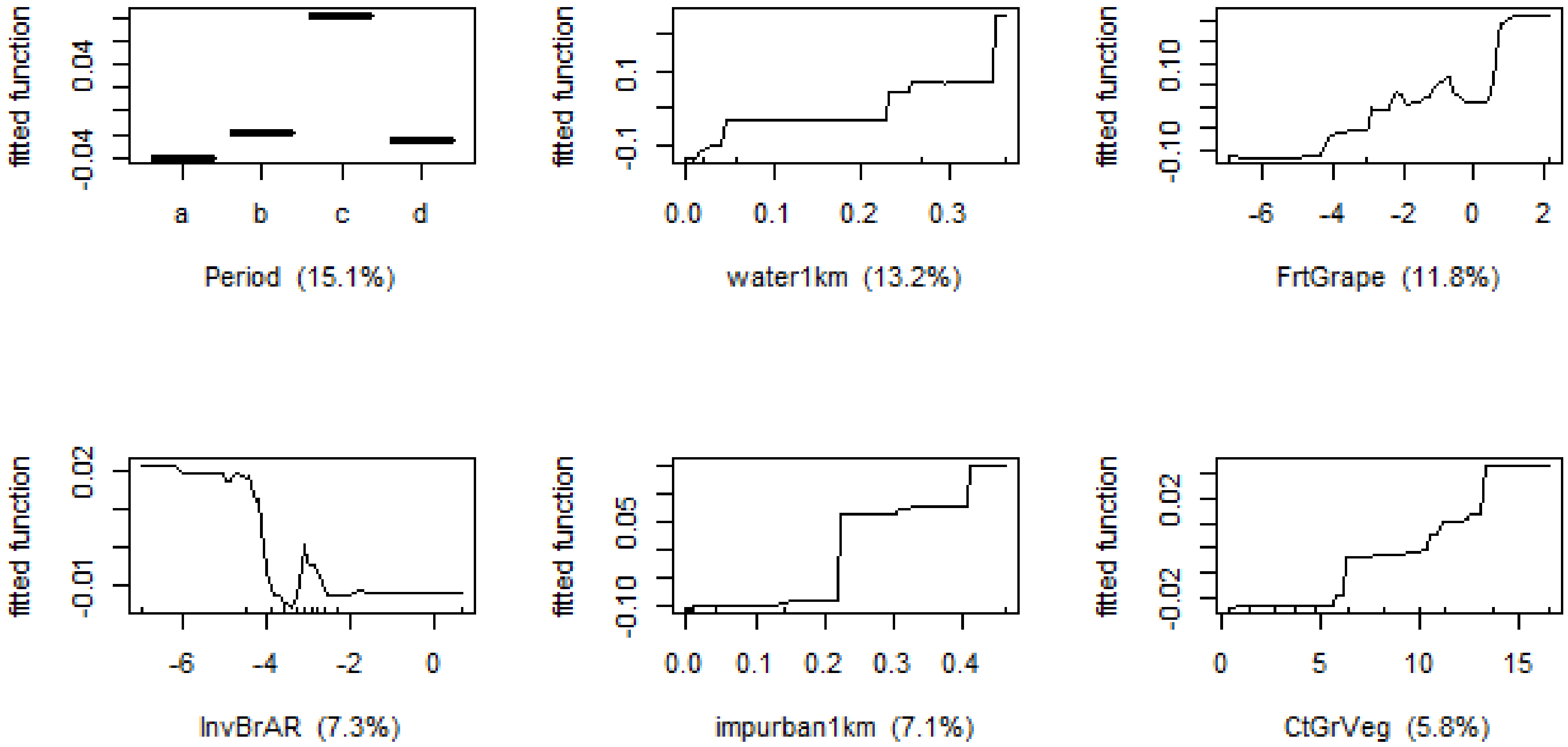


Fig. 34. Partial dependence plots for the six most influential variables that predict Gray Catbird density. Rug plots located at the bottom of plots show the distribution of data, in deciles, for the *X*-axis variable. Relative influence is in parentheses. See Table 1 for predictor variable descriptions.

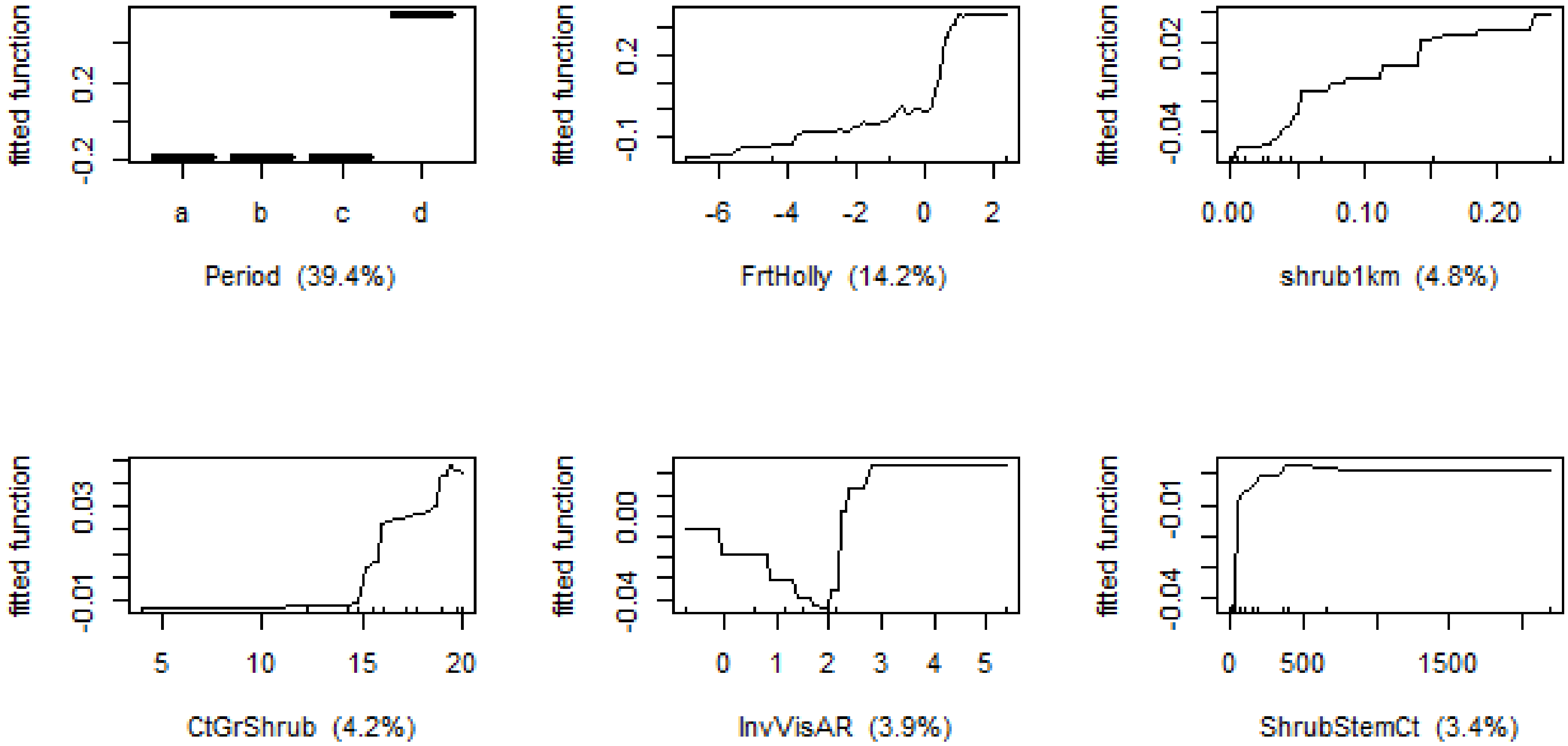


Fig. 35. Partial dependence plots for the six most influential variables that predict Hermit Thrush density. Rug plots located at the bottom of plots show the distribution of data, in deciles, for the *X*-axis variable. Relative influence is in parentheses. See Table 1 for predictor variable descriptions.

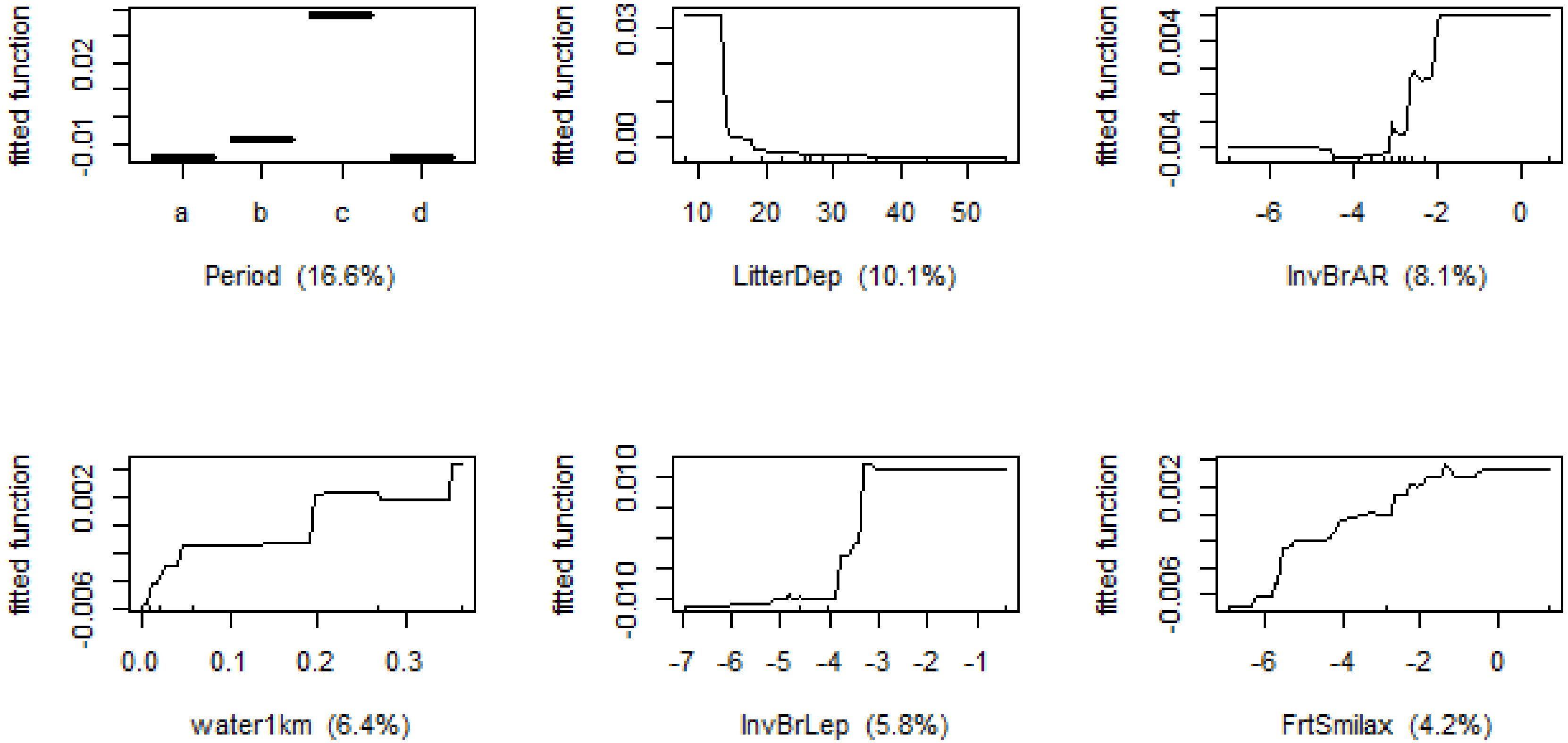


Fig. 36. Partial dependence plots for the six most influential variables that predict Northern Parula density. Rug plots located at the bottom of plots show the distribution of data, in deciles, for the *X*-axis variable. Relative influence is in parentheses. See Table 1 for predictor variable descriptions.

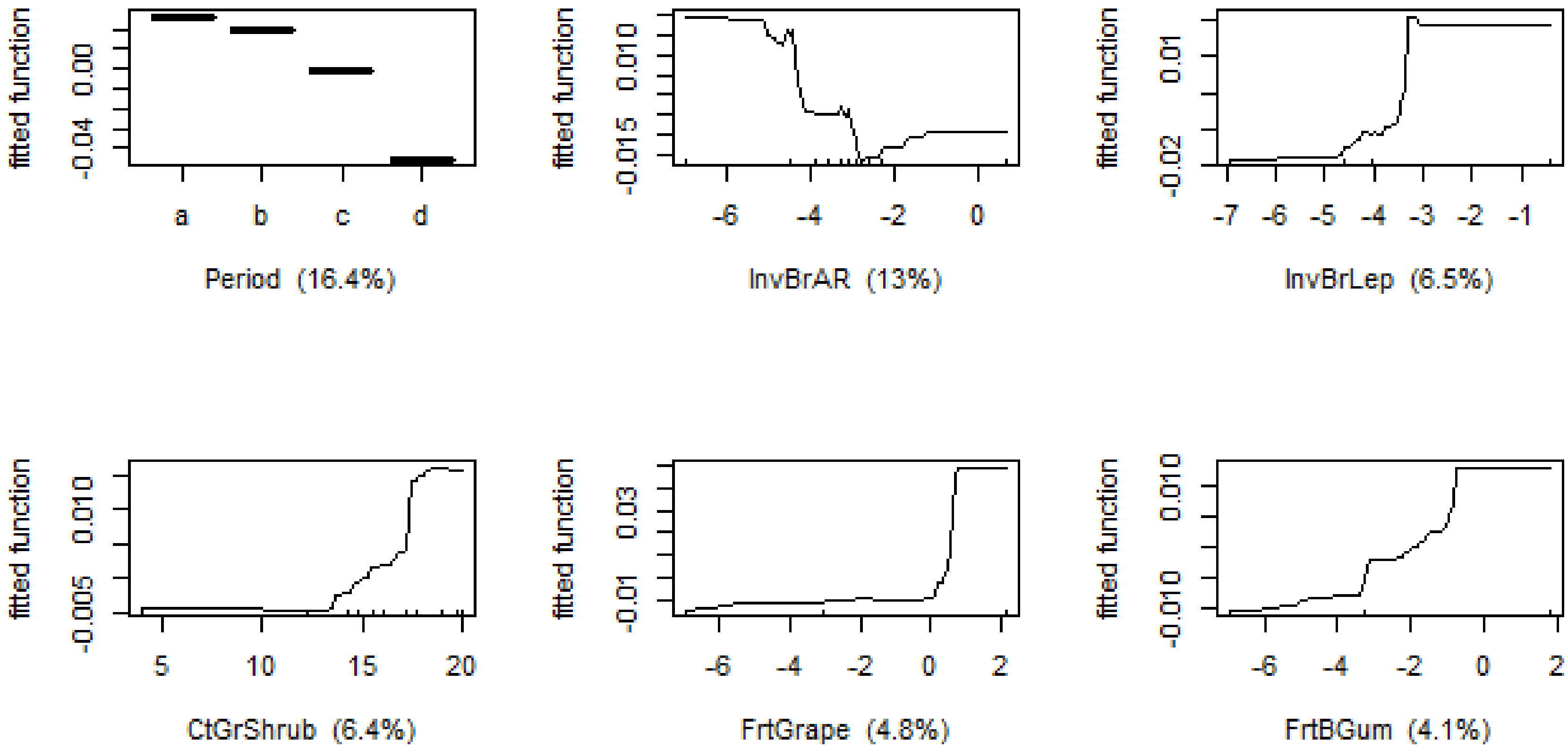


Fig. 37. Partial dependence plots for the six most influential variables that predict Ovenbird density. Rug plots located at the bottom of plots show the distribution of data, in deciles, for the *X*-axis variable. Relative influence is in parentheses. See Table 1 for predictor variable descriptions.

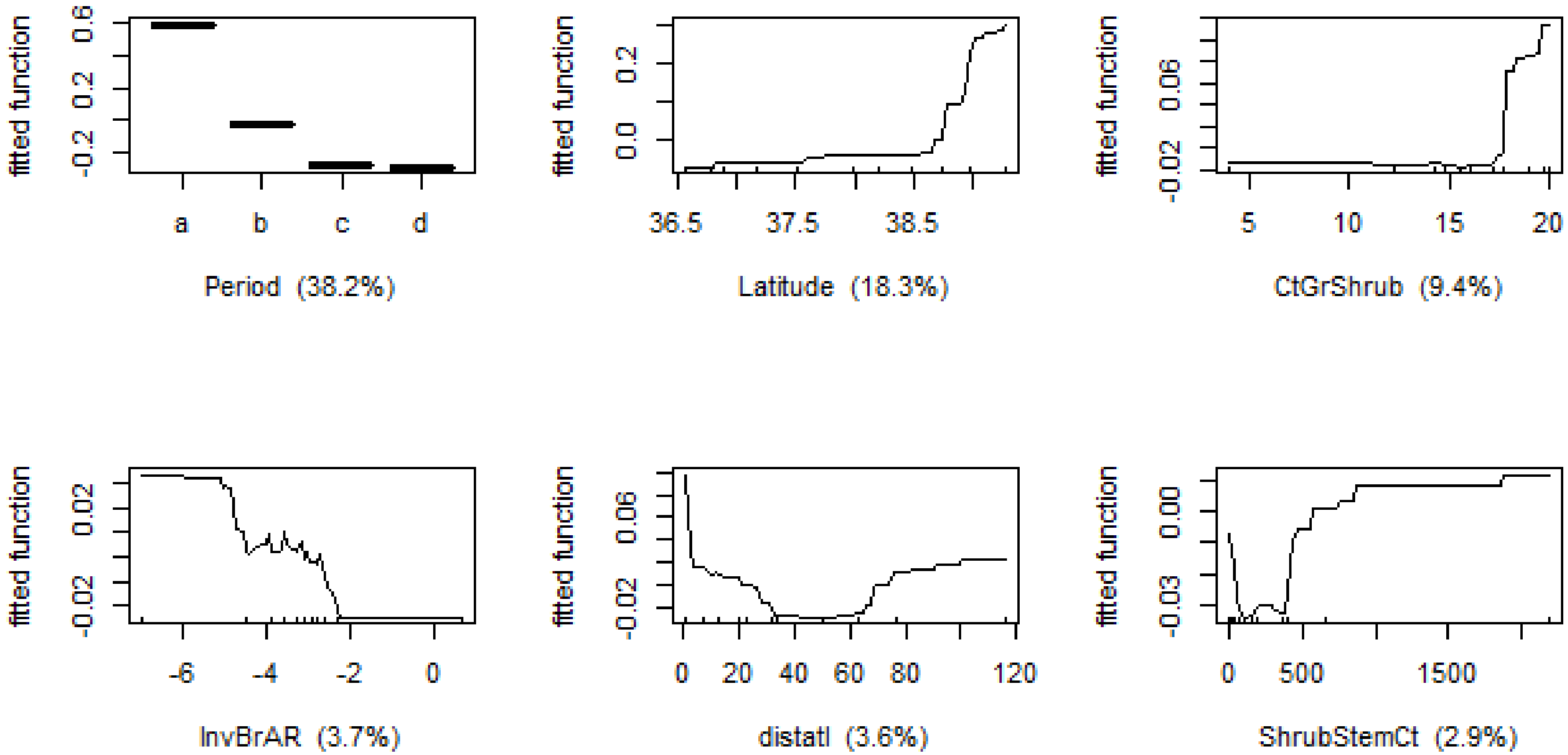


Fig. 38. Partial dependence plots for the six most influential variables that predict Red-eyed Vireo density. Rug plots located at the bottom of plots show the distribution of data, in deciles, for the *X*-axis variable. Relative influence is in parentheses. See Table 1 for predictor variable descriptions.

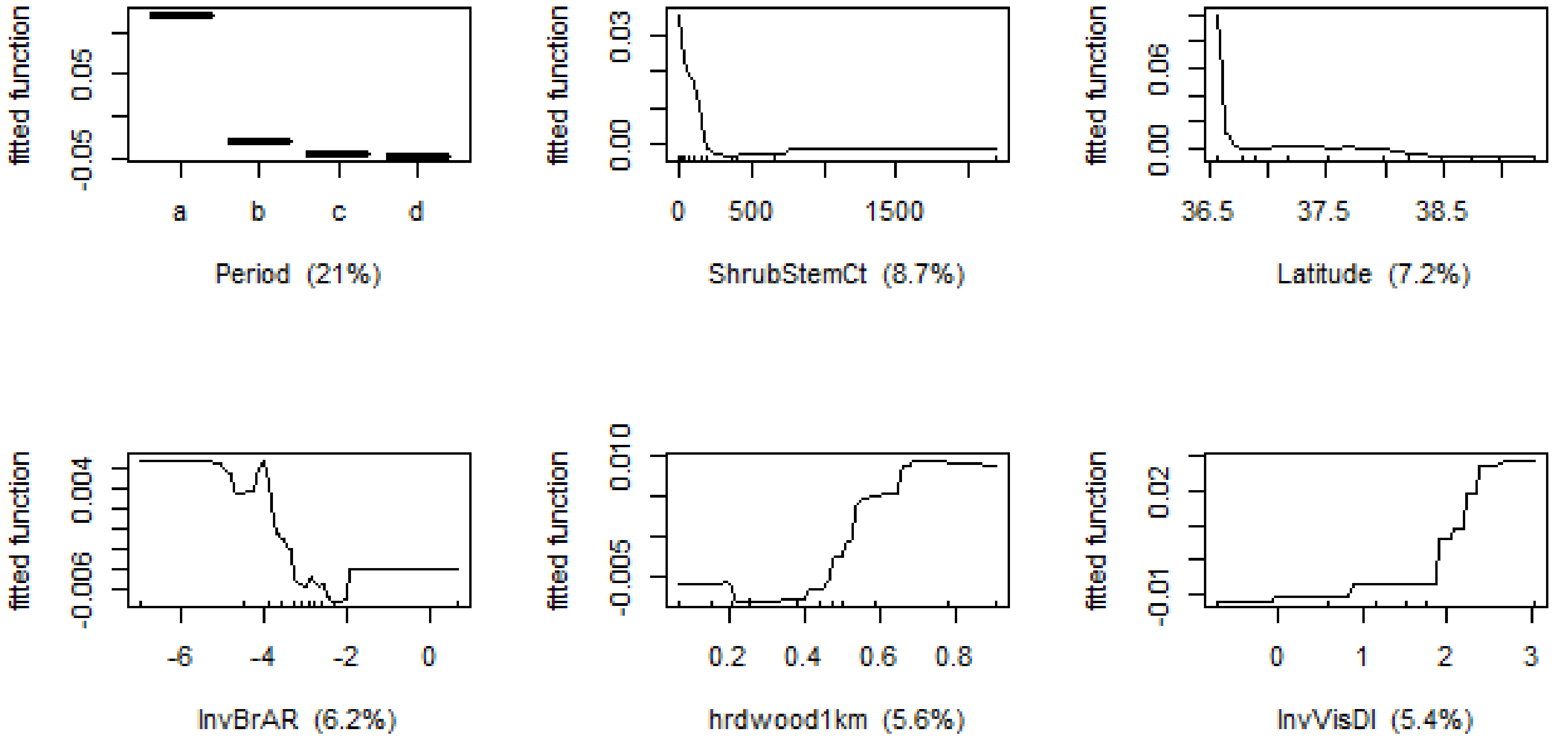


Fig. 39. Partial dependence plots for the six most influential variables that predict Yellow-billed Cuckoo density. Rug plots located at the bottom of plots show the distribution of data, in deciles, for the *X*-axis variable. Relative influence is in parentheses. See Table 1 for predictor variable descriptions.

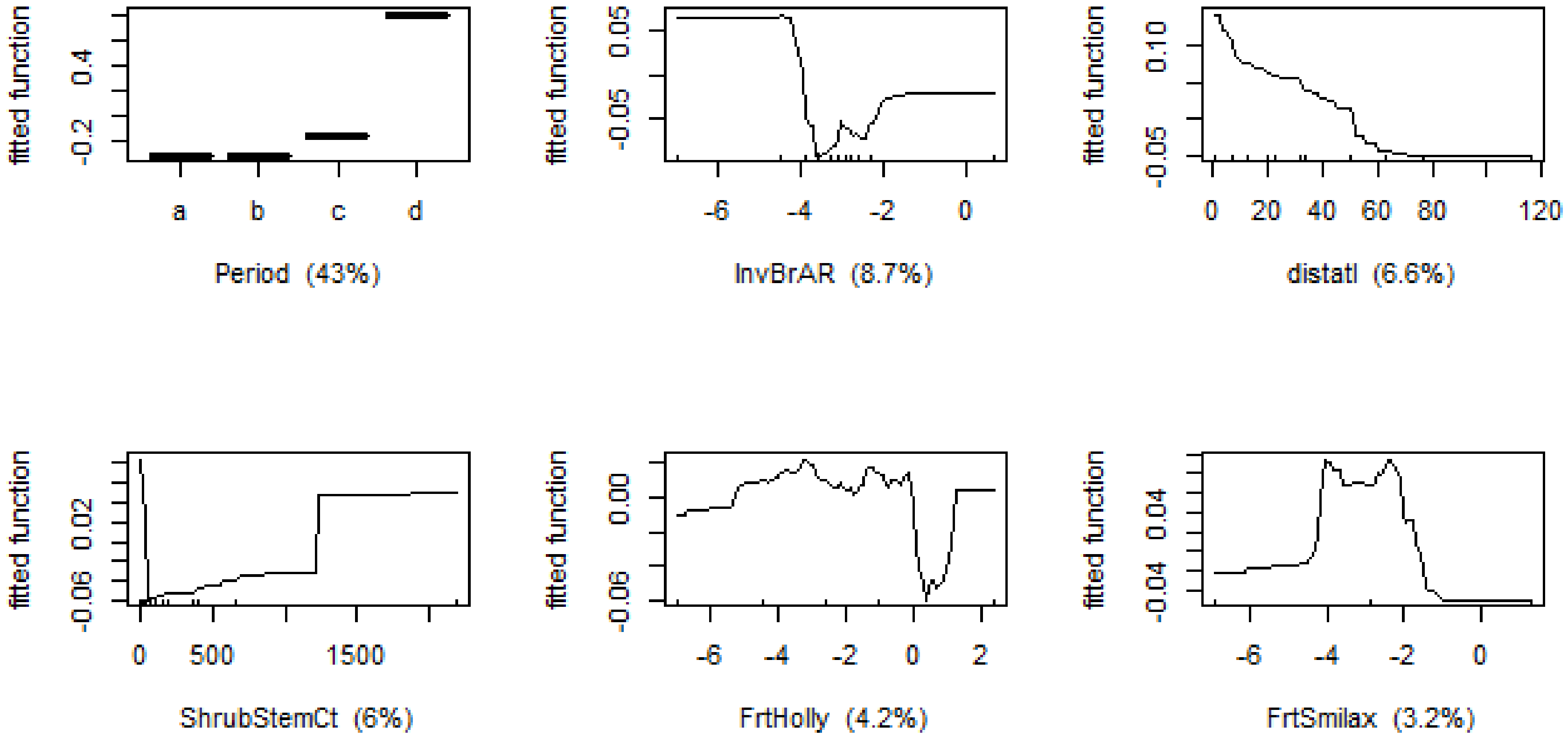


Fig. 40. Partial dependence plots for the six most influential variables that predict Yellow-rumped Warbler density. Rug plots located at the bottom of plots show the distribution of data, in deciles, for the *X*-axis variable. Relative influence is in parentheses. See Table 1 for predictor variable descriptions.

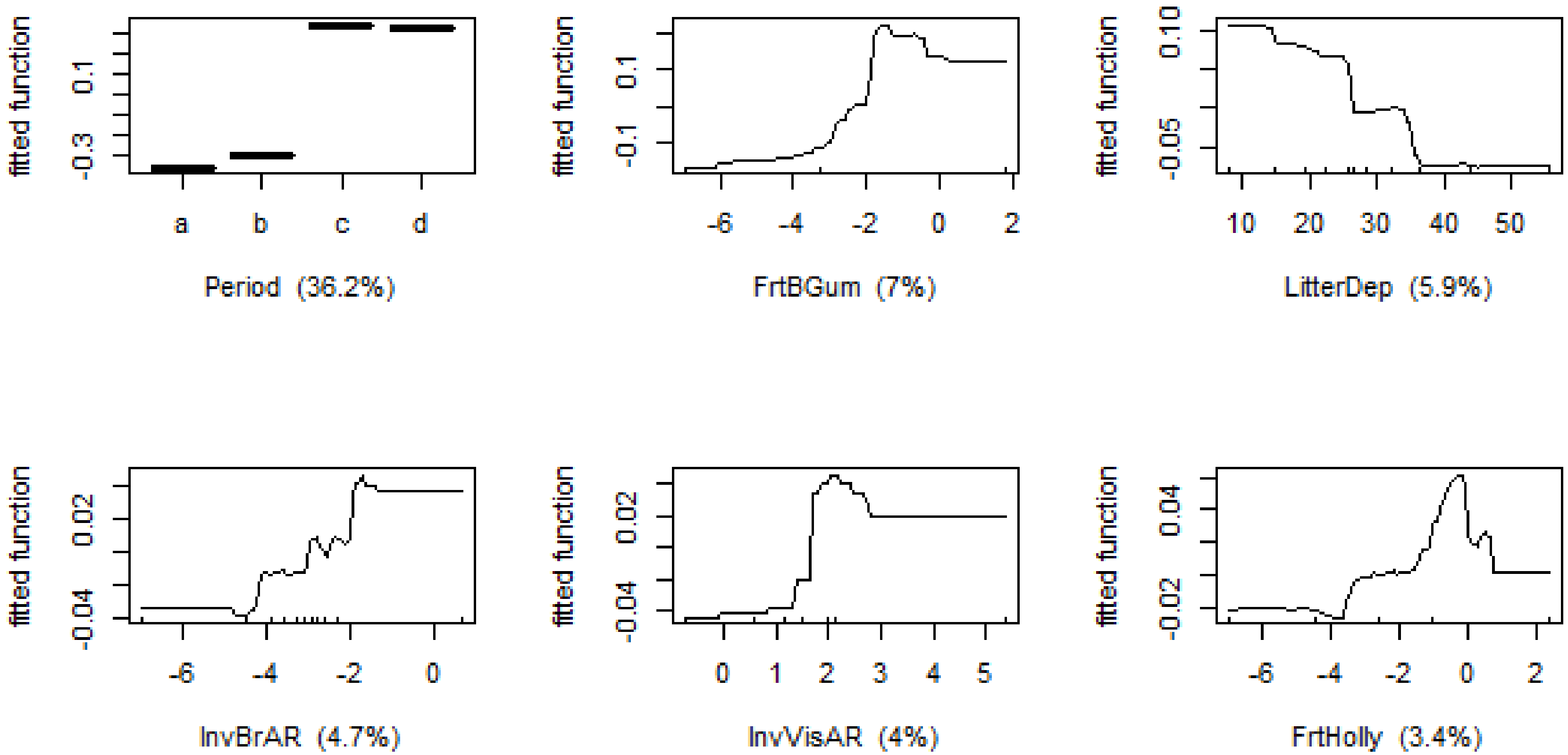


Fig. 41. Partial dependence plots for the six most influential variables that predict (Yellow-shafted) Northern Flicker density. Rug plots located at the bottom of plots show the distribution of data, in deciles, for the *X*-axis variable. Relative influence is in parentheses. See Table 1 for predictor variable descriptions.

density and migrant density (Figs. 28-30, 32, 34, 37, 39-40). Yellow-billed Cuckoo (*Coccyzus americanus*) density was positively related to Diptera per m^2 of ground surveyed (Fig. 39), while Black-throated Blue Warbler, Northern Parula, and Ovenbird densities were positively related to branch Lepidoptera density (Figs. 31, 36-37). Ripe fruit was found to influence the densities of select migrants as well. Density of ripe Grape fruit showed a strong positive relationship with migrant densities of both American Redstart and Gray Catbird (*Dumetella carolinensis*) (Figs. 30, 34). Ripe Black Gum fruit density was a strong positive predictor of Northern Flicker (*Colaptes auratus*) density (Fig. 41). Hermit Thrush was the only species to have ripe American holly rank as an important predictor variable (Fig. 35).

For patch-scale habitat features, the predictor variables litter depth, shrub stem count, count of ground vegetation, count of ground shrubs, and canopy cover were considered influential predictors for explaining migrant density in at least one model. Litter depth was an important predictor in the models for Acadian Flycatcher (*Empidonax virescens*), Northern Parula, and Northern Flicker, with each species' density declining with increasing litter depth (Figs. 29, 36, 41). The count of ground vegetation was positively related to Gray Catbird density (Fig. 34). Shrub stem count was an important predictor for three species, showing a strongly positive relationship to Great Crested Flycatcher (*Myiarchus crinitus*) density, a positive relationship to Yellow-rumped Warbler density, and a negative relationship to Yellow-billed Cuckoo density (Figs. 32, 39-40). The most common patch-scale habitat structure variable influencing migrant density was count of ground shrubs, which was positively related to densities of the season-wide grouped migrants' model as well as the densities of Black-throated Blue Warbler, Ovenbird, and Red-eyed Vireo (Figs. 28, 31, 37-38).

At the landscape scale, all four land cover types exhibited strong yet variable influence on migrant densities. The proportion of impervious surface within the 1-km buffer was related negatively to Acadian Flycatcher density, yet related positively to Black-throated Blue Warbler and Gray Catbird densities (Figs. 29, 31, 34). The proportion of water within the 1-km buffer was positively related to the densities of American Redstart, Gray Catbird, and Northern Parula (Figs. 30, 34, 36). The proportion of hardwood forest within the 1-km buffer was shown to have a weakly negative relationship with the density of migrants in the grouped migrant model (Fig. 28), gradually decreasing in density with increased proportion of hardwood within the buffer, while alternatively showing a positive relationship with densities of Acadian Flycatcher, Great Crested Flycatcher, and Yellow-billed Cuckoo (Figs. 29, 32, 39).

Predictor variables at the regional scale showed influence on a select few migrant densities. Acadian Flycatcher and Red-eyed Vireo densities both showed a positive relationship with latitude, whereas Yellow-billed Cuckoo density was negatively related to latitude (Figs. 29, 38-39). Yellow-rumped Warbler density was negatively related to distance to the Atlantic Ocean and decreased as distance from the ocean was increased (Fig. 40).

3.2 Period-specific Analyses

Two models of migrant density were developed, one for each sampling period of interest (period 1 [15 Aug – 4 Sep] and period 3 [26 Sep – 16 Oct]), with both including grouped nocturnal landbird migrant density as the variable of interest. Adjustment of model parameters resulted in use of a learning rate of 0.001 for both models, and number of trees in each final optimized model set at 1,900 for period 1 and 1,600 for period 3 (Table 20). Out of the 30 total predictor variables that were included in each BRT model, 13 variables (added across all models)

Table 20. Parameters and predictive performance metrics for BRT models, separated by sampling period (Period 1 (15 Aug – 4 Sep) and Period 3 (26 Sep – 16 Oct)), obtained from 10-fold cross-validation and using the 30 predictor variables detailed in Table 1. Table values indicate: the response variable for each model, each model's optimal learning rate, number of trees fitted for the final ensemble model, proportion of total deviance explained of the training data, and cross validation correlation. For both models, bag fraction was left at 0.5 and tree complexity at 5. See Table 1 for codes.

Response Variable (Model)		Learning Rate	No. of Trees	Proportion Deviance Explained	CV Correlation
AllMigPerHa	(15 Aug – 4 Sep)	0.001	1900	0.43	0.47
	(26 Sep – 16 Oct)	0.001	1600	0.29	0.31

showed a relative contribution of 5% or greater, the arbitrary cutoff for signifying predictor variables determined to be influential in explaining migrant density (Table 21). Model fit, based on proportion of deviance explained, was moderate for the 15 Aug – 4 Sep analysis (0.43, cross-validated correlation of 0.47), and to a lesser degree for the 26 Sep – 16 Oct analysis (0.29, cross-validated correlation of 0.31).

For the analysis of 15 Aug – 4 Sep, eight influential predictors of nocturnal migratory landbird density were identified: proportion impervious surface within a 1-km buffer, proportion hardwood forest within a 1-km buffer, proportion shrub / scrubland within a 1-km buffer, ground shrub count, ground vegetation count, basal area, Arachnids per g of branch, and Diptera ground density (Table 21). Partial response plots illustrate that the density for all nocturnal migratory landbirds during period 1 (15 Aug – 4 Sep) was negatively related to proportion of surrounding impervious surface, and increased with higher proportions of both surrounding shrub / scrubland and hardwood forest (Fig. 42). Density also increased with higher ground shrub and ground vegetation counts, was greatest at sites with generally low basal area, and decreased with increasing branch Arachnid and visual (ground survey) Dipteran densities. The strongest

Table 21. Summary table for the relative contributions (%) of each predictor variable included in boosted regression tree models developed to identify which factors were most influential in determining migrant density, and includes modeling results for nocturnal migrant analyses during Period 1 (15 Aug – 4 Sep) and Period 3 (26 Sep – 16 Oct). Species and predictor variable codes defined in Table 1.

	Predictor	Response Variable (%)	
		AllMigPerHa	
		(15 Aug – 4 Sep)	(26 Sep – 16 Oct)
Patch / Food Resources	InvBrAR	**6.09**	**5.29**
	InvVisAR	2.57	**7.96**
	InvBrLep	2.04	3.35
	InvVisLep	0.03	0.00
	InvBrDI	2.13	**10.46**
	InvVisDI	**5.24**	2.64
	InvBrOR	3.88	0.01
	InvVisOR	1.06	1.34
	FrtBGum	0.19	0.22
	FrtHolly	0.79	1.92
	FrtBlueB	0.08	0.00
	FrtDogw	0.00	0.00
	FrtGrape	0.74	3.28
	FrtParB	0.07	1.96
	FrtSmilax	0.00	2.21
Patch / Habitat Features	CanopyC	0.91	**6.99**
	LitterDep	1.52	1.97
	CtGrLeaf	1.35	4.39
	CtGrVeg	**7.00**	2.27
	CtVine	2.47	1.85
	CtGrShrub	**12.64**	4.49
	ShrubStemCt	2.22	2.42
	basalarea	**6.94**	3.24
Landscape	impurban1km	**15.82**	2.72
	water1km	1.72	**5.02**
	hrdwood1km	**6.43**	3.39
	shrub1km	**6.65**	**5.96**
Regional	Latitude	4.70	**10.78**
	distatl	2.29	2.64

Table 21. Continued.

	Predictor	Response Variable (%)	
		AllMigPerHa	
		(15 Aug – 4 Sep)	(26 Sep – 16 Oct)
Temporal	Year	2.25	1.12

Note: All numbers in bold represent variables whose contributions accounted for at least 5% of the respective model’s total, and were considered the most influential predictor variables for determining migrant density.

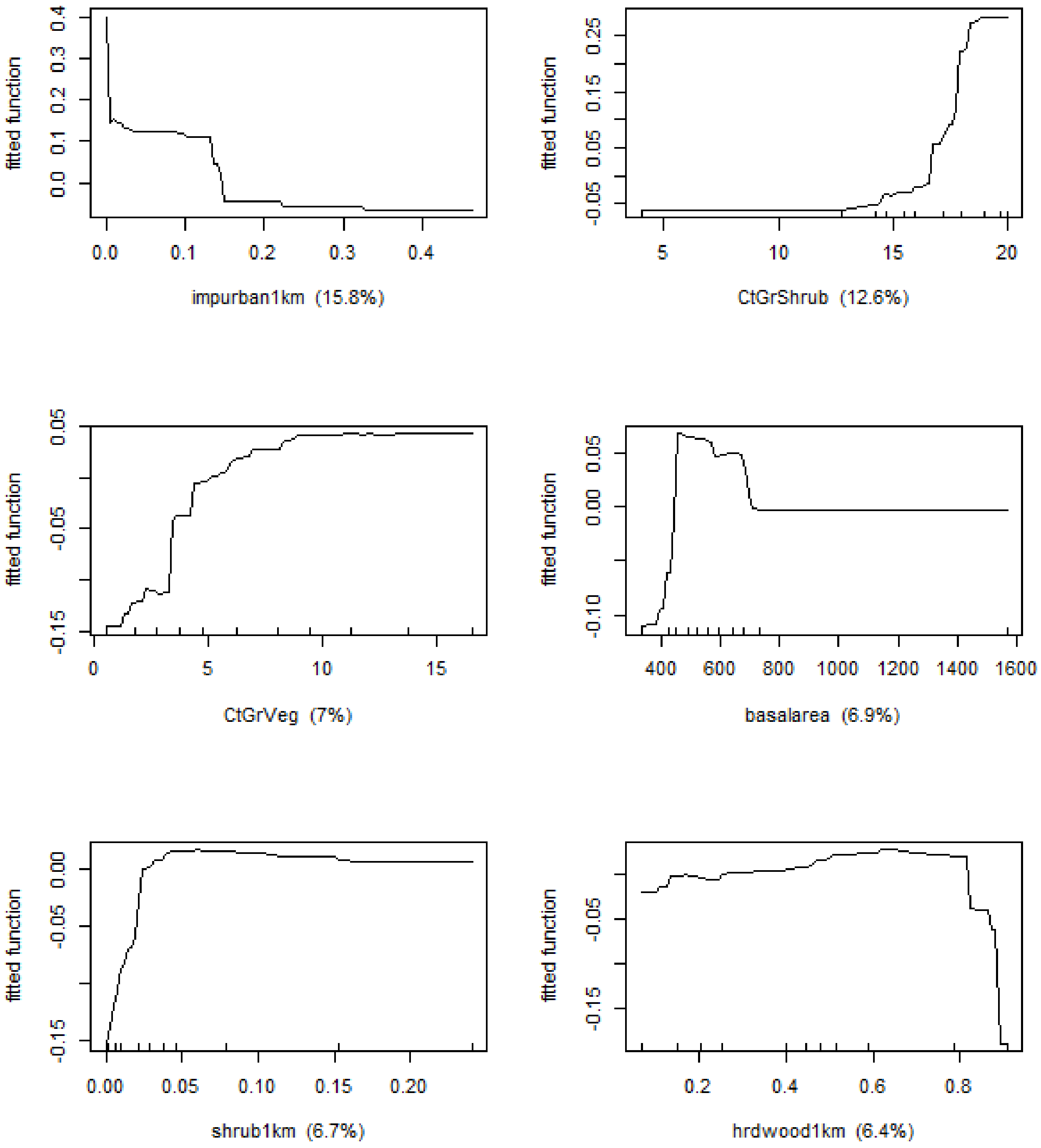


Fig. 42. Partial dependence plots for the six most influential variables that predict migrant density for all nocturnal landbird species included in the Period 1 analysis. Rug plots located at the bottom of plots show the distribution of data, in deciles, for the *X*-axis variable. Relative influence is in parentheses. See Table 1 for predictor variable descriptions.

interaction occurring among predictor variables for the density of all nocturnal migrants during 15 Aug – 4 Sep, while generally weak, included the count of ground vegetation and density of branch Arachnid, such that migrant density increased at sites with more dense ground vegetation and reduced branch Arachnid density (Table 22).

Table 22. Ranked interaction sizes for the ten most influential predictor variable interactions for the BRT analysis of all nocturnal migrant density during Period 1 (15 Aug – 4 Sep). See Table 1 for predictor variable descriptions.

Rank	Variable 1	Variable 2	Interaction Size
1	CtGrVeg	InvBrAR	0.39
2	CtGrShrub	InvVisDI	0.36
3	CtGrVeg	Year	0.22
4	CtGrShrub	CtGrVeg	0.14
5	shrub1km	CtGrShrub	0.12
6	impurban1km	InvVisDI	0.10
7	InvVisDI	InvBrDI	0.07
8	CtGrShrub	InvBrOR	0.05
9	shrub1km	InvVisDI	0.04
10	impurban1km	basalarea	0.04

For the analysis of 26 Sep – 16 Oct, seven influential predictors of nocturnal migratory landbird density were identified: latitude, proportion permanent water within a 1-km buffer, proportion shrub / scrubland within a 1-km buffer, canopy cover, Diptera per g of branch, Arachnids per g of branch, and Arachnid ground density (Table 21). Partial response plots illustrate that the density for all nocturnal migratory landbirds during period 3 (26 Sep – 16 Oct) increased with latitude, was greatest at high canopy cover, increased with proportion of surrounding permanent water (up to ~0.3), and was greatest at low proportions of surrounding shrub / scrubland (Fig. 43). Migrant density also increased with higher visual (ground survey)

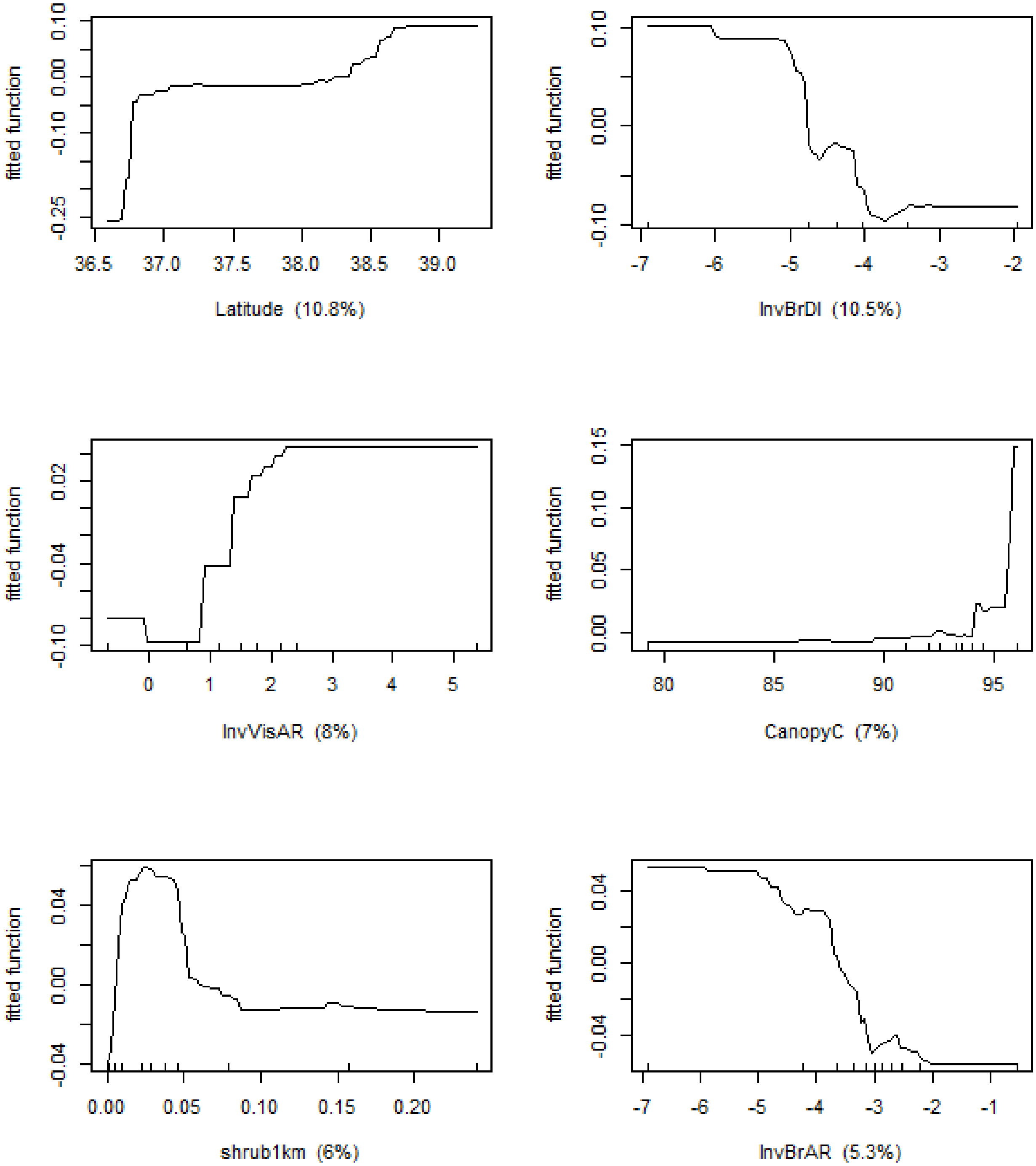


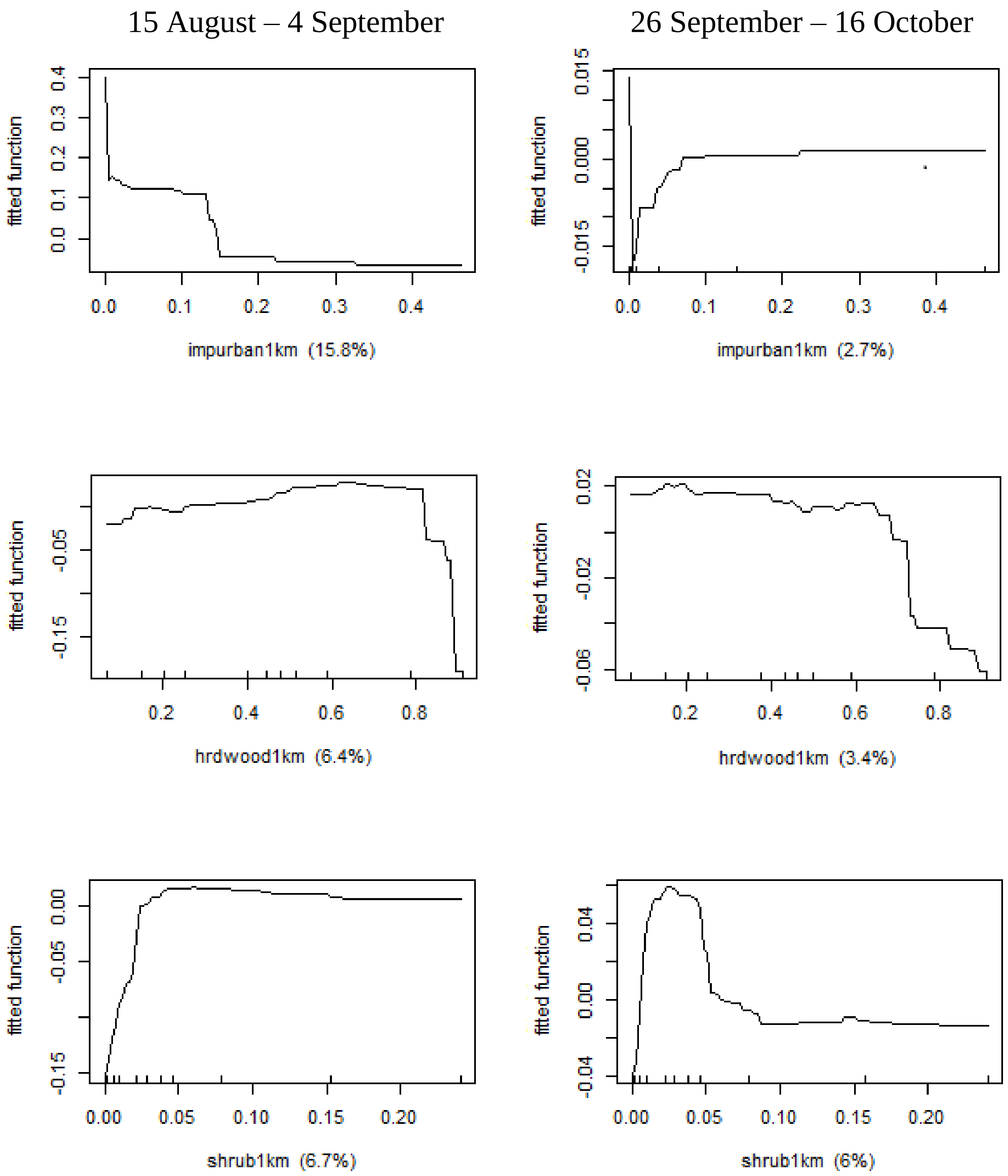
Fig. 43. Partial dependence plots for the six most influential variables that predict migrant density for all nocturnal landbird species included in the Period 3 analysis. Rug plots located at the bottom of plots show the distribution of data, in deciles, for the *X*-axis variable. Relative influence is in parentheses. See Table 1 for predictor variable descriptions.

Arachnid density, and conversely decreased with increasing branch Arachnid and branch Dipteran densities. The strongest interaction occurring among predictor variables for the density of all nocturnal migrants during 26 Sep – 16 Oct, while generally weak, included densities of branch Diptera and branch Lepidoptera, such that migrant density increased at sites with a lower density of both branch Dipterans and branch Lepidopterans (Table 23).

Table 23. Ranked interaction sizes for the ten most influential predictor variable interactions for the BRT analysis of all nocturnal migrant density during Period 3 (26 Sep – 16 Oct). See Table 1 for predictor variable descriptions.

Rank	Variable 1	Variable 2	Interaction Size
1	InvBrDI	InvBrLep	0.36
2	InvBrDI	InvVisAR	0.26
3	Latitude	InvBrDI	0.25
4	InvVisAR	InvBrAR	0.08
5	FrtSmilax	InvBrDI	0.07
6	basalarea	InvBrDI	0.06
7	CanopyC	InvBrDI	0.06
8	CtGrLeaf	InvVisDI	0.05
9	shrub1km	InvBrDI	0.04
10	shrub1km	InvVisAR	0.04

The influence and response of predictor variables to migrant density showed noteworthy variation between the two sampling periods (Figs. 44-46). Distance to the Atlantic coast, a regional variable, went from being positively related to density during the early portion of migration (15 Aug – 4 Sep) to negatively related by mid-season (26 Sep – 16 Oct) (Fig. 46). Latitude, another regional variable, was far more influential during the mid-season peak in migration (26 Sep – 16 Oct) than early (15 Aug – 4 Sep), although showed a positive relationship with density during both periods. At the landscape-scale, migrant density was strongly negatively related to surrounding impervious surface early in the season (15 Aug – 4 Sep), and was conversely far more positively related to density later in the season (26 Sep – 16 Oct). Migrant densities during both period 1 (15 Aug – 4 Sep) and period 3 (26 Sep – 16 Oct) were influenced by the proportion of scrub /shrubland within the 1-km buffer as well, with shrubland showing a strongly positive influence during 15 Aug – 4 Sep and inverse negative relationship during 26 Sep – 16 Oct (Fig. 44). At the patch-scale, migrant density was positively related to ground vegetation count during 15 Aug – 4 Sep, while showing a negative relationship during 26 Sep – 16 Oct (Fig. 45). Similarly, patch-scale food density variables showed inverse relationships according to sampling period (Fig. 46).


15 August – 4 September

26 September – 16 October

Fig. 44. Partial dependence plots for the response of nocturnal migrant density, separated by sampling periods (Period 1 on the left, Period 3 on the right) to select predictor variables used in both analyses. Rug plots located at the bottom of plots show the distribution of data, in deciles, for the *X*-axis variable. Relative influence is in parentheses. See Table 1 for predictor variable descriptions.

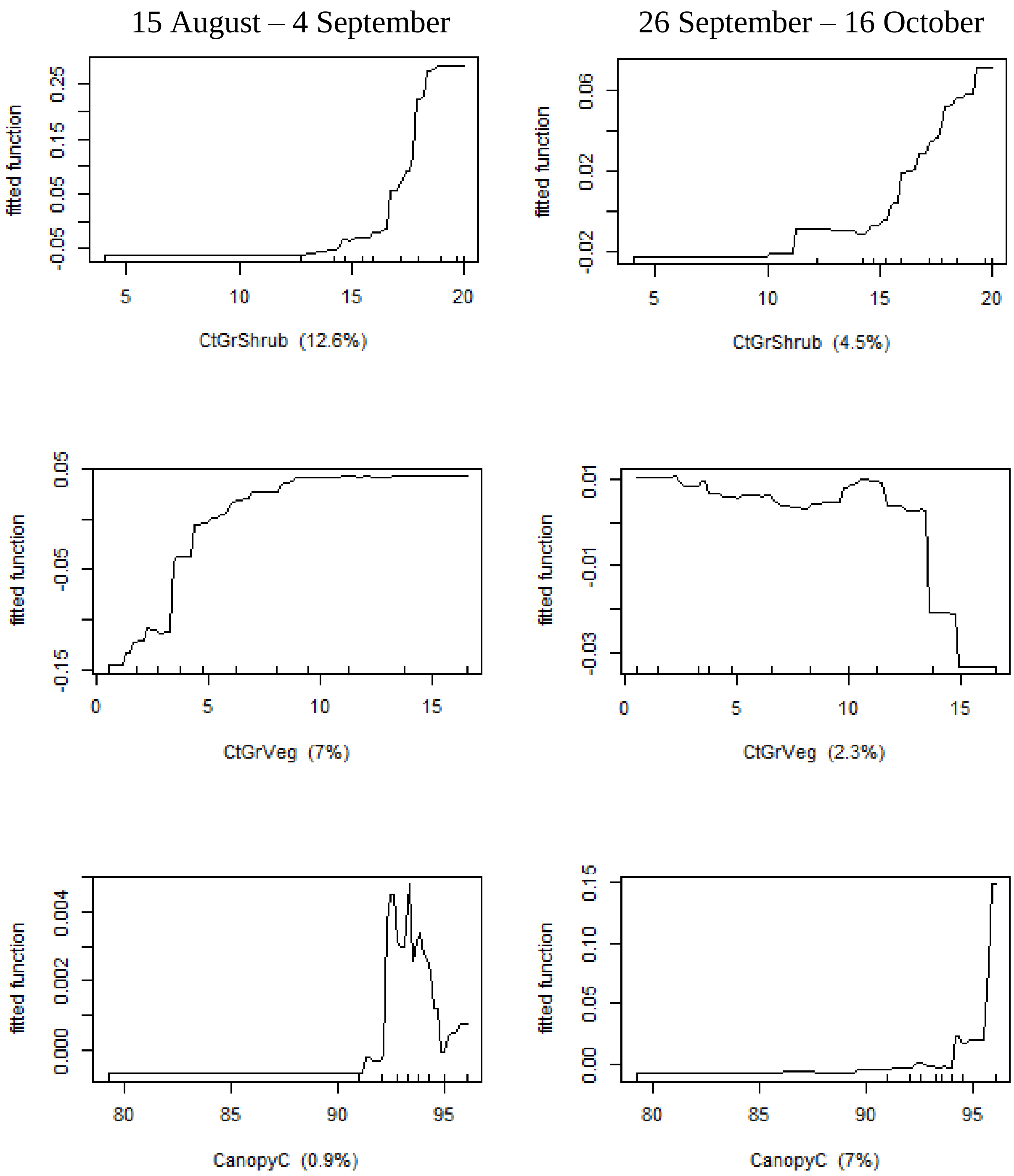


Fig. 45. Partial dependence plots for the response of nocturnal migrant density, separated by sampling periods (Period 1 on the left, Period 3 on the right) to select predictor variables used in both analyses. Rug plots located at the bottom of plots show the distribution of data, in deciles, for the *X*-axis variable. Relative influence is in parentheses. See Table 1 for predictor variable descriptions.

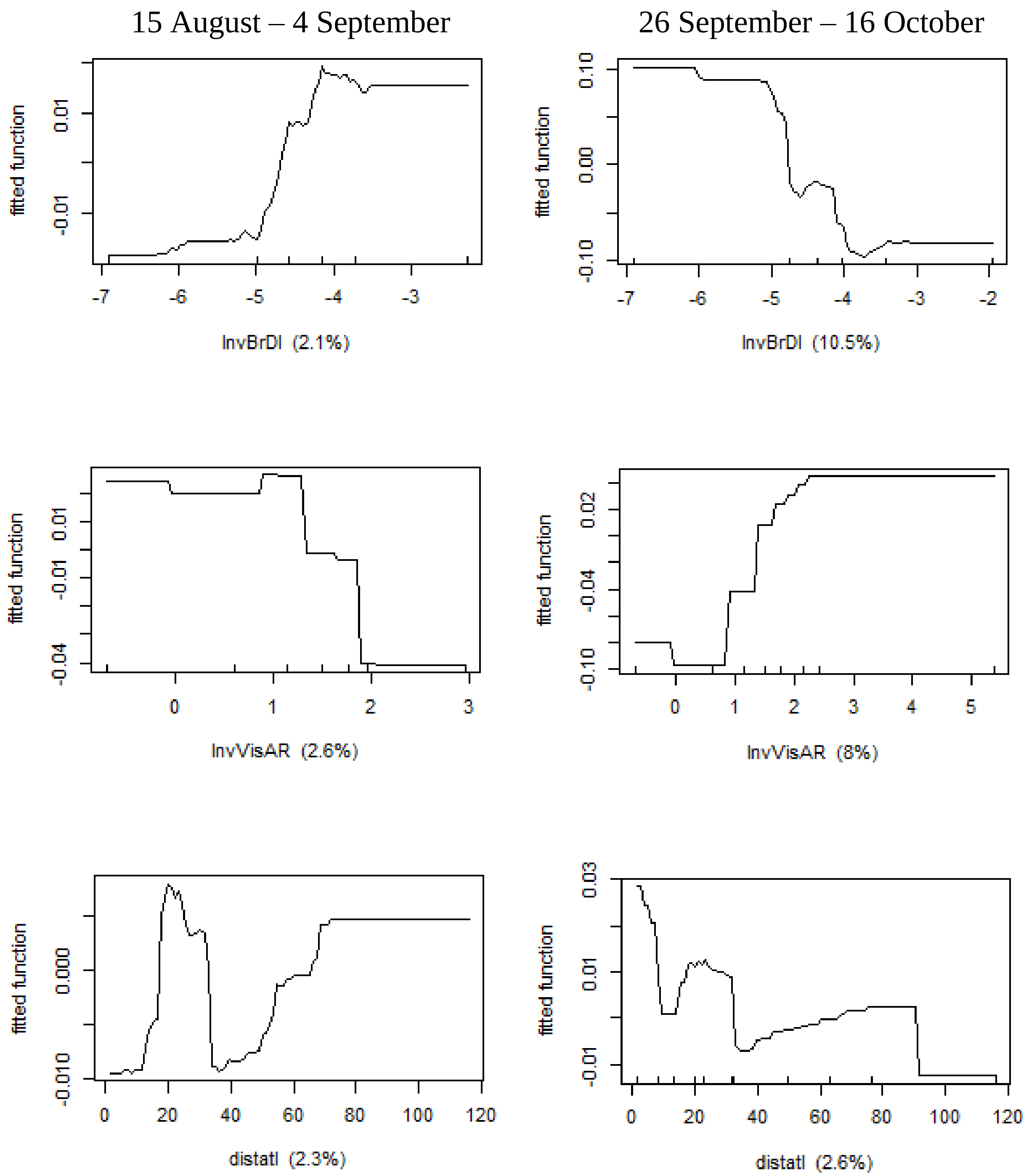


Fig. 46. Partial dependence plots for the response of nocturnal migrant density, separated by sampling periods (Period 1 on the left, Period 3 on the right) to select predictor variables used in both analyses. Rug plots located at the bottom of plots show the distribution of data, in deciles, for the *X*-axis variable. Relative influence is in parentheses. See Table 1 for predictor variable descriptions.

CHAPTER 4

DISCUSSION

The multi-scale and multi-temporal analyses of forested stopover site use by migratory landbirds during autumn migration revealed that migratory landbird use of forested stopover habitat was influenced by factors operating across multiple spatial scales, including food availability and habitat characteristics at the patch-scale, land cover composition surrounding sites at the landscape-scale, and proximity to oceanic barriers and latitude at the regional-scale. My findings, consistent with similar studies (e.g., Cushman and McGarigal 2002, Buler et al. 2007, Buler and Moore 2011) demonstrate the influence of extrinsic variables across multiple scales on landbird migrants, and reaffirm the overwhelming need to consider multiple spatial and temporal scales when assessing stopover habitat use.

Obtaining enough fuel at stopover sites to continue migration is arguably the most important goal for an individual, the results of which can influence behavioral decisions such as departure time, travel speed, and direction, and ultimately determines migratory success (Smith and McWilliams 2014). Branch Arachnid density was positively related to Northern Parula density, and likely reflects their known strong preference for spiders as a food source (Moldenhauer and Regelski 2012). Negative relationships with species to branch Arachnid density, while somewhat unexpected given the overall positive association between invertebrate abundance and migrant density found in prior studies (e.g., Hutto 1985, Buler et al. 2007), may possibly be explained by considering which particular species showed this negative relationship. For example, of the seven migrant species that had branch Arachnid density ranked as an important predictor variable with a negative relationship, four of those species (Acadian

Flycatcher, Great Crested Flycatcher, Ovenbird, and Yellow-billed Cuckoo) were present at the beginning of the first sampling period in mid-August, and were potentially individuals still using prior breeding territory habitats. If this were the case, their time and familiarity with the area may have allowed them the opportunity to reduce a portion of the invertebrate food supply (Moore and Wang 1991, Marquis and Whelan 1994). One must also consider that, given a migrant's unfamiliarity with resource distribution among stopover sites across a landscape, high-quality habitat with ample resources may actually be used less than expected in relation to nearby low-quality habitat if migrants do not have perfect information on the distribution of resources (Shochat et al. 2002). Alternatively, use of sites with low Arachnid densities may simply reflect a weak preference by forested migratory species for these invertebrates relative to other taxa available, as was concluded in one sweeping review on bird consumption of Arachnids, specifically spiders (Gunnarsson 2008). Branch Lepidopteran density, another influential invertebrate predictor variable, was positively related to migrant densities of Black-throated Blue Warbler, Northern Parula, and Ovenbird, each of which are known to consume Lepidopterans (Porneluzi et al. 2011, Moldenhauer and Regelski 2012, Holmes et al. 2017). Dipteran ground density was also related positively to Yellow-billed Cuckoo density. This was an interesting, somewhat unexpected result, as Yellow-billed Cuckoos are known to glean insects from leaves, with caterpillars (Lepidoptera) recognized as being by far their most preferred food source (Hughes 2015). For the sampling period-specific analyses, branch Diptera during 15 Aug – 4 Sep and ground Arachnid during 26 Sep – 16 Oct both showed a positive relationship to migrant density. This positive relationship between migrant density and invertebrate abundance has been found prior (Hutto 1985, Buler et al. 2007), supporting my finding that arthropod abundance appeared to influence stopover site use for some migratory taxa. But, of course, my study is somewhat biased in that invertebrates were only collected near the ground and thus likely do not reflect invertebrate diversity and abundance found higher in the upper canopy. The aforementioned positive influence of ground Dipterans on Yellow-billed Cuckoo density may provide a prime example of this potential bias, as Yellow-billed Cuckoos primarily reside and forage in the midstory and canopy regions of forests (Hughes 2015). Given this potential bias, the influence of invertebrate density on other primarily higher-foliage gleaning species analyzed (flycatchers, select warblers) should be interpreted with caution, while similar future research should strongly consider including food sampling at multiple strata within the forest.

The abundance of various fruiting species was also important in explaining migrant bird densities for particular species, possibly a result of migrants increasing their fruit intake, as has been reported prior (Parrish 1997, Smith et al. 2007b, Alan et. al 2013). Some migrant associations found with ripe fruit are well established. For example, Grape was positively related to Gray Catbird density, and a preference for this fruit has been well documented in both Gray Catbirds (Smith et al. 2011) as well as many other landbirds (Baird 1980). Black Gum was positively related to Northern Flicker density, and is also a food shown in prior literature, albeit scarce, to be consumed by them (Beal 1911). However, many of the migrant species in the study were not necessarily known to consume those fruit species found to be influential. For example, American holly was strongly positively related to Hermit Thrush density, and while this species does substantially increase their fruit consumption during migration and into winter, few studies have found that they consume American holly (Dellinger et al. 2012). Given the paucity of observations reporting consumption, in addition to the fact that overwintering Hermit Thrush arrived late in the survey season when American holly began to ripen, this result could potentially reflect an artifact of the timing of fruiting and migration rather than any actual fruit preference. Although this may be the case for Hermit Thrush, the importance of these late-season fruits should not be dismissed. Native fruiting species such as American holly can retain ripe fruits into winter and provide a valuable resource for numerous species during a time when food may be scarce (McCarty et al. 2002), and can even influence the distribution and abundance of overwintering birds (Borgmann et al. 2004). Greenbrier showed a moderately influential relationship with Northern Parula density, although not listed as a preferred fruit in prior research (Moldenhauer and Regelski 2012). Grape was found to be influential to American Redstart density, and to a lesser degree the densities of Black-throated Blue Warbler and Ovenbird. Ovenbird density also showed a moderately influential positive relationship with Black Gum. Interestingly, Ovenbirds maintain an almost completely insectivorous diet during migration (Porneluzi et al. 2011). While both American Redstarts and Black-throated Blue Warblers have been found to include various small fruits in their diets (see Sherry et al. 2016, Holmes et al. 2017), Grape consumption has not been described. Most information on fruit consumption for these latter warbler species comes solely from winter habitat studies, highlighting a gap in our collective stopover knowledge that warrants attention and further research.

It is important to recognize that plants and invertebrates at each site form part of a continuously changing community, one influenced by factors across multiple spatial scales, which ultimately could contribute to both the biodiversity and ecosystem function of each habitat (Kruess 2003). Patch-scale site characteristics, for example, can influence the growth and thus quality of fruits available for migrants (Smith et al. 2015). In the same way, the abundance and quality of plants, including those producing fruit, can influence the abundance and diversity of invertebrates inhabiting these microhabitats. For those species that appear to be influenced by the presence of fruit without any previously published records of consumption, there is the possibility that they are secondarily attracted to fruit in their search for invertebrates, which may be feeding on the fruit. For example, Black-throated Blue Warbler, Northern Parula, and Ovenbird all were influenced by branch Lepidopterans. Black Gum, Grape, and Greenbrier, those fruiting species that predicted density of at least one of these migrant species, may have supported large numbers of Lepidopterans at these sites. Hardwood forests are known to contain a higher fruiting species abundance and diversity than alternative pine-dominated forests (Greenberg et al. 2012), and perhaps this is an artifact of migrants' demonstrated hardwood habitat preference (Buler et al 2007). While the presence of hardwood forested habitat may have some degree of influence on site selection, hardwoods should not be considered the only important forest type. There is great diversity in the types of fruiting species found between hardwood and pine forests, and preferences for food type must be considered on a species-by-species basis if assessments of habitat quality are to accurately represent their true value for migrant species (Moore et al. 1995, Greenberg et al. 2011). Furthermore, non-forested habitat such as shrubland needs consideration as well when assessing fruit available for migrants, given this habitat generally supports more fruit diversity and abundance than forested areas (Suthers et al. 2000). In addition to valuable food resources, shrubland also provides necessary cover and protection for migrants (McCabe and Olsen 2015b), with fall migrant abundance correlating to stem density in prior research (Suthers et al. 2000).

Localized site structure and vegetative characteristics showed a fair degree of influence on migrant density, despite similar multi-scale stopover research done prior in the southeast, which found weak relationships between migrant abundance and habitat structure (Buler et al. 2007). At the patch-scale, canopy cover positively influenced migrant density during sampling period 3 (26 Sep – 16 Oct), when transient migrants were predominately detected, and may infer migrants are cueing in on dense forest cover to identify stopover habitat (Buler et al. 2007, McCabe and Olsen 2015a). Similarly, dense understories were preferred by migrants in the present study. This general association with a denser understory structure may reflect the desire for stopover habitat that provides more shelter to hide and move within (Moore et al. 2005), especially for insectivorous birds using the dense substrate and foliage to search for prey (Martin and Karr 1986). Given the cryptic nature of invertebrates, in addition to a migrant's unfamiliarity with a new area, insectivorous migrants may use habitat features such as vegetative structure when selecting stopover habitat (Wolfe et al. 2014). The reason for preferring a dense understory is likely highly variable among different migratory species. For Great Crested Flycatcher, a species that utilize branches as overhead lookout spots when searching for prey (Miller and Lanyon 2014), their positive relationship between density and shrub stem density may reflect a preference for appropriate perching locations from which to sally for aerial insects. For species known to glean regularly from foliage in low canopy and understory shrubby areas, such as Black-throated Blue Warbler and Yellow-rumped Warbler (Hunt and Flaspohler 1998, Holmes et al. 2017), their positive association with increasing shrub density may possibly be due to this increased opportunity for finding potential food items within shrubs. Additionally, these migrating birds need to avoid predators during stopover, and may be selecting habitat with dense shrubbery primarily for this reason (Sapir et al. 2004). Given that localized habitat features associated with vegetative density were more important earlier in migration (15 Aug – 4 Sep) than later (26 Sep – 16 Oct), one possibility worth considering is that these early-season results may simply reflect continued use of preferred breeding habitat into the first portion of autumn migration (Mitchell et al. 2012). This may be the best explanation for a positive relationship with shrub density for species such as the Red-eyed Vireo, one known to prefer shrubby deciduous habitat during breeding, yet who often forage via gleaning among the canopy of the forest (Cimprich et al. 2000). Alternatively, Red-eyed Vireos also increase their fruit intake substantially during migration, including many plant species that occur in the lower portions of the forest. Clearly, the influence of local habitat features can vary greatly among species, justifying the need to assess stopover habitat selection on a species-by-species basis. Furthermore, it is critical to recognize that these habitat characteristics at the localized scale can influence the abundance and quality of available foods such as fruiting species (Smith et al. 2015), potentially affecting individual refueling rates at a stopover site.

Migrants en route to wintering habitats may use hardwood forest in the landscape as a cue to land (Buler et al. 2007, McCabe and Olsen 2015a), thus potentially providing a signal of habitat quality (Cohen et al. 2014). At the landscape-scale, a positive early-season (15 Aug – 4 Sep) relationship with hardwood and shrubland within a 1-km buffer, as well as the negative relationship to impervious surface, may again simply be an artifact of breeding site preference (Mitchell et al. 2012), as these early-season migrant species may simply be individuals that bred at the sites prior to sampling. This potential residual relationship with breeding habitat is best exemplified by Acadian Flycatchers, an early-season migrant whose density was positively related to hardwood and negatively related to impervious surface, a species that prefers large undisturbed forestland, especially during breeding (Allen et al. 2017). Alternatively, the mid-season (26 Sep – 16 Oct) negative relationships with hardwood, as well as the positive relationships with impervious surface and permanent water, may reflect migratory landbirds being pushed into particular forest sites to avoid poor, unsuitable landscape in neighboring areas (Buler and Dawson 2014). Given that migrants are densely packing into areas with less forest cover, this perhaps suggests that these birds are not necessarily responding to forest cover at the landscape scale when migrating, a result not supported by previous stopover research (Buler et al. 2007, McCabe and Olsen 2015a). If this is the case, a better understanding of the functional connectivity among stopover habitats is critical, as fragmentation across the landscape substantially increases the costs and risks associated with attempted dispersal to alternative habitats (Baguette and Van Dyck 2007).

Fragmented habitats, such as those studied here with large amounts of surrounding urbanization, are generally lower-quality than larger, contiguous forests (Moore et al. 1995, Faaborg et al. 2010a, Matthews and Rodewald 2010). Results from the present study, however, do not show a significant reduction in food availability, a potential metric of habitat quality, among sites with reduced surrounding hardwood and increased impervious surface (urbanization). Furthermore, studies of stopover habitat where site-specific individual measurements were used find that anthropogenic woodlots can substitute as high quality stopover habitat in the place of larger, natural woodlands (Liu and Swanson 2014a,b).

At the regional-scale, stopover sites in proximity to the coastline have been shown to support higher migrant densities (Lafleur et al. 2016). The influence of distance to the Atlantic coast shifted among periods, with sites further from the coast generally supporting greater migrant densities during 15 Aug – 4 Sep, possibly an artificact of prior breeders remaining at the sites (Mitchell et al. 2012), and those closer to the coast supporting greater densities during 26 Sep – 16 Oct. Yellow-rumped Warbler density was also negatively related to distance to the Atlantic Ocean and decreased as distance from the ocean increased. Prior studies show similar results, with near-coastal stopover sites containing greater migrant densities (Diehl et al. 2003, Buler et al. 2007, Buler and Dawson 2014, Lafleur et al. 2016). Recent research utilizing radar found significant evidence that wind drift can cause nocturnal migrants to become displaced over the Atlantic during flight, forcing a reorientation inland known as “morning flight” that can result in higher migrant densities along the coast (Van Doren et al. 2016). This may also be supportive evidence for the “coastal effect” caused by misdirection of inexperienced migrants (Ralph 1978). Many near-coastal landings are undoubtedly the result of other influencing factors such as adverse weather conditions (Gauthreaux and Belser 1999, Schaub et al. 2004) which may cause a funneling of individuals towards the coast (Bruderer 1997), or individual body condition and subsequent metabolic needs en route (Moore and Aborn 2000, Moore et al. 2005).

My research demonstrates the complex and highly variable use of forested stopover habitat along the mid-Atlantic Flyway during autumn migration. Migrant density early in the season (15 Aug – 4 Sep), which primarily consisted of post-breeding Neotropical migrants, was most strongly influenced by patch-scale habitat features and landscape-scale land covers. This specific influence of habitat factors (at both the landscape and patch scale), may be representative of continued use of preferred breeding habitat by individuals present prior to sampling (Mitchell et al. 2012), although merely speculative as data collected did not include prior captures to identify individuals, and thus I was not able to address this issue. Migrant density during the middle of the migratory season (26 Sep – 16 Oct), when observations were predominantly of both transient and early overwintering (temperate) migrants, was influenced more by patch-scale food resources, different landscape-scale land covers, and overall region.

Future stopover habitat research conducted in areas where late-season breeding and early-season migration of species overlap would greatly benefit from sampling prior to the onset of migration, as this data would shed light on changes in resource availability and use, and thus site quality across multiple seasons. Similar extensions of survey efforts into winter would allow for a better understanding of the importance of resources, notably overwintering fruits, for both temperate migrants and year-round residents, as well as provide the platform for comparing the degree of competition occurring between migrants and residents at different times of the year. Given the importance as well as variability in choice of food resources to migrants, including efforts to record consumption is recommended. Similarly, increasing the scope of food data captured by additionally sampling higher into the midstory and canopy may provide more insight into the quality of these sites, especially for species regularly utilizing elevated strata of the forest. Better understanding this relationship between migrants and habitat is critical for making successful management decisions. Given migrants showed a preference for dense understory, as well as notably consuming more fruits during migration and winter periods, future efforts aimed at providing more fruit-producing shrubby understory plants may prove a successful patch-scale management tool in the mid-Atlantic region. Not only can these plants provide more fruit resources for migrants, but can also result in more habitat for populations of invertebrates to utilize across the landscape (Tscharntke and Brandl 2004), thereby increasing invertebrate food availability and subsequently overall habitat quality. Pursuing further research into the diets of migrant species of interest when using mid-Atlantic stopover sites is encouraged, as this information can lead to valuable insight related to their behaviors and decisions and thus positively influence future management decisions. Additional future considerations should also be given to other localized factors such as predation pressures (Aborn 1994), and level of competition for resources (Moore and Wang 1991), however, as these and many other variables undoubtedly influence migrant use of sites. Furthermore, predation pressures specifically from raptors may be underrepresented in forested stopover research, given their diurnal migration patterns (Newton 2010), and should be properly addressed.

Prior multi-scale analysis of stopover habitat use found a positive relationship between hardwood forest cover at the landscape-scale and understory arthropod abundance, as well as higher migrant densities at sites with greater proportions of surrounding hardwood (Buler et al 2007). These results suggest that nearby hardwood forest surrounding the site could be acting as a high-quality site indicator for landbird migrants, even conveying to them where to land (Buler et al. 2007, McCabe and Olsen 2015a). Fragmented habitat in landscapes with high surrounding urbanization are generally considered lower quality than larger undisturbed forests (Moore et al. 1995, Faaborg et al. 2010a), containing a reduced arthropod food supply (Matthews and Rodewald 2010). The present study, however, did not show a reduction in food availability in fragmented habitat with reduced surrounding hardwood. Additionally, sites with more surrounding hardwood forest in the landscape did not support the greatest migrant densities in this study. Much of this may be attributed simply to variations in the regional availability of landscape types. For example, the most similar multi-scale study on stopover habitat use (see Buler et al. 2007), took place along the Gulf Coast. In this region, the amount of surrounding forest within 5-km of survey sites was much greater on average (mean 0.59) than the mid-Atlantic sites (mean 0.28) used in the present study. Migrants traveling along the mid-Atlantic coast have less forested habitat to locate and use than other stopover regions. Migrants packing into these smaller forests likely face greater degrees of competition for resources and thus a more challenging overall migratory journey (Askins and Askins 2002). Moreover, fragmented urban landscapes limit the potential for an individual to successfully seek out more suitable stopover habitats via morning flight, possibly extending the length of stopover bouts as birds search for suitable patches, and may result in even more time and energy being expended (Moore at al. 1995).

In many cases, increasing the quality of available habitat across fragmented areas is the best strategy for protecting vulnerable populations (Harrisson et al. 2012). However, if food is not a limiting resource among sites irrespective of location and surrounding environment, increasing the ability of migrants to move among sites is of high priority in the mid-Atlantic region. The cost of travelling among habitats greatly increases as the connectivity among those sites decreases, thus influencing an individual's decision to move across the landscape (Baguette and Van Dyck 2007). Urbanization of much of the United States, especially including the northeast and mid-Atlantic regions, has been steadily increasing for over 100 years, with little decline expected as human populations continue to grow and expand (Boustan et al. 2013). Given this pattern, further research into the quality of habitat found along the mid-Atlantic, especially in areas facing heavy anthropogenic influence and limited habitat connectivity is highly recommended. Additionally, increasing efforts to provide functional connections among stopover sites occurring across a fragmented landscape is important. Providing connections in fragmented habitats across a human-modified landscape can ease the stress on individuals searching for alternative habitat, and ultimately help conserve vulnerable species (Olivier and Van Aarde 2017). Identifying mechanisms responsible for stopover site selection and use along the mid-Atlantic Flyway is extremely important research necessary for properly identifying and addressing current and future migratory landbird conservation challenges, and one requiring use of a multi-scale approach.

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APPENDIX

Appendix A. Complete list of all bird species detected during transect surveys, their migration status classifications (mi – transient, su – summer breeder, wi – winter resident, yr – year-round), number of raw detections, and if the species was included in formation of detection probabilities used for analyses of stopover habitat use (N – no, Y – yes).

Common Name	Scientific Name	Migration Status	Detections	In Analyses (Y/N)
Great Blue Heron	*Ardea herodias*	yr	12	N
Great Egret	*Ardea alba*	yr	3	N
Canada Goose	*Branta canadensis*	yr	54	N
Snow Goose	*Chen caerulescens*	wi	5	N
Wood Duck	*Aix sponsa*	yr	3	N
Black Vulture	*Coragyps atratus*	yr	5	N
Turkey Vulture	*Cathartes aura*	yr	58	N
Cooper's Hawk	*Accipiter cooperii*	yr	5	N
Sharp-shinned Hawk	*Accipiter striatus*	yr	4	N
Unknown Accipiter	*Accipiter sp.*	yr	5	N
Red-shouldered Hawk	*Buteo lineatus*	yr	85	N
Red-tailed Hawk	*Buteo jamaicensis*	yr	10	N
Unknown Buteo	*Buteo sp.*		2	N
Unknown Hawk			6	N
Bald Eagle	*Haliaeetus leucocephalus*	yr	11	N
Osprey	*Pandion haliaetus*	su	3	N
Northern Bobwhite	*Colinus virginianus*	yr	3	N
Wild Turkey	*Meleagris gallopavo*	yr	26	N
Killdeer	*Charadrius vociferus*	yr	9	N
Greater Yellowlegs	*Tringa melanoleuca*	mi	3	N
American Woodcock	*Scolopax minor*	yr	5	Y
Herring Gull	*Larus argentatus*	yr	5	N
Laughing Gull	*Leucophaeus atricilla*	su	2	N
Unknown Gull			5	N
Caspian Tern	*Hydroprogne caspia*	su	3	N
Mourning Dove	*Zenaida macroura*	yr	140	N
Black-billed Cuckoo	*Coccyzus erythropthalmus*	mi	3	Y
Yellow-billed Cuckoo	*Coccyzus americanus*	su	80	Y
Barn Owl	*Tyto alba*	yr	1	N
Barred Owl	*Strix varia*	yr	28	N
Eastern Screech-Owl	*Megascops asio*	yr	8	N
Great Horned Owl	*Bubo virginianus*	yr	7	N
Unknown Owl		yr	2	N
Belted Kingfisher	*Megaceryle alcyon*	yr	7	N

Appendix A. Continued.

Common Name	Scientific Name	Migration Status	Detections	In Analyses (Y/N)
Chimney Swift	*Chaetura pelagica*	su	30	N
Ruby-throated Hummingbird	*Archilochus colibris*	su	20	N
Unknown Hummingbird		mi	1	N
Downy Woodpecker	*Picoides pubescens*	yr	600	N
Hairy Woodpecker	*Picoides villosus*	yr	199	N
Northern Flicker	*Colaptes auratus*	wi	542	Y
Pileated Woodpecker	*Dryocopus pileatus*	yr	418	N
Red-bellied Woodpecker	*Melanerpes carolinus*	yr	1033	N
Red-headed Woodpecker	*Melanerpes erythrocephalus*	yr	34	N
Yellow-bellied Sapsucker	*Sphyrapicus varius*	wi	25	Y
Unknown Woodpecker			132	N
Eastern Wood-Pewee	*Contopus virens*	su	345	Y
Acadian Flycatcher	*Empidonax virescens*	su	240	Y
Yellow-bellied Flycatcher	*Empidonax flaviventris*	mi	1	Y
Unknown Empidonax	*Empidonax sp.*		15	Y
Eastern Phoebe	*Sayornis phoebe*	su	18	Y
Great Crested Flycatcher	*Myiarchus crinitus*	su	105	Y
Blue-headed Vireo	*Vireo solitarius*	mi	12	Y
Red-eyed Vireo	*Vireo olivaceus*	su	395	Y
Warbling Vireo	*Vireo gilvus*	su	3	Y
White-eyed Vireo	*Vireo griseus*	su	90	Y
Yellow-throated Vireo	*Vireo flavifrons*	su	50	Y
Unknown Vireo	*Vireo sp.*		7	Y
American Crow	*Corvus brachyrhynchos*	yr	438	N
Fish Crow	*Corvus ossifragus*	yr	23	N
Unknown Crow	*Corvus sp.*	yr	1	N
Blue Jay	*Cyanocitta cristata*	yr	805	N
Horned Lark	*Eremophila alpestris*	yr	2	N
Purple Martin	*Progne subis*	su	12	N
Tree Swallow	*Tachycineta bicolor*	su	8	N
Bank Swallow	*Riparia riparia*	su	1	N
Barn Swallow	*Hirundo rustica*	su	4	N
(Eastern) Tufted Titmouse	*Baeolophus bicolor*	yr	1210	N
Carolina Chickadee	*Poecile carolinensis*	yr	1010	N
Brown Creeper	*Certhia americana*	wi	67	Y
Brown-headed Nuthatch	*Sitta pusilla*	yr	14	N
Red-breasted Nuthatch	*Sitta canadensis*	wi	4	Y
White-breasted Nuthatch	*Sitta carolinensis*	yr	293	N
Carolina Wren	*Thryothorus ludovicianus*	yr	1538	N

Appendix A. Continued.

Common Name	Scientific Name	Migration Status	Detections	In Analyses (Y/N)
House Wren	*Troglodytes aedon*	su	4	Y
Winter Wren	*Troglodytes hiemalis*	wi	94	Y
Unknown Wren			1	N
Blue-gray Gnatcatcher	*Polioptila caerula*	su	5	Y
Golden-crowned Kinglet	*Regulus satrapa*	wi	439	Y
Ruby-crowned Kinglet	*Regulus calendula*	wi	112	Y
Unknown Kinglet	*Regulus sp.*	wi	1	Y
Eastern Bluebird	*Sialia sialis*	yr	73	N
American Robin	*Turdus migratorius*	yr	861	N
Wood Thrush	*Hylocichla mustelina*	su	117	Y
Gray-cheeked Thrush	*Catharus minimus*	mi	10	Y
Hermit Thrush	*Catharus guttatus*	wi	193	Y
Swainson's Thrush	*Catharus ustulatus*	mi	16	Y
Veery	*Catharus fuscescens*	mi	68	Y
Unknown *Catharus*	*Catharus sp.*	mi	3	Y
Wood/*Catharus* Thrush			16	Y
Brown Thrasher	*Toxostoma rufum*	yr	27	Y
Gray Catbird	*Dumetella carolinensis*	su	62	Y
Northern Mockingbird	*Mimus polyglottos*	yr	10	N
European Starling	*Sturnus vulgaris*	yr	12	N
American Pipit	*Anthus rubescens*	wi	2	N
Cedar Waxwing	*Bombycilla cedrorum*	yr	74	N
American Redstart	*Setophaga ruticilla*	mi	127	Y
Bay-breasted Warbler	*Setophaga castanea*	mi	2	Y
Black-and-white Warbler	*Mniotilta varia*	mi	76	Y
Blackburnian Warbler	*Setophaga fusca*	mi	3	Y
Blackpoll Warbler	*Setophaga striata*	mi	19	Y
Black-throated Blue Warbler	*Setophaga caerulescens*	mi	138	Y
Black-throated Green Warbler	*Setophaga nigrescens*	mi	5	Y
Blue-winged Warbler	*Vermivora cyanoptera*	su	1	Y
Canada Warbler	*Cardellina canadensis*	mi	2	Y
Cape May Warbler	*Setophaga tigrina*	mi	2	Y
Chestnut-sided Warbler	*Setophaga pensylvanica*	mi	10	Y
Hooded Warbler	*Setophaga citrina*	su	45	Y
Magnolia Warbler	*Setophaga magnolia*	mi	9	Y
Northern Parula	*Setophaga americana*	mi	28	Y
Palm Warbler	*Setophaga palmarum*	mi	1	Y
Pine Warbler	*Setophaga pinus*	yr	268	Y
Prothonotary Warbler	*Protonotaria citrea*	su	9	Y

Appendix A. Continued.

Common Name	Scientific Name	Migration Status	Detections	In Analyses (Y/N)
Worm-eating Warbler	*Helmitheros vermivorus*	su	14	Y
Yellow-rumped Warbler	*Setophaga coronata*	wi	270	Y
Swainson's Warbler	*Limnothlypis swainsonii*	su	1	Y
Common Yellowthroat	*Geothlypis trichas*	su	10	Y
Northern Waterthrush	*Parkesia noveboracensis*	mi	7	Y
Ovenbird	*Seiurus aurocapillus*	su	59	Y
Yellow-breasted Chat	*Icteria virens*	su	3	Y
Unknown Warbler			424	Y
Scarlet Tanager	*Piranga olivacea*	su	42	Y
Summer Tanager	*Piranga rubra*	su	37	Y
Northern Cardinal	*Cardinalis cardinalis*	yr	1104	N
Blue Grosbeak	*Passerina caerulea*	su	6	Y
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	mi	8	Y
Indigo Bunting	*Passerina cyanea*	su	10	Y
Eastern Towhee	*Pipilo erythrophthalmus*	yr	83	Y
Chipping Sparrow	*Spizella passerina*	su	2	Y
Field Sparrow	*Spizella pusilla*	su	8	N
Dark-eyed (Slate-colored) Junco	*Junco hyemalis*	wi	14	Y
Fox Sparrow	*Passerella iliaca*	wi	4	Y
White-throated Sparrow	*Zonotrichia albicollis*	wi	70	Y
Song Sparrow	*Melospiza melodia*	yr	5	N
Swamp Sparrow	*Melospiza georgiana*	wi	3	Y
Bobolink	*Dolichonyx oryzivorus*	mi	23	N
Brown-headed Cowbird	*Molothrus ater*	yr	12	N
Red-winged Blackbird	*Agelaius phoeniceus*	yr	51	N
Rusty Blackbird	*Euphagus carolinus*	wi	3	N
Unknown Blackbird			65	N
Common Grackle	*Quiscalus quiscula*	yr	132	N
Northern (Baltimore) Oriole	*Icterus galbula*	su	9	Y
Unknown Oriole	*Icterus sp.*	su	1	Y
Unknown Icterid	*Icterid sp.*	su	2	N
House Finch	*Carpodacus mexicanus*	yr	12	N
American Goldfinch	*Spinus tristis*	yr	240	N
Pine Siskin	*Spinus pinus*	wi	6	Y
Unknown Bird			594	N

VITAE

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EDUCATION

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Spring 2012 – TA in Ornithology, Auburn University, Auburn, Alabama
Spring / Summer 2011 and 2012 – Research Assistant, Auburn University, Auburn, Alabama

THESIS-RELATED PRESENTATIONS

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November 2014 – Tidewater Chapter of Sigma Xi’s Poster Session, Christopher Newport University, Newport News, Virginia (poster)
July 2014 – North American Congress for Conservation Biology, Missoula, Montana (oral)
May 2014 – Hastings Natural History Reservation Plenary Lecture Series, Carmel Valley, California (oral)
March 2014 and 2015 – Virginia Coastal Avian Partnership, Eastern Shore, Virginia (oral)

PUBLICATIONS

Ç. Akçay, **J. A. Arnold**, K. L. Hambury, and J. L. Dickinson. 2016. Age based discrimination of rival males in western bluebirds. Animal Cognition 19:999-1006.

Ç. Akçay, K. L. Hambury, **J. A. Arnold**, A. M. Nevins, and J. L. Dickinson. 2014. Song sharing with neighbours and relatives in a cooperatively breeding songbird. Animal Behaviour 92:55-62.

J. A. Arnold, J. A. Trent, and E. C. Soehren. 2012. Joint Nesting by the Eastern Bluebird (*Sialia sialis*) in Southeast Alabama. Alabama Birdlife 58(2):32-35.

AWARDS

2014 – Washington Biologists Field Club Research Grant, $2,700
2014 – Sigma Xi GIAR, $700
2014 – J.J. Murray Award, Virginia Society of Ornithology, $1,000