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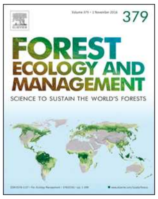

Habitat resilience for songbirds: The role of topographic position in a mixed deciduous forest

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ABSTRACT

Climate change is altering patterns of resource availability and this may have negative effects on insectivorous forest birds in the US upper Midwest. As invertebrate life cycle phenology shifts due to earlier spring leaf-out, nesting birds are vulnerable to phenological mismatches between food supply and demand. Areas with complex topography, and thus a variety of thermal and humidity conditions, may support a greater variety of plant and invertebrate phenological rates and stages within close proximity than are found in areas with simple topography. However, the extent and magnitude of this phenomenon is unclear, as is the degree to which topographic position may influence the ability of species to persist during extreme conditions. We examined the effects of topographic position on the phenology of a tri-trophic forest system over two years from spring through mid-summer. We hypothesized that in cool microsites the likelihood of trophic mismatches and late season food shortages is lower than in warm microsites. At 70 sites in the Baraboo Hills, part of the Driftless Area of the US Midwest, we recorded leaf-out timing of over 700 deciduous trees, measured weekly changes in invertebrate biomass on understory foliage, and conducted bird point counts to assess avian species richness and density. In stream gorges, cooler temperatures were associated with slight but significant delays in leaf-out timing of canopy and understory deciduous trees relative to upland sites. At all sites, invertebrate biomass was distributed relatively evenly across the study period, in contrast to other temperate zone sites where phenological mismatches have been reported between birds and their invertebrate prey. Invertebrate biomass was similar in stream gorges and uplands in both study years. Insectivorous bird species richness was greater in stream gorges than in the surrounding upland forest during both seasons and was positively related to Lepidoptera larvae biomass in the understory. Among eight abundant insectivorous bird species, density was similar in uplands and stream gorges, among four species density was higher in uplands, and density of two species was higher in stream gorges. These results suggest that insectivorous birds within this study area are unlikely to experience trophic mismatches, and that despite having cooler microclimates and higher avian species richness, stream gorges did not provide more invertebrate food resources than uplands under the climate conditions of the years in which we sampled this tri-trophic system.

1. Introduction

Climate change is projected to affect species and ecosystems globally, but changes can be difficult to extrapolate to local scales that are experienced by organisms (Sears et al. 2011). Heterogeneity within landscapes, and a high degree of habitat connectivity are two attributes that may confer resilience to the impacts of climate change (Anderson et al. 2014). Specifically, variation in topographic features (slope, aspect, position) within close spatial proximity, may mitigate the acute effects of climate change on species by creating multiple distinct microclimates simultaneously within landscapes (Sears et al. 2011). In this paper, we examine how topographic variation introduces an important source of phenological asynchrony into multiple trophic levels within a temperate forest ecosystem, potentially influencing food availability for nesting insectivorous songbirds.

At local scales, topography is important in shaping the effects of warming spring temperatures due to climate change. This is particularly important in temperate forest ecosystems of the northern hemisphere, where spring phenology has advanced measurably in recent decades (Badeck et al. 2004; Richardson et al. 2006; Friedl et al. 2014). Areas of highly varied topography provide a variety of thermal conditions (Fisher et al. 2006), and because trees are dependent on local temperatures to break dormancy in the spring, the pace of tree phenology is not uniform across heterogeneous landscapes (Fisher et al. 2006; Sears et al. 2011). In

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New England, small valleys (< 40 m loss of elevation) resulted in 10–14 day leaf-out delays in the cool microclimates created by cold air drainage relative to adjacent uplands (Fisher et al. 2006). Additionally, different tree species do not leaf-out synchronously, or have identical phenophase lengths (Donnelly et al. 2017), and so tree species diversity also contributes to phenological asynchrony.

The life cycles of herbivorous forest invertebrates are closely tied to spring tree phenology. Lepidoptera larvae, in particular, feed most efficiently on young leaves that have not yet developed defensive compounds or tough outer layers (Murakami et al. 2005; Roslin and Salminen 2009). In forests where predictable Lepidoptera seasonal peaks have been documented, these peaks often coincide with tree budburst and are most pronounced in forests with low tree species diversity (Both et al. 2009). Often, habitats with highly seasonal invertebrate resources are also sites with low tree species diversity, where young leaves are only present briefly on the landscape. Additionally, tree species diversity is positively related to Lepidoptera species diversity (Stireman et al. 2014). Although the population dynamics of forest caterpillars are often synchronized within species (Stange et al. 2011), in mixed deciduous forests of New Hampshire (Lany et al. 2015) and mixed deciduous-coniferous forests of northern Europe (Burger et al. 2012) the varied life histories of the multitude of invertebrate species contribute to relatively stable invertebrate abundance throughout the spring and summer. These two contrasting forest types (high tree species richness with stable invertebrate abundance vs. low tree species richness with highly seasonal invertebrate abundance) greatly shape the food resources available to insectivorous forest birds.

Changes in the abundance and seasonality of Lepidoptera larvae in temperate regions may drive population dynamics of insectivorous forest songbirds (Jones et al. 2003; Gonzalez-Braojos et al. 2017). Lepidoptera larvae make up a major portion of the diets of many insectivorous forest bird species (Holmes and Schultz 1988) and have been shown to comprise 60–90% of the food provisioned to nestlings (Goodbred and Holmes 1996), and peak food demand by birds during the nesting cycle historically co-occurs with peaks in Lepidoptera larvae abundance (Lany et al. 2015). In years with early spring onset, tree leaf-out and Lepidoptera hatch dates are also earlier (Both et al. 2009; Burger et al. 2012; Lany et al. 2015), however long-distance migrant bird species, which rely on circannual programming to begin spring migration (Akesson et al. 2017) arrive at the breeding grounds on a relatively inflexible date each year that is independent of local food supply (Both and Visser 2001). The resulting trophic mismatch can reduce nesting success for many long-distance migrant species (Visser et al. 2006; Knudson et al. 2011; Saino et al. 2011; Gienapp et al. 2014) and have negative demographic effects on populations, particularly related to nestling recruitment (Sillet et al. 2000) and female immigration (Gonzalez-Braojos et al. 2017). Alternatively, if invertebrate abundance is more evenly distributed throughout the spring and summer, advancing spring phenology may expand the period of high food availability in temperate habitats (Dunn et al. 2011). This could make it possible for long-distance migrant species to reproduce successfully even if their arrival is not synchronized perfectly with peak invertebrate availability. Additionally, extended periods of food availability later into the nesting season could allow double-brooded bird species to complete two successful nesting cycles, even in northern areas of their range where the breeding season is shorter (Halupka et al. 2008; Townsend et al. 2013; McDermott and DeGroote 2016; Townsend et al. 2016; Halupka and Halupka 2017). Thus, although global climate change is the driving force behind phenological changes, local-scale factors (i.e. food resource diversity and availability) and selection pressures may have a stronger influence on bird populations (Knudson et al. 2011; Dunn and Moller 2014; Wesolowski and Rowinski 2014; Senner et al. 2016).

The goal of this study was to investigate how topographic position interacts with climate to influence microhabitat suitability for breeding insectivorous forest birds in a mixed deciduous forest. Specifically, we wanted to determine whether, during the period from spring through midsummer, phenology of trees and invertebrates differs in stream gorges versus upland sites, and how this in turn influences bird species richness and density patterns. The first objective was to determine if topographic position results in distinct microclimates, and if the pace of spring tree phenology reflects these differences. We hypothesized that uplands and south-facing slopes are consistently warmer than stream gorges, and that tree leaf-out is slower and occurs later in stream gorges than in uplands. The second objective was to compare seasonal patterns of invertebrate biomass in stream gorges and upland sites. We hypothesized that invertebrate biomass is greater and more stable throughout the season in stream gorges because lower ambient temperature and higher water availability prevent desiccation and water-stress in terrestrial invertebrates (Ramey and Richardson 2017) and thus potentially support greater species diversity. Additionally, we predicted that in both habitat types invertebrate biomass does not exhibit a strong seasonal peak due to high tree species diversity. The third objective was to determine the degree to which forest bird density and richness is associated with invertebrate biomass and topographic position throughout the season. We hypothesized that sites with higher invertebrate biomass support greater avian species richness and density. Understanding how topographic position shapes phenology, invertebrates, and bird habitat quality will provide insight about the effectiveness of explicitly incorporating topographic complexity in climate adaptation plans.

2. Materials and methods

2.1. Study area

We established 8, 15-ha study sites (Table 1) in forests of the 585 km^2 Baraboo Hills of southern Wisconsin on properties owned by the State of Wisconsin, The Nature Conservancy, The Wisconsin Society for Ornithology, and private landowners. Elevation of the study sites ranged from 297 to 408 m above sea level. Many areas in the Baraboo Hills have been identified as having above average resilience (Anderson et al., 2016), due to extensive habitat connectivity and topographic diversity, which provide space for a range of species responses to future climate changes (Anderson et al. 2014). Additionally, this region has a high diversity of tree and bird species (Mossman and Lange 1982). The eight sites were selected and paired such that each pair of sites included one upland and one stream gorge site and had uniform geologic substrate (sandstone or quartzite), similar forest age, tree species composition, and management history. Elevation of upland sites ranged from 355 to 408 m above sea level (mean = 374 m), and elevation of stream gorge sites ranged from 297 to 344 m (mean = 316 m), resulting in an elevation difference between upland and stream gorge sites ranging from 25 to 108 m (mean = 57 m).

Table 1
Study sites arranged in pairs by proximity and geologic substrate, with each site name followed by an acronym in parentheses. N indicates the number of sampling points at each site. Mean elevation of each site (in meters above sea level) is reported. All sites are approximately 15 ha.

Upland Site	N	Elevation	Stream Gorge Site	N	Elevation	Substrate
South Bluff (SB)	7	369	Pine Glen (PG)	8	344	Quartzite
Schara Road (SR)	8	408	Baxter's Hollow (BH)	10	300	Quartzite
Natural Bridge (NAT)	8	359	Pine Hollow (PH)	9	323	Sandstone
Honey Creek (HC)	10	355	Hemlock Draw (HD)	10	297	Sandstone

Each site was located at least 100 m from any hard forest edge (i.e. road or agricultural field), to avoid influence of fragmentation on invertebrate biomass (Burke and Nol 1998; Stireman et al. 2014) and area-sensitive bird species (Fraser and Stutchbury 2003). Paired sites were separated by 0.2–10 km. We established 7–10 sampling points per site (70 points total) by placing points randomly but with the constraint that each point had a 75 m buffer that did not extend beyond the boundary of the study site or overlap the buffers of other points. Points located in uplands sites were on flat hilltops or the upper slopes of hills, and points in stream gorge sites were located near creeks or in mesic forests on the ravine floor, on steep hillsides along the walls of the ravines, and in mesic forests with gradual sloping topography above the steep areas of each ravine. Habitat type refers to stream gorge or upland sites.

2.2. Data collection

2.2.1. Temperature

We used dataloggers (DS1921 iButtons) to record temperature every 30 min from June until August in 2017, and April until August in 2018. Two iButtons were distributed in each study site in locations that characterized the overall topography, aspect, and vegetation of the site. We placed the iButtons in waterproof capsules 1.5 m off the ground, to capture temperatures in the understory where invertebrate surveys occurred. Each capsule was suspended from a branch of a sapling using fishing line and was at least one meter away from large tree trunks, rocks, or patches of direct sunlight. Hubbart et al. (2005) found that iButtons were accurate to within 1 °C 99% of the time.

2.2.2. Tree phenology

At each sampling point we selected 4–8 reference canopy trees, picking from a set of focal species widely distributed in the study area including: Sugar Maple, Red Maple, Red Oak, White Oak, White Ash, Black Ash, Shagbark Hickory, Bitternut Hickory, American Elm, Slippery Elm, Yellow Birch, Basswood, Bigtooth Aspen (scientific names in Table 2). Additionally, at each point we selected 4–8 reference understory trees or shrubs, including the species listed above, as well as Black Cherry, Ironwood, Blue Beech and Witch Hazel (scientific names in Table 2). We defined canopy trees as > 10-cm in diameter at 1.37 m ("breast height") and not overtopped by surrounding trees, and we defined understory trees as > 2-m tall and overtopped by surrounding trees (Wood and Pidgeon 2015). Each tree was marked with flagging and revisited every 10 days in 2017 and every 5 days in 2018 from mid-April until early June for a total of 4 visits in 2017 and 8 visits in 2018. During visits, for these selected canopy and understory trees we estimated the proportion of the crown displaying the following categories: Winter condition, Budding, Budbreak, Young Leaf, Mature Leaf (following methods in Wood and Pidgeon 2015).

Table 2
Common and scientific names of tree and shrub species included in phenology surveys.

Common Name	Scientific Name
Sugar Maple	*Acer saccharum*
Red Maple	*Acer rubrum*
Red Oak	*Quercus rubra*
White Oak	*Quercus alba*
White Ash	*Fraxinus americana*
Black Ash	*Fraxinus nigra*
Shagbark Hickory	*Carya ovata*
Bitternut Hickory	*Carya cordiformis*
American Elm	*Ulmus americana*
Slippery Elm	*Ulmus rubra*
Yellow Birch	*Betula alleghaniensis*
Basswood	*Tilia americana*
Bigtooth Aspen	*Populus grandidentata*
Black Cherry	*Prunus serotina*
Ironwood	*Ostrya virginiana*
Blue Beech	*Carpinus caroliniana*
Witch Hazel	*Hamamelis virginiana*

2.2.3. Invertebrate biomass seasonality

We sampled invertebrates on foliage every two weeks from mid-May until late-July in 2017, and every week from late-April until late-July in 2018. At each visit we randomly chose 7 of the 7–10 established sampling points at each site to focus efforts on. At each point we randomly chose and sampled 2 branches in the lower understory (< 3-m) and 2 in the upper understory (3–6 m). Thus we collected 28 branch samples per site, following precedent of Johnson (2000). At each point, we sampled a variety of shrub and tree species to capture a wide range of invertebrates. Each sample consisted of 100 leaves at the end of a branch and the twigs, bark, and flowers contained in the area encompassed by the leaves. To sample the low understory, we visually examined a 100-leaf sample and tallied all invertebrates we encountered (Holmes and Schultz, 1988). For upper understory samples, we used a large fabric net (1-m diameter) on a telescoping pole. We positioned the net to surround the end of a branch bearing live foliage, so that approximately 100 leaves were contained within the net. By shaking the net, we dislodged invertebrates from the foliage and then collected them from the net. We identified invertebrates to taxonomic order and assigned them to an order-specific size class based on their length (excluding legs and antennae; Appendix A). If we were unable to identify a specimen to order, we preserved it in ethanol for later identification.

2.2.4. Avian species richness and density

We conducted variable-radius point counts during 3 periods in 2017 and 2018: late May/early June, mid-June, and late June/early July. Point counts were conducted at all 70 sampling points during favorable weather conditions starting within 15 min of sunrise, and ending by 1100. We recorded species, direction, and distance from the center of the point for all birds detected by sight or sound during 10-min observation periods.

2.2.5. Vegetation characteristics

We characterized microhabitat in July and August of 2017 and 2018. At each sampling point, we measured the understory woody species richness and density (stems/m^2) within a 5-m radius circle centered on the point. Additionally, we measured the foliage height diversity of the understory by recording the number of times vegetation touched a 4-meter pole marked in 30-cm increments placed in 4 clusters of 4 points spaced 2-m apart in each cardinal direction from the center of the 5-m radius circle. We measured the tree species richness and basal area in m^2/ha at each point using a BAF 2 metric prism in a variable radius plot. We estimated the canopy height at each sampling point by measuring 3 representative trees with a clinometer and then averaging them.

2.3. Analysis

2.3.1. Temperature

We averaged readings from the 2 iButtons at each site by week, distinguishing between daytime (sunrise to sunset) and nighttime (sunset to sunrise) temperature. We also averaged the daytime and nighttime temperature across all stream gorge sites and all upland sites. We plotted the weekly minimum and maximum temperatures recorded at each site to look for differences between habitat types. We analyzed differences between weekly mean temperatures at stream gorge and upland sites using paired t-tests.

2.3.2. Tree phenology

We considered the leaf emergence date for an individual shrub or tree to be the Julian date when 40% of the crown was in the young leaf phase because at this date a large amount of young leaf habitat was available and the transition from 40 to 90% young leaf phase for each tree often occurred rapidly. We analyzed the understory and canopy layers separately. For both layers, we calculated the mean leaf emergence date across all species between habitat types and tested for significant differences in mean leaf emergence dates using the Wilcoxon test. We used the same methods to separately analyze differences in leaf out of the three canopy and understory species with the most phenology observation between stream gorge and upland sites. We ranked the study sites in order of mean canopy leaf emergence date and used this rank-order as a covariate in the avian species richness model.

2.3.3. *Invertebrate biomass seasonality*

To characterize resource availability from an avian perspective, we converted invertebrate abundance into estimated dry biomass, using allometric equations (Rogers 1977; Sabo et al. 2002; Gruner 2003; Appendix B). We did not include dragonflies (*Odonata*), walking sticks (*Phasmida*), cicadas (*Cicadellidae*), or large (> 16 mm length) bees and wasps (*Hymenoptera*), because these are not likely a food source of forest songbirds. We also excluded slugs (*Stylommatophora*) and millipedes (*Myriapoda*) because these rarely occurred in foliage samples. We calculated the biomass of invertebrates collectively, as well as separately for the most common invertebrate orders: Lepidoptera larvae (caterpillars), Diptera (flies), and Aranaea (spiders). We calculated the average invertebrate biomass at each point by averaging data collected from the four branch samples during each visit. Within each of three time periods that roughly correspond to the timing of bird nesting- May (territory establishment), June (first nest attempts), and July (fledging and second nest attempts) - we calculated the mean invertebrate biomass of each sampling point, study site, and habitat type. We tested for significant differences in biomass between habitat types and between the three time periods using Wilcoxon rank sum tests.

2.3.4. *Avian species richness and density*

We calculated avian species richness at each study site by summing the number of species detected during all point count rounds within each year. However, we excluded species only detected on the first point count round, because it is likely they were late migrants. Additionally, we excluded non-insectivorous species including raptors, corvids, turkeys, waterfowl, wading birds, kingfishers, and strictly granivorous species (Mourning Dove and American Goldfinch). We tested for differences in richness of the resulting set of insectivore species between upland and stream gorge sites. To determine the influence of habitat we developed explanatory models of insectivorous bird species richness at the site level using linear regression (R version 3.5.3), after determining that the data were distributed normally and met model assumptions including independent and normally distributed residuals (R package "olsrr"). Our explanatory variable set included habitat type, study year, biomass of the 3 invertebrate orders with greatest abundance, mean daytime and nighttime temperature, and tree phenology rank of the study sites. We tested for multicollinearity between explanatory variables using variance inflation factors (R package "car") and used VIF > 5 as a cutoff for multicollinearity, so that only unrelated variables were included in the global model. We used an exhaustive search based on Baysian Information Criterion values (R package "leaps") to select a set of top models. We conducted a likelihood ratio test (R package "lmtest") to test goodness of fit of the top models.

To estimate avian density within each habitat type, we developed hierarchical distance-based density models (Buckland et al. 2001) using R package "unmarked" (Chandler, 2017). We selected a subset of four sampling points per site that were separated by at least 300 m, and only included point count data from these to avoid double-counting individual birds. We estimated the density of 14 widespread insectivorous species (those with > 45 detections in the reduced data set; common and scientific names of these target bird species in Appendix E). We recorded the distance to each bird at the location where it was first observed, within the categories 0–25, 26–50, 51–75, and 76–150 m. Because of a systematic estimation bias in field-recorded distances that resulted in unrealistically high density estimates, we corrected distance measurements with a calibration equation of *field distance + 10 m* (Buckland et al. 2001) after comparing histograms of detection distances with those recorded by other experienced observers in similar habitat conditions.

We found that patterns of relative density between habitat types were consistent between years for the14 focal species, and so we built models with data from two years. Our models used distance data to estimate a detection function within a Poisson framework, and we included covariates that may influence density, availability, and detection (Kery and Royle, 2016; Royle et al. 2004; Chandler, 2017). In the model for each species, we first compared the fit of half-normal, hazard rate, and uniform detection key functions using Akaike's Information Criterion (AIC) (Buckland et al. 2001) and selected a key function. We then tested support for null models and models with all combinations of covariates, including hours since sunrise and Julian date as availability covariates and distance to the nearest creek as a detection covariate. To account for nonlinear effects of time of day on detection probability we also tested models with a quadratic term of hours since sunrise (Farwell et al. 2016). We included habitat type as a density covariate in all models. This resulted in 24 models per species. We used AIC values to determine the top candidate models, i.e. those with ΔAIC < 2, and from among these we selected the most parsimonious model. We evaluated goodness of fit of top models using 100 simulations of a parametric bootstrap test (Kery and Royle, 2016; Reidy et al. 2014) based on the Chi-squared statistic.

2.3.5. *Vegetation characteristics*

We calculated understory foliage height diversity (Erdelen 1984) and averaged the four measurements taken at each sampling point. For the six vegetation characteristics, we averaged measurements or mean values taken at every sampling point within study sites. We compared the mean values of stream gorge and upland study sites using Wilcoxon signed-rank tests. We considered differences between groups to be significant if $p < 0.05$.

3. Results

3.1. *Microclimates*

Our iButton data showed that stream gorges maintained lower understory air temperature than the surrounding upland forests. Mean daytime and nighttime temperatures were consistently 1–3 °C lower in stream gorge sites than upland sites ($p < 0.01$; mean temperatures across all study sites, from April–July, ranged from $12-24$ °C in both years).

To determine the climatic context of our study years, we checked how the mean temperature during our study seasons compared to averages from 1950-present, examining data from the Baraboo weather station (NOWData) which is within 30 km of all the study sites. Monthly mean temperatures recorded at the Baraboo weather station during April-August 2017 were typical of long-term temperature records. However, the mean temperature in April of 2018 was 2.3 °C, which is the coldest on record and deviates from a long-term monthly average of 7.3 °C. May 2018 was the warmest on record, with a mean temperature of 18.3 °C, compared to a long-term monthly average of 13.9 °C. Mean temperatures during June-August 2018 were typical of long-term temperature records (Appendix C).

3.2. *Tree phenology*

We monitored 634 shrubs and trees in 2017 and 774 shrubs and trees in 2018 of 17 canopy and understory species (Appendix D). In 2017, we detected no differences in phenology between habitat types, perhaps because we conducted only 4 surveys, and each survey took multiple days to complete. In 2018, canopy and understory species as a whole experienced budbreak and leaf emergence earlier in upland sites than in stream gorge sites by 1–3 days ($p < 0.01$; Fig. 1). This pattern was consistent when we examined species patterns individually. Red

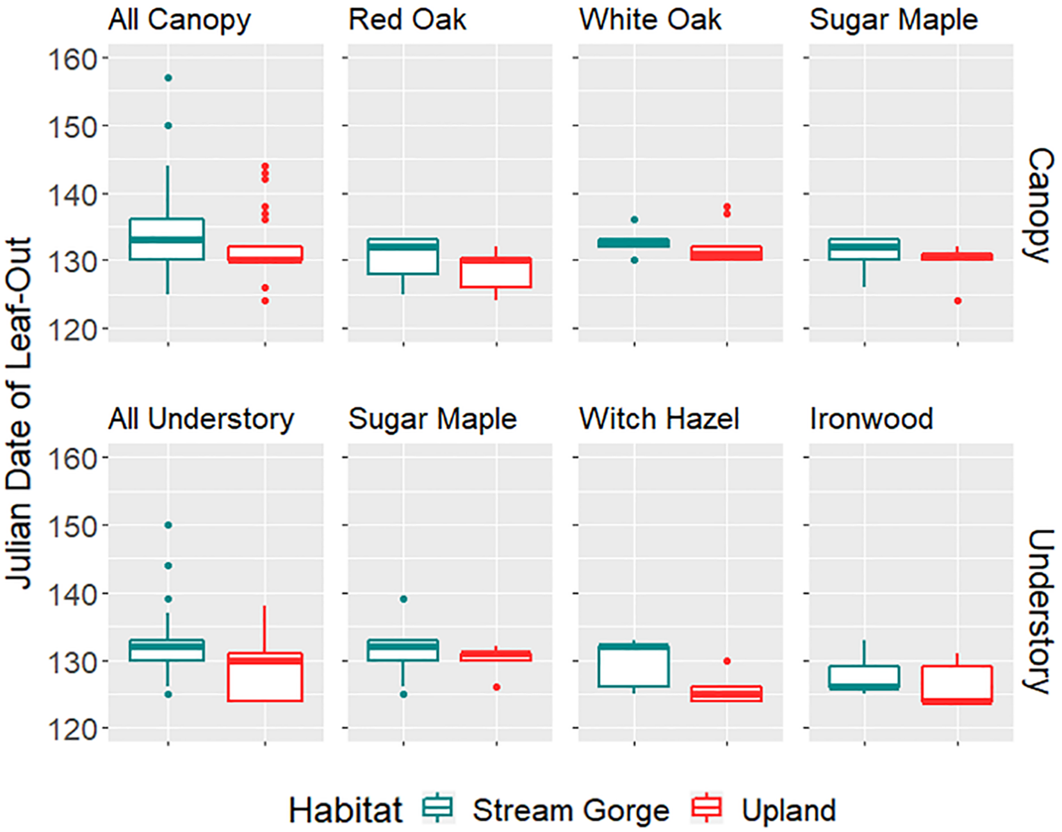

Fig. 1. Boxplots of Julian date indicating when 40% of the leaves of canopy and understory trees were in the young leaf stage in upland and stream gorge sites during 2018. All canopy and understory trees are combined in the left boxplots, and the three canopy and understory species with the most phenology records are shown individually. Middle lines indicate median, lower and upper hinges correspond to the 1st and 3rd quartiles (25th and 75th percentiles), vertical lines correspond to 1.5*interquartile range from the nearest quartile, and the dots beyond this represent outliers. In all comparisons, the difference between uplands and stream gorges was significant at $p < 0.05$.

Oak, White Oak, and Sugar Maple in the canopy and Sugar Maple, Witch Hazel, and Ironwood in the understory all leafed out earlier in upland sites ($p < 0.05$; Fig. 1). Red Oak, White Oak, and sugar Maple were the most abundant canopy tree species in the study sites and so their phenology had a large effect on forest conditions.

3.3. *Invertebrate biomass seasonality*

During 2017 mean invertebrate biomass was higher at stream gorge sites than at upland sites (12.0 vs. 10.8 mg per 100 leaves; $p = 0.02$). However, during 2018 mean biomass was distributed equally between habitat types (12.0 vs. 12.0 mg per 100 leaves; $p = 0.28$). Biomass seasonality exhibited a different seasonal pattern between years (Fig. 2). In both uplands and stream gorges in 2017, mean invertebrate biomass was higher in June than it was in May or July ($p < 0.05$), while in 2018 it was higher in both June and July than in May ($p < 0.05$). During June 2017, mean biomass was higher at stream gorge sites than at uplands ($p < 0.01$). Within all other months, invertebrate biomass did not differ between stream gorges and uplands.

3.4. *Avian species richness and density*

Mean insectivorous bird species richness tallied over both years was greater in stream gorge sites than upland sites (30.25 vs. 24.75 respectively; $p = 0.02$; species detected in each habitat type are reported in Appendix E). In 2017, mean species richness of stream gorge sites was 26.75 (range 25 to 30) compared to 21.25 (range 18 to 24) at upland sites ($p = 0.03$), while in 2018, mean species richness was 33.5 (range 32 to 37) at stream gorge sites, compared to 28.25 at upland sites (range 26 to 32; $p = 0.03$; Fig. 3). Additionally, mean species richness of long-distance migrant birds was greater in stream gorge sites than upland sites (20 vs. 16.88 respectively; $p = 0.02$).

We found that four models were similar in their ability to explain species richness, with adjusted R^2 values of 0.76–0.82. Three of these models included invertebrates among the explaining variables, and three models demonstrated a positive association between bird species richness and Lepidoptera biomass ($p = 0.03$–0.13, Table 3). The top model from this group, as indicated by being the most parsimonious of two models with the lowest BIC score, included habitat, year and mean Lepidoptera biomass as covariates (Table 3).

Avian density of 14 common and widely distributed insectivorous species, corrected for imperfect detection (see Appendix F), varied between habitat types (Table 4). Four species were more abundant in upland sites in both years, two were more abundant in stream gorge sites in both years, and eight were equally abundant in both habitats (Table 4). Of the seven insectivorous species that typically raise two sets of young each year in this study area, two were more abundant in stream gorges (Acadian Flycatcher and Chipping Sparrow $p < 0.01$), one was more abundant in uplands (Blue-gray Gnatcatcher $p = 0.06$), three were equally distributed (Eastern Wood-pewee $p = 0.22$; Wood Thrush $p = 0.88$; American Robin $p = 0.14$), and one was not detected frequently enough to estimate abundance (Eastern Towhee). The raw average abundances of 35 most frequently detected bird species are reported in Appendix G.

3.5. *Vegetation characteristics*

Two of the six vegetation characteristics differed between habitat types ($p < 0.05$, Table 5). Mean understory tree and shrub density was 1.0 stems/m^2 in stream gorge sites and 1.9 stems/m^2 in upland sites ($p = 0.03$). Mean basal area was also lower in stream gorge sites (20.4 vs. 26.8 m^2/ha, $p = 0.03$). Understory woody species richness, foliage

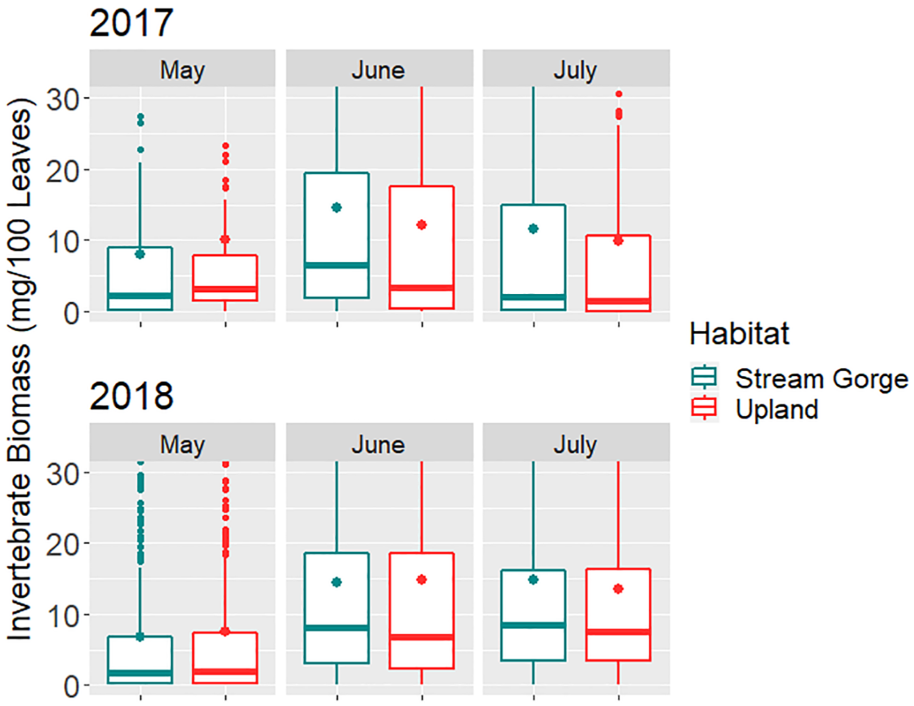

Fig. 2. Boxplots of mean invertebrate biomass (mg/100 leaves) from May – July 2017 and 2018 in upland and stream gorge sites. Middle lines indicate median, lower and upper hinges correspond to the 1st and 3rd quartiles (25th and 75th percentiles), whiskers correspond to 1.5*interquartile range from the nearest quartile, and the dots beyond this represent outliers. The Y-axis is truncated at 30 and therefore some outlying points are not shown. Stars indicate mean values for each group.

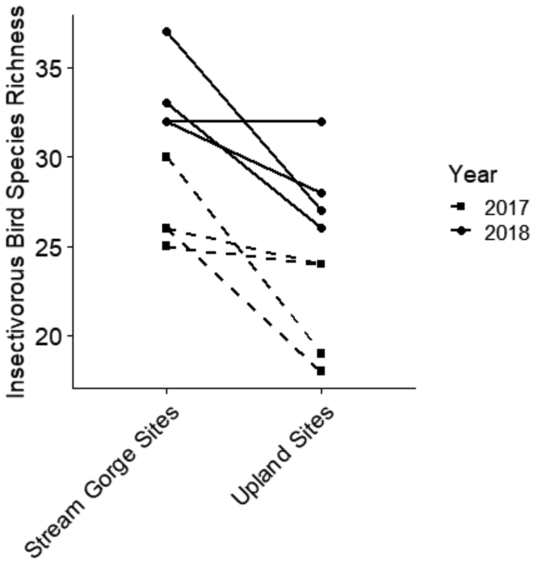

Fig. 3. Insectivorous bird species richness in upland and stream gorge sites in 2017 and 2018. Lines connect study sites paired by proximity and geologic substrate, and line type represents year.

height diversity, canopy species richness, and canopy height were consistent between habitat types (Table 5).

4. Discussion

Areas with a variety of topographic contexts in close proximity are thought to offer greater resilience to climate change than areas with uniform topography (Anderson et al. 2014). We measured three links of a food chain with the goal of determining whether the phenological timing of resources for breeding birds differed according to topographic position. We found that small-scale differences in topographic position separated by as little at 150 m elevation create different microclimates, as we had expected. The pace of tree and shrub phenology at the cooler stream gorge sites was slower, in that spring leaf-out was delayed by 1–3 days relative to nearby warmer upland sites. In both warm and cool microclimates, seasonal patterns of invertebrate abundance were not characterized by a pronounced seasonal peak, but rather increased gradually throughout the spring and summer. We found that cool microclimates in sheltered valleys supported greater insectivorous bird species richness than upland sites, which we expected, but contrary to our hypothesis did not clearly support higher invertebrate biomass or avian density.

Small scale differences in topographic position separated by 40 m elevation have been shown to delay leaf-out timing of canopy trees in southern New England by as much as 14 days, due to the frost pocket effect in valleys (Fisher et al. 2006). And yet, we found more modest differences of 1–3 days between leaf-out timing in upland and stream gorge sites, despite elevation differences between study sites ranging from 25 to 108 m. This could be attributable to the unusual temperature extremes of spring 2018 during which leaf-out timing was compressed into a period of just a few days for most tree species. Alternatively, the elevation of the study sites, which ranged from 297 to 408 m above sea level, may have caused some confounding effects. In the mid-Atlantic states, there is evidence for a ‘phenology breakpoint’ around 275 m above sea level, below which leaf-out is delayed by a *loss* of elevation and above which it is delayed by a *gain* in elevation (Elmore et al. 2012). Because the sites in this Baraboo Hills study occur close to this breakpoint, it is possible that both effects may have been operating (i.e. frost pocket effect as well as cooler temperatures at the higher elevations of our upland sites). Fisher et al. (2006) found pronounced differences in the timing of leaf-out between valleys and uplands that were located 50–225 m above sea level, and thus below the breakpoint.

Invertebrate biomass in the Baraboo Hills study area did not exhibit a strong seasonal peak timed to leaf-out in May, in agreement with our expectations. The gradual increase in invertebrate biomass that we observed in both upland and stream gorge sites is characteristic of a mixed deciduous forest with high tree species richness (Burger et al. 2012), exactly the conditions of our study area. Each tree species is thought to support a unique invertebrate community, consisting of invertebrate species that emerge at different times throughout the season (Futuyma and Gould 1979; Holmes and Schultz 1988; Tallamy and Schropshire 2009). Therefore, high tree species diversity may contribute to relatively stable invertebrate abundance throughout the season, and a low likelihood of trophic mismatches between birds and their invertebrate prey in this study

Table 3
Estimates, standard errors of the estimates, and p-values of the coefficients in the top species richness models (Δ BIC = within 2 of the top model). Adjusted R^2, BIC and likelihood ratio test p-values for overall model significance are also reported.

Variable	Definition	Estimate	Standard Error	p-value	Adj. R^2	BIC	LR test p-value
Model 1					0.80	−18	< 0.01
(Intercept)		−1080	2684	< 0.01			
Habitat	Stream gorge (0) or upland site (1)	−5.26	1.14	< 0.01			
Year	2017 or 2018	5.37	1.33	< 0.01			
Lepid.	Mean Lepidoptera Biomass (mg/100 leaves)	1.45	0.74	0.07			
Model 2					0.82	−18	< 0.01
(Intercept)		−6132	4244	0.18			
Habitat		−6.73	1.52	< 0.01			
Year		3.05	2.10	0.17			
Lepid.		1.87	0.77	0.03			
Diptera	Mean Diptera Biomass (mg/100 leaves)	−1.22	0.88	0.19			
Model 3					0.76	−17	< 0.01
(Intercept)		−13588	2514	< 0.01			
Habitat		−5.50	1.25	< 0.01			
Year		6.75	1.25	< 0.01			
Model 4					0.81	−16	< 0.01
(Intercept)		−4799	4605	0.32			
Habitat		−6.77	1.54	< 0.01			
Invert.	Mean Invertebrate Biomass (mg/100 leaves)	0.33	0.40	0.43			
Lepid.		1.49	0.91	0.13			
Dipt.		−1.41	0.92	0.15			

Table 4
Estimated density (territories per hectare) of 14 common bird species by habitat type, corrected for imperfect detection. DB indicates whether or not a species is double-brooded in this study area. P-value indicates the significance of habitat type as a density covariate in the distance model.

		Upland		Stream Gorge		
Species	DB	Density	Standard Error	Density	Standard Error	p-value
Long-distance Migrant Species						
Eastern Wood-Pewee	Y	1.61	0.19	1.31	0.17	0.21
Acadian Flycatcher	Y	0.18	0.06	1.30	0.21	< 0.01
Yellow-throated Vireo	N	0.31	0.09	0.31	0.09	0.96
Red-eyed Vireo	N	1.21	0.21	0.83	0.17	0.15
Blue-gray Gnatcatcher	Y	1.43	0.27	0.80	0.21	0.06
Wood Thrush	Y	0.74	0.37	0.77	0.39	0.88
Ovenbird	N	0.56	0.09	0.17	0.04	< 0.01
American Redstart	N	1.52	0.31	0.96	0.23	0.07
Scarlet Tanager	N	0.52	0.11	0.27	0.07	0.02
Rose-breasted Grosbeak	N	0.42	0.11	0.52	0.18	0.27
Short-distance Migrant Species						
American Robin	Y	0.41	0.09	0.59	0.11	0.14
Chipping Sparrow	Y	0.09	0.07	0.84	0.55	< 0.01
Resident Species						
Black-capped Chickadee	N	0.98	0.28	0.80	0.24	0.61
White-breasted Nuthatch	N	0.36	0.23	0.22	0.13	0.33

area. However, the connection between tree species richness and invertebrate biomass is speculative and this study was not designed to test the influence of tree species diversity, but rather to capture conditions at different topographic positions, at sites with tree composition typical of the Baraboo Hills. Different invertebrate taxonomic orders exhibited differences in biomass seasonality trends (see Appendix H), and Lepidoptera larvae appeared to have a gradual peak in biomass during June. In European forests, three bird species specialized to feed on caterpillars experienced phenological mismatches, while two bird species that feed on a wider variety of insects did not (Dunn and Moller 2014). Although the peak in Lepidoptera larvae biomass that we measured was not abrupt in either 2017 or 2018, the trend of peaking in June suggests that the possibility for phenological mismatches may exist under certain weather conditions for bird species in this study area that feed exclusively on caterpillars.

A caveat of this study is that we were unable to characterize canopy invertebrate biomass but were limited to sampling the lowest 6 m of forest vegetation. Many bird species forage exclusively in the canopy, and so the understory invertebrate surveys we conducted may or may not provide a true index of food resources available for those species. In some mixed deciduous forests, understory invertebrate communities have been shown to be similar to those in the canopy (Holmes and Schultz 1988; Rodenhouse and Holmes 1992), however, other studies have found that there is a high degree of vertical stratification in folivorous invertebrate communities (Murakami et al. 2005; Ulyshen 2011). Additionally, some insectivorous birds sally for aerial insects, which we did not quantify beyond those resting on foliage, thus it is possible this food source was not fully detected.

The two-season length of field data collection likely contributed to lack of precision in measures of phenology and invertebrates. It is possible that with additional years of data collection under a greater set of climate contexts, patterns would become more differentiated. Regional weather conditions and yearly variation in timing of invertebrate biomass may play an important role in shaping annual avian communities. Because Lepidoptera larvae are an important food source for nesting songbirds, it follows that habitats with rich invertebrate food resources would support more songbird species. However, the coefficient for habitat type was substantially larger than for Lepidoptera biomass, indicating that habitat plays an additional role, beyond abundance of lepidopterans, in patterns of bird species diversity.

Among the 14 bird species for which we were able to estimate density, patterns were not consistent between habitat types, likely because species are adapted to different forest microsite conditions. For example, Ovenbirds tend to avoid especially rocky areas (Mossman and Lange 1982) and this may have contributed to their lower density in stream gorge sites, which tend to have more outcroppings than upland sites. Additionally, some bird species do not forage in tree species in proportion to the amount of invertebrate biomass those tree species support, and they may instead be responding to the structure of the leaves and branches (Holmes and Schultz 1988). To take this research question further, it would be

Table 5

Mean woody vegetation characteristics measured at 7–10 sampling points per study site in July- August of 2017 and 2018. Averages are reported for each habitat type. Stars indicate significant differences between habitat types at the $p < 0.05$ level.

Study Site	Understory Density (stems/m^2)	Foliage Height Diversity	Understory Species Richness	Basal Area (m^2/ha)	Canopy Species Richness	Mean Canopy Ht. (ft)
Stream Gorge	1.0*	1.4	10.2	20.4*	4.7	87.7
BH	1.4	1.6	14.2	19.2	4.9	84.5
HD	0.6	1.3	8.3	23.6	5.3	91.2
PG	1.4	1.6	11.1	19.5	4.3	83.3
PH	0.7	1.0	7.1	19.1	4.2	91.8
Upland	1.9*	1.3	10.5	26.8*	4.3	82.6
HC	2.0	1.4	10.4	31.4	5.0	85.1
NAT	2.0	1.0	10.1	25.3	5.0	78.4
SB	1.7	1.5	12.0	24.9	3.4	81.9
SR	1.9	1.3	9.6	25.5	3.8	85.0

necessary to understand how habitat structure, species composition, and invertebrate biomass interact to shape habitat quality for forest songbirds.

5. Conclusions

As the climate of the Midwestern US is characterized by increasingly warm spring and summer temperatures, cool microclimates within forests may provide important habitat elements for bird species. Focusing conservation efforts on forest areas with a diversity of microclimates could mitigate some of the negative impacts of climate change on insectivorous bird species by providing stable food resources throughout the nesting season. However, not all bird species in this study were positively associated with the forest conditions in stream gorge sites with cool microclimates. There are many factors that influence the quality of bird habitat and preserving a variety of habitat and microclimate conditions is likely to result in habitat for the largest range of species responses in a changing climate.

CRediT authorship contribution statement

Maia E. Persche: Conceptualization, Investigation, Formal analysis, Writing - original draft. **Anna M. Pidgeon:** Conceptualization, Methodology, Resources, Writing - review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

Median length of invertebrates of each size class, excluding antennae and legs.

Invertebrate Groups	Median Length of Size Classes (mm)				
	Class 1	Class 2	Class 3	Class 4	Class 5
Lepidoptera larvae	4	10	16	22	30
Coleoptera, Diptera, Aranea, Opiliones, Hemiptera, Hymenoptera, Neuroptera, Acari, Collembola	2	5	10	16	22
Adult Lepidoptera, Ephemeroptera, Orthoptera, Plecoptera, Trichoptera	5	10	16	22	25+

Appendix B

Order-specific allometric equations used to calculate invertebrate biomass based on length (L).

Taxonomic Order	Allometric Equation	Source	Times Cited
Lepidoptera larvae	0.004(Lˆ2.64)	Rogers 1977	145
Adult Lepidoptera	0.012(Lˆ2.69)	Sabo et al. 2002	130
Coleoptera	0.04(Lˆ2.64)	Sabo et al. 2002	130
Diptera	0.04(Lˆ2.26)	Sabo et al. 2002	130
Aranae and Opiliones	0.05(Lˆ2.74)	Sabo et al. 2002	130
Hymenoptera (Formicidae)	0.027(Lˆ2.666)	Sabo et al. 2002	130
Hymenoptera (Sphecidae)	0.166(Lˆ1.797)	Sabo et al. 2002	130
Hemiptera	0.005(Lˆ3.33)	Sabo et al. 2002	130
Ephemeroptera	0.014*(Lˆ2.49)	Sabo et al. 2002	130
Orthoptera	0.03*(Lˆ2.55)	Sabo et al. 2002	130
Neuroptera	0.007*(Lˆ2.739)	Gruner 2003	51
Plecoptera	0.26*(Lˆ1.69)	Sabo et al. 2002	130
Acari	0.0562*(Lˆ2.332)	Gruner 2003	51
Collembola	0.0056*(Lˆ2.809)	Gruner 2003	1
Trichoptera	0.01*(Lˆ2.9)	Sabo et al. 2002	130

Appendix C

Average monthly temperature recorded at the Baraboo weather station from 1950 to 2018. Mean temperatures are reported in degrees Celsius with standard error. Maximum and minimum monthly average temperatures and they years they occurred are also shown.

	April	May	June	July	August
Mean Temperature	7.3	13.9	19	21.3	20
Standard Error	0.23	0.23	0.17	0.18	0.18
Maximum (Year)	12.7 (1985)	18.3 (2018)	22.0 (2005)	25.3 (2012)	23.2 (1955)
Minimum (Year)	2.3 (2018)	9.9 (1996)	14.9 (1969)	18 (1996)	17.3 (1994)

Appendix D

Breakdown of 774 trees monitored for phenology in 2018, by species in each study site, habitat type, and forest layer. A subset of 634 trees was monitored during 2017. Upland site name acronyms are italicized. Refer to Table 1 for site names and descriptions, and Table 2 for scientific names of tree species.

	BH	*SR*	HD	*HC*	PH	*NAT*	PG	*SB*	Stream Gorge	*Upland*	**Total**
Canopy Species											
Am. Elm	2	1	1	2	0	3	0	1	3	7	**10**
Aspen	3	3	0	4	0	4	2	0	5	11	**16**
Basswood	2	0	3	3	3	2	4	1	12	6	**18**
Bit. Hickory	2	2	4	3	3	2	1	2	10	9	**19**
Black Ash	5	0	4	0	2	0	5	0	16	0	**16**
Red Maple	1	3	3	1	1	6	6	1	11	11	**22**
Red Oak	10	8	9	10	8	8	8	9	35	35	**70**
Sh. Hickory	3	6	4	3	2	4	1	3	10	16	**26**
Slippery Elm	0	1	3	6	1	1	1	0	5	8	**13**
Sugar Maple	8	5	6	5	7	1	5	1	26	12	**38**
White Ash	0	2	0	5	4	1	6	2	10	10	**20**
White Oak	10	9	9	11	7	13	4	13	30	46	**76**
Yellow Birch	7	0	6	0	8	0	0	0	21	0	**21**
Total	**53**	**40**	**52**	**53**	**46**	**45**	**43**	**33**	**194**	**171**	**365**
Understory Species											
Am. Elm	2	3	5	3	2	4	1	1	10	11	**21**
Basswood	4	2	1	3	2	4	4	1	11	10	**21**
Bit. Hickory	1	0	3	3	5	6	1	2	10	11	**21**
Black Ash	9	0	2	0	1	0	5	0	17	0	**17**
Black Cherry	3	5	1	8	2	3	4	4	10	20	**30**
Blue Beech	7	1	7	2	4	0	7	0	25	3	**28**
Ironwood	2	10	0	11	2	5	6	4	10	30	**40**
Red Maple	1	2	4	4	1	5	3	3	9	14	**23**
Red Oak	1	3	1	2	1	5	2	4	5	14	**19**
Sh. Hickory	4	1	1	3	0	2	6	5	11	11	**22**
Slippery Elm	0	1	4	4	3	1	3	2	10	8	**18**
Sugar Maple	6	9	10	6	10	1	3	5	29	21	**50**
White Ash	1	4	3	2	3	4	3	2	10	12	**22**
White Oak	5	3	1	2	1	1	3	4	10	10	**20**
Witch Hazel	9	1	7	3	8	0	7	2	31	6	**37**
Yellow Birch	5	0	8	0	7	0	0	0	20	0	**20**
Total	**60**	**45**	**58**	**56**	**52**	**41**	**58**	**39**	**228**	**181**	**409**

Appendix E

Common and scientific names of insectivorous bird species included in species richness and density estimates.

Common Name	Scientific Name	Stream Gorge	Upland
Long-distance Migrant Species			
Yellow-billed Cuckoo	*Coccyzus americanus*	X	X
Ruby-throated Hummingbird	*Archilochus colubris*	X	X
Great Crested Flycatcher	*Myiarchus crinitus*	X	X
Eastern Wood-Pewee	*Contopus virens*	X	X
Acadian Flycatcher	*Empidonax virescens*	X	X
Least Flycatcher	*Empidonax minimus*	X	X
Eastern Phoebe	*Sayornis phoebe*	X	
Yellow-throated Vireo	*Vireo flavifrons*	X	X
Red-eyed Vireo	*Vireo olivaceus*	X	X
Blue-gray Gnatcatcher	*Polioptila caerulea*	X	X
Veery	*Catharus fuscescens*	X	X
Wood Thrush	*Hylocichla mustelina*	X	X
Baltimore Oriole	*Icterus galbula*	X	X
Ovenbird	*Seiurus aurocapillis*	X	X

Worm-eating Warbler	*Helmitheros vermivorum*	X	
Louisiana Waterthrush	*Parkesia motacilla*	X	
Blue-winged Warbler	*Vermivora cyanoptera*	X	X
Common Yellowthroat	*Geothlypis trichas*	X	X
American Redstart	*Setophaga ruticilla*	X	X
Cerulean Warbler	*Setophaga fusca*	X	X
Blackburnian Warbler	*Setophaga fusca*	X	
Yellow Warbler	*Setophaga petechia*	X	X
Chestnut-sided Warbler	*Setophaga pensylvanica*		X
Black-throated Green Warbler	*Setophaga virens*	X	
Hooded Warbler	*Setophaga citrina*	X	X
Scarlet Tanager	*Piranga olivacea*	X	X
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	X	X
Indigo Bunting	*Passerina cyanea*	X	X
Short-distance Migrant Species			
House Wren	*Troglodytes aedon*	X	X
Winter Wren	*Troglodytes hiemalis*	X	
Carolina Wren	*Thryothorus ludovicianus*	X	
Eastern Bluebird	*Sialis sialis*		X
American Robin	*Turdus migratorius*	X	X
Gray Catbird	*Dumetella carolinensis*	X	X
Cedar Waxwing	*Bombycilla cedrorum*	X	X
Eastern Towhee	*Pipilo erythrophthalmus*	X	X
Chipping Sparrow	*Spizella passerina*	X	X
Song Sparrow	*Melospiza melodia*	X	
Brown-headed Cowbird	*Molothrus ater*	X	X
Resident Species			
Black-capped Chickadee	*Poecile atricapillus*	X	X
Tufted Titmouse	*Baeolophus bicolor*	X	X
White-breasted Nuthatch	*Sitta carolinensis*	X	X
Brown Creeper	*Certhia americana*	X	X
Northern Cardinal	*Cardinalis cardinalis*	X	X

Appendix F

Top distance-based density model for each species. Key function, availability and detection covariates, estimates, and p-values are shown ~1 indicates null variable in model.

Species	Key Function	Availability Covariates	Est.	p-value	Detection Covariates	Est.	p-value
Eastern Wood-Pewee	Hazard-rate	Sun.hour	5.87	0.855	~1	–	–
Acadian Flycatcher	Hazard-rate	~1			~1	–	–
Yellow-throated Vireo	Hazard-rate	Sun.hour	9.57	0.85	~1	–	–
Red-eyed Vireo	Hazard-rate	Sun.hour	7.78	0.64	~1	–	–
		Sun.hour^2	−1.59	0.63			
		Julian	−0.06	0.29			
Black-capped Chickadee	Hazard-rate	Sun.hour	2.96	0.90	creek	−0.00	0.52
White-breasted Nuthatch	Hazard-rate	~1	–	–	creek	0.00	0.76
Blue-gray Gnatcatcher	Hazard-rate	~1	–	–	creek	−0.00	0.95
Wood Thrush	Halfnormal	Julian	0.06	0.00	~1	–	–
American Robin	Hazard-rate	~1	–	–	~1	–	–
Chipping Sparrow	Hazard-rate	~1	–	–	~1	–	–
Ovenbird	Hazard-rate	~1	–	–	~1	–	–
American Redstart	Halfnormal	~1	–	–	~1	–	–
Scarlet Tanager	Hazard-rate	Sun.hour	9.29	0.87	~1	–	–
Rose-breasted Grosbeak	Halfnormal	Sun.hour	−2.06	0.06	~1	–	–
		Sun.hour^2	0.40	0.13			
		Julian	0.17	0.03			

Appendix G

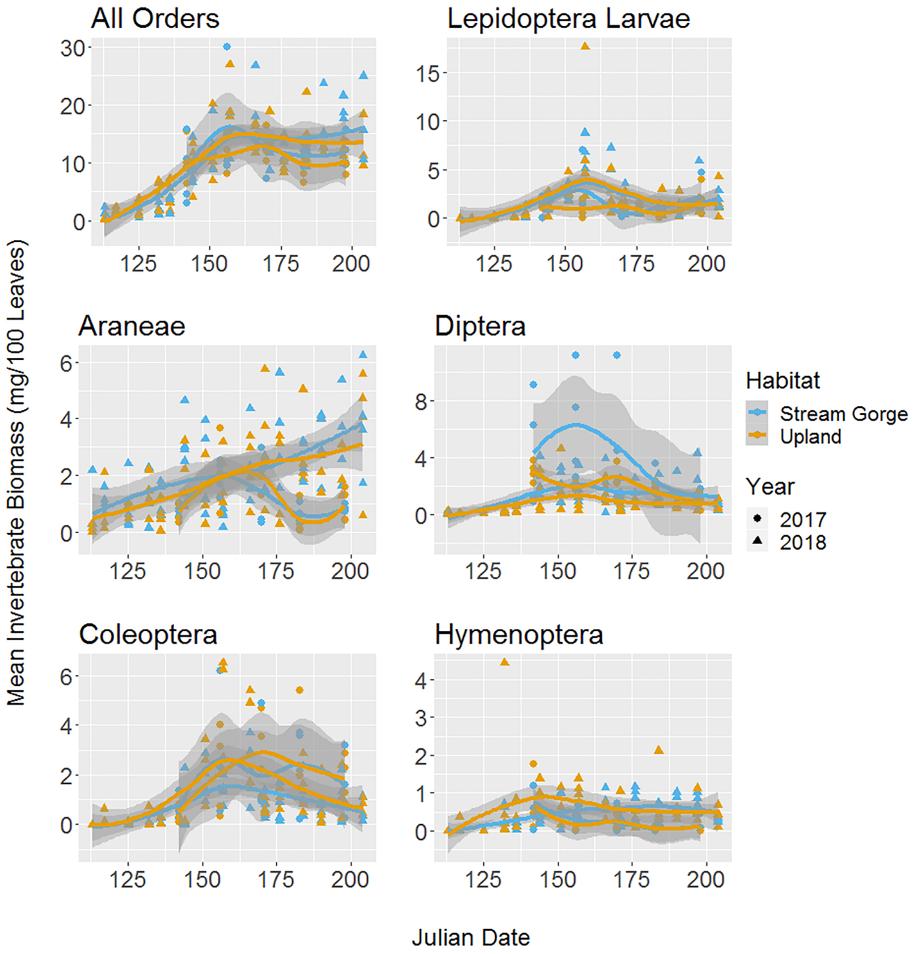
Raw average density (territories per hectare) by habitat type of all insectivorous bird species with at least 20 detections on point counts between late May and early July 2017 and 2018. P-values of Welch's t-tests with Bonferroni corrections are reported to compare density between habitat types.

Species	Stream Gorge Density	Standard Deviation	Upland Density	Standard Deviation	p-value
Yellow-billed Cuckoo	0.06	0.18	**0.17**	0.34	0.02
Red-bellied Woodpecker	0.04	0.14	**0.33**	0.47	0.00
Yellow-bellied Sapsucker	0.08	0.22	**0.09**	0.29	0.83
Downy Woodpecker	0.12	0.28	**0.18**	0.30	0.19
Hairy Woodpecker	0.10	0.27	**0.12**	0.29	0.67
Great Crested Flycatcher	0.19	0.36	**0.30**	0.47	0.13
Eastern Wood-Pewee	1.46	0.88	**2.13**	0.99	0.00
Acadian Flycatcher	**1.44**	0.72	0.40	0.59	0.00
Least Flycatcher	0.28	0.72	**0.30**	0.75	0.84

Eastern Phoebe	**0.33**	0.50	0.00	0.00	0.00
Red-eyed Vireo	0.93	0.71	**1.47**	0.76	0.00
Yellow-throated Vireo	**0.35**	0.41	0.30	0.46	0.48
Black-capped Chickadee	**0.34**	0.56	0.30	0.45	0.67
Tufted Titmouse	**0.18**	0.42	0.17	0.34	0.95
White-breasted Nuthatch	0.15	0.31	**0.34**	0.41	0.00
House Wren	0.18	0.44	**0.28**	0.66	0.26
Winter Wren	**0.25**	0.48	0.00	0.00	0.00
Blue-gray Gnatcatcher	0.47	0.56	**0.96**	0.76	0.00
Veery	**1.31**	1.23	0.24	0.52	0.00
Wood Thrush	0.25	0.48	**0.35**	0.45	0.21
American Robin	**0.78**	0.81	0.60	0.63	0.14
American Goldfinch	**0.48**	0.50	0.40	0.48	0.29
Eastern Towhee	0.18	0.55	**0.21**	0.42	0.71
Chipping Sparrow	**0.71**	0.73	0.03	0.17	0.00
Song Sparrow	**0.21**	0.47	0.00	0.00	0.00
Baltimore Oriole	**0.12**	0.27	0.06	0.20	0.17
Brown-headed Cowbird	**0.78**	0.69	0.72	0.58	0.58
Ovenbird	0.38	0.64	**1.21**	0.74	0.00
Louisiana Waterthrush	**0.74**	0.60	0.00	0.00	0.00
American Redstart	0.60	0.88	**0.79**	0.86	0.19
Cerulean Warbler	0.08	0.22	**0.42**	0.62	0.00
Black-throated Green Warbler	**0.26**	0.52	0.01	0.07	0.00
Scarlet Tanager	0.43	0.50	**0.62**	0.61	0.05
Northern Cardinal	0.10	0.29	**0.24**	0.46	0.03
Rose-breasted Grosbeak	**0.43**	0.56	0.41	0.44	0.84

Appendix H

Biomass seasonality of five abundant invertebrate orders, and all orders combined (including orders not analyzed separately). Each point represents mean invertebrate biomass (mg/100 Leaves) of a study site, with different shapes indicating study year. Habitat types are represented by different colors. Samples were taken from 16 understory tree and shrub species at heights ranging from 0.5 to 6 m.



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