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THE COMPARATIVE EFFECTS OF LANDSCAPE-LEVEL FOREST FRAGMENTATION, FOREST AREA AND LOCAL HABITAT MEASURES ON CONNECTICUT BIRD COMMUNITIES

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Abstract. I studied how breeding and wintering forest bird communities across Connecticut responded to variation in landscape attributes and habitat characteristics. I hypothesized that increasing forest fragmentation would result in 1) declines in the richness and density of breeding communities, as well as in neotropical migrant, ground nesting, interior forest-associated and arboreal and ground foraging richness and density, 2) population and richness increases in breeding short-distance migrant and resident, foraging generalist and edge/successional and habitat generalist species, including population increases in the nest parasitic Brown-headed Cowbird, 3) forest area loss effects predominating over fragmentation effects, 4) fragmentation effects predominating over local habitat effects, 5) natural forest breaks having fewer community effects than human-associated ones, and 6) winter effects of fragmentation on species richness, community density and species composition showing little community consequence. Using the Variable Circular Plot technique, I surveyed birds at 1,815 points along 121 transects that traversed ca. 400 km of forest. From these data, I computed sampled species richness and community density as well as individual species' population densities for each transect. Moreover, I classified species encountered as to their nest site selection, macrohabitat use, microhabitat use, migratory strategy and trophic affiliation. I also made 12,705 habitat measurements at survey points on: 1) forest type, 2) moisture regime, 3) diameter of canopy trees at breast height, 4) canopy cover, 5) understory density, 6) elevation and 7) vertical vegetation complexity. I employed QGIS 3.16 on aerial orthophotos to characterize the landscapes near study sites by constructing an 800 m wide corridor around each and distinguishing the following: 1) forest, 2) human-associated, 3) agricultural, 4) open water, 5) marshes and 6) beaches. Once delineated, I computed areas of forest, non-forest and core forest and perimeter/area ratios for 31,550 ha of study area. To evaluate temporal variation in community relationships, I duplicated surveys at 50 sites in eastern Connecticut during separate years. Based on observations of 36,702 summering individuals of 123 species and 13,742 wintering individuals of 63 species, hypothesis 1 was supported in each instance by population density results although species richness results were often more closely associated with habitat measures. Among landscape measures, forest fragmentation-associated measures had the closest association with summer community measures 67% of the time, strongly suggesting that fragmentation effects were the predominant driver of such community patterns. Hypothesis 2 had only limited support, with short-distance migrant density and richness, foraging generalist density and richness, edge/successional density and richness, habitat generalist density and Brown-headed Cowbird density showing little response to landscape measures. Hypothesis 3 was supported by evidence that the effects of fragmentation appeared to predominate over those of simply forest extent in predicting

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summer and winter bird community characteristics even in the comparatively extensive forests of southern New England. Evidence supporting hypothesis 4 was weak, with community and individual species measures tending to be more closely associated with habitat measures. Hypothesis 5 was generally supported, with few summer or winter community measures or species patterns showing any significant relationship to natural forest breaks. Hypothesis 6 was also supported, with winter community and species density patterns showing little relationship to any landscape measures, with particularly elevation appearing to be a principal driver of winter patterns. Duplicate observations for eastern Connecticut showed that, although a number of observations were consistent with statewide patterns, temporal variation did occur in some ecological relationships, much as reported for other temperate bird communities.

Investigation of the effects of forest fragmentation on bird communities originated in studies of species-area and island biogeographic effects observed in woodlots, where more species occurred in larger tracts and community composition shifted with increasing tract size from generalist and edge/ successional to forest interior species (Galli et al. 1976, Ambuel and Temple 1983, Blake and Karr 1987, Robbins et al. 1989). Forest interior-breeding species that migrate to the neotropics appeared particularly susceptible to fragmentation effects (Lynch and Whigham 1984, Askins and Philbrick 1987, Zipkin et al. 2009), with fragmented forests described as having reduced food supply (Gibbs and Faaborg 1990, Burke and Nol 1998), greater brood parasitism (Robinson et al. 1995, Donovan et al. 1997, Hobson and Bayne 2000), greater predation (Wilcove 1985, King et al. 1997, Hobson and Bayne 2000) and greater rates of local extinction (Boulinier et al. 2001, Hames et al. 2001).

Despite such assertions, much contrary data on the effects of fragmentation exist. Edge effects are often thought to impact communities negatively (George and Brand 2002, Manolis et al. 2002, Hoover et al. 2006), but amount of edge does not always relate to species composition (Hawrot and Niemi 1996, Drapeau et al. 2000) or nest success (Hanski et al. 1996, Matthysen and Adriaensen 1998). Moreover, community richness and abundance may not vary with fragmentation (Manuwal and Manuwal 2002), as microhabitat conditions can be important in determining the presence of individual species (Lynch and Whigham 1984, Dorazio et al. 2015). In addition, the amount of nest parasitism can be unrelated to fragmentation (Askins and Philbrick 1987, Fauth 2000, Morimoto et al. 2012), as parasitism levels are related to geographic differences in Brown -headed Cowbird (*Molothrus ater*) density (Hanski et al. 1996). With respect to predation, DeGraaf et al. (1999) found no difference in nest predation between edge and interior forest, although ground nesters were more heavily predated, and Rodewald et al. (2012) found nest survival unrelated to urbanization for most species. All species groups are also not equally affected by fragmentation, with generalist (Telleria and Santos 1994), edge/successional and short-distance migrant species (Lynch and Whigham

1984, Hobson and Bayne 2000) appearing less affected. Furthermore, natural forest breaks (Drapeau et al. 2000) and silvicultural practices do not appear to have the same impact on communities as agricultural and human development (Thompson et al. 2002) and forest gaps can have positive community effects (Blake and Hoppes 1986). Fragmentation effects also diverge geographically, with less fragmented forests in the eastern U.S. showing the lowest effects (Rosenberg et al. 1999, Thompson et al. 2002, Rittenhouse et al. 2010), whereas highly fragmented midwestern landscapes are thought to function as population sinks (Robinson et al. 1995, Brawn and Robinson 1996, Tittler et al. 2006).

Another issue concerning studies of forest fragmentation is that delineation of which species belong in such categories as forest interior inhabitants (e.g., Butcher et al. 1981) is not always based on sound evidence as, considering species accounts in Birds of the World (Billerman et al. 2022; see also Villard 1998), quantitative data on species' habitat use are often limited, with little study of the basic natural history of many species occurring since the 1980s. Indeed, the recent reticence of many top-tier scientific journals even to consider publishing basic studies has not served the cause of scientific inquiry well. Moreover, population phenomena among forest species, particularly those at their range limits, may have local distributions and populations closely related to factors unrelated to fragmentation in summer (Craig et al. 2022) and winter (Craig 2012).

Most studies on forest fragmentation have dealt with breeding birds. Those few that have examined winter communities have sometimes found that richness, evenness (Hamel et al. 1993) or abundance (Yahner 1993) have no relation to a variety of fragmentation-related metrics, although Yahner (1993) found that richness increased in heavily logged area. Moreover, in experiments to get wintering birds to cross forest breaks, Black-capped Chickadees (*Poecile atricapillus*) were less likely to cross gaps as width increased (St Clair et al. 1998). In addition, Pearson et al. (1993) found that landscape matrix and within-patch vegetation explained most differences in winter richness and abundance, Doherty and Grubb (2000) found that richness, density and species composition were positively related to forest
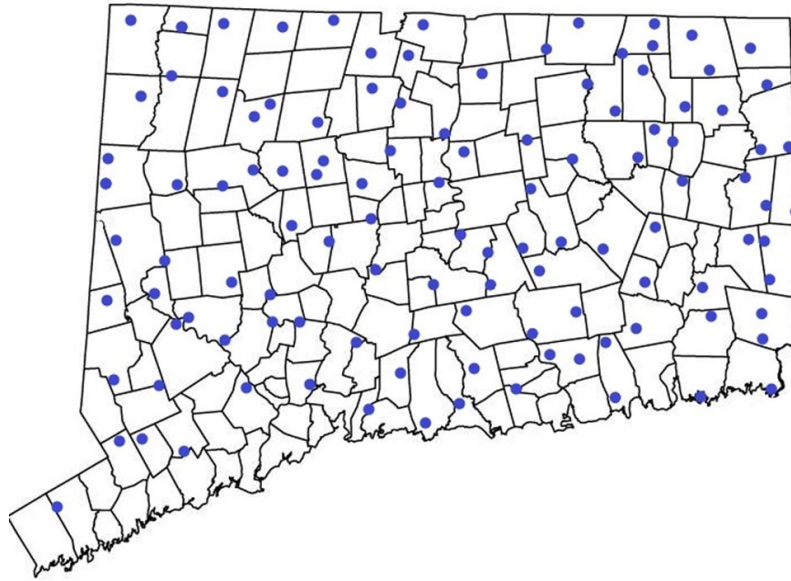
FIG. 1. Location of 121 study sites across Connecticut.

area and Craig (2012) and Craig and Klaver (2013) found that habitat associations were inconsistent except that energetically less expensive lower, more southerly elevations were related to population increases.

Although the term fragmentation tends to be used synonymously with habitat loss, the two terms can be argued to have separate meanings (D'Eon 2002), with habitat loss relating to the amount of a particular habitat remaining in an area once completely covered by it, whereas fragmentation relates specifically to such measures as isolation and edge. In practice, however, fragmentation and habitat loss tend to be highly correlated, so separating their effects is difficult, although D'Eon (2002) asserted that studies have indicated that habitat loss effects predominate over those of fragmentation. In any event, one also might argue that the consequence of habitat loss is fragmentation, so they are parts of one phenomenon.

As noted by D'Eon (2002), landscape-scale empirical data are needed to evaluate hypotheses concerning the effects of fragmentation. As such, I surveyed forest birds in both summer and winter at what is generally considered to be the landscape scale (Askins and Philbrick 1987, Drapeau et al. 2000, Thompson et al. 2002) for the entire state of Connecticut. Although large scale surveys of this sort may analyze patterns using relative species detections such as the North American Breeding Bird Survey (Boulinier et al. 2001, Rittenhouse et al. 2010), in this case I employed quantitative surveys to produce measures of absolute population density for all forest species present. With such data, I sought to determine whether within the context of a largely forested New England landscape if fragmentation

and habitat loss effects were still observable in larger forested tracts and, if so, what were these effects? Specifically, based on the previous research of those cited above, I hypothesized that increasing fragmentation would result in 1) declines in the richness and density of breeding communities, as well as in neotropical migrant, ground nesting, interior forest-associated and arboreal and ground foraging richness and density, 2) population and richness increases in breeding short-distance migrant and resident, foraging generalist and edge/successional and habitat generalist species, including population increases in the Brown-headed Cowbird, 3) habitat loss (i.e., forest area) effects predominating over edge (i.e., fragmentation) effects, 4) fragmentation effects predominating over local habitat effects, 5) natural forest breaks having fewer community effects than human-associated ones, and 6) winter effects of fragmentation on species richness, community density and species composition showing little community consequence due to the prevalence of ecological generalist species at this season.

METHODS

Study areas. Connecticut is the 4th most populous state, with a current population of 3.605 million inhabiting 13183 km². Of this population, 26.6% is in the southwestern metropolitan New York City region and 48.9% is in the state's central valley (U.S. Census Bureau 2020). The remainder of the state, particularly the hilly uplands of eastern and northwestern Connecticut, is comparatively rural. Mean summer temperatures range from 18.9°C in the northwest to 21.7°C on the southwest coast. In winter, mean temperature ranges from -4.4°C in the

northwest to 0.3°C on the Atlantic Ocean-facing southeast coast. Topography ranges from a mean elevation of 381 m in the steeply hilly northwest to <122 m in the low hills of the southeast coast. (Dowhan and Craig 1976, NOAA 2020).

Much of Connecticut is characterized by a bedrock geology of gneisses, schists and granites in hilly uplands, although marble exposures pass through the northwest and sandstones predominate in the central Connecticut valley. These are overlain in numerous locations by glacial sediments of varying depths (Stone et al. 1999) and major drainages are characterized by glacial outwash (Ilgen et al. 1966, Roberts 1981). Eastern Connecticut in particular is covered with extensive deposits of glacial sand and gravel associated in part with recessional moraines (Stone et al. 1999). The differences that arise in soils from their underlying geology exert significant influences on the forests that grow upon them (Foster and O'Keefe 2000, Craig 2017).

Despite its urbanization, Connecticut forest cover varies from 75% in the rural northwest to 37% in the urbanized southwest. Also urbanized central Connecticut averages ca. 50%, whereas more rural eastern Connecticut averages ca. 67% forest. However, the extent of forest cover is declining as urbanization proceeds (Alerich 2000, Butler 2017).

Forest community composition varies with elevation and microhabitat conditions. On more mesic sites, Northern Red Oak (*Quercus borealis*) occurs in varying mixtures with other oaks, hickories (*Carya* spp.), Black Birch (*Betula lenta*) and Red Maple (*Acer rubrum*). Toward the south and east and in more xeric locations, Black Oak (*Q. velutina*) progressively replaces Northern Red Oak. At the most xeric sites, particularly on sandy, glacial deposits and rocky ridges, Chestnut Oak (*Q. prinus*) and Scarlet Oak (*Q. coccinea*) often become predominant.

Mesic deciduous forests of richer soils and coves are vegetated particularly by Sugar Maple (*A. saccharum*), White Ash (*Fraxinus Americana*), Tulip Poplar (*Liriodendron tulipifera*), and Yellow Birch (*B. lutea*) in association with oaks and hickories. Deciduous associations of swamp soils are frequently dominated by Red Maple, which is joined in these situations by such species as Yellow Birch and Swamp White Oak (*Q. bicolor*). Floodplain communities, especially along the extensive floodplains of the Connecticut River, are dominated by Red Maple, American Elm (*Ulmus americana*), Silver Maple (*A. saccharinum*) and Pin Oak (*Q. prinus*).

Particularly in the north, deciduous trees of mesic environments are joined by Eastern White Pine (*Pinus strobus*) and Eastern Hemlock (*Tsuga canadensis*) to form conifer-transition hardwood associations. These conifers may form nearly pure hemlock-white pine stands. Moreover, in cove sites associated with rivers and streams, Eastern Hemlock can occur in nearly pure groves. Particularly in northern

Connecticut and near the Connecticut-Rhode Island border on xeric, glacial sands and gravels, Eastern White Pine joins with oaks and hickories to form pine-oak associations. In hydric situations, Eastern White Pine and Eastern Hemlock may co-occur with deciduous swamp species to form conifer-swamp hardwood associations. Conifers also are important elements of successional forests. Eastern White Pine is a common to predominant member of forests regenerating after logging or abandonment, with its prevalence tending to increase from south to north. Eastern Redcedar (*Juniperus virginiana*) is also common in successional forests, with its prevalence increasing from north to south (Craig 2017).

Bird surveys. I established 121 survey transects, with each traversing 3.2−4 km of forest depending upon terrain and other local conditions (Fig. 1). Each transect had 15 survey points—the maximum I could visit during the peak of morning bird activity. Hence, I surveyed 1815 points through ca. 400 km of forest. Survey points were ca. 200 m apart, a distance that I empirically determined to minimize detecting the same bird from two successive points. I recorded locations, elevations and horizontal distances between points with a Garmin Etrex global positioning device (Garmin, Inc. Olathe, KS). Transects were situated on public land, private land with public access or on private land for which I had owner-granted access. Within these constraints, transect placement followed a randomized block protocol, with sites occupied in all geographic regions of the state.

I surveyed transects in random order in northeast Connecticut (26 transects) during the summer of 2001 and winter of 2001−2002, surveyed southeast Connecticut (24 transects) in 2002−2003, and repeated these observations in 2004−2005 and 2005−2006 for northeast and southeast Connecticut, respectively. I surveyed central Connecticut (25 transects) in 2006−2007, northwest Connecticut (28 transects) in 2007−2008 and southwest Connecticut (18 transects) in 2008−2009. The size of these regions varied, so the number of transects established in each region also varied, such that sampling intensity was similar for each region.

Routes began at first light (05:15 in summer, 07:00 in winter) and lasted 3.5−4 hr. I performed surveys year-round under conditions of low wind and at most minimal precipitation. In winter, surveys proceeded regardless of snow depth or minimum temperature, which on occasion dropped to −26°C. Survey routes followed existing hiking trails where possible in order to travel expeditiously between points and to re-locate survey points easily. Except for old logging roads that did not break the forest canopy, I avoided using forest roads. When no paths were available, I followed compass bearings through the forest. I limited summer field observations to between 20 May and 5 July, the height of the local

breeding season, to minimize alteration of survey results due to behavioral changes (Skirvin 1981). Similarly, I limited winter observations from mid-December to the end of February—the heart of the local winter season.

I used the Variable Circular Plot (VCP) technique to survey. It has wide utility in evaluating populations over a variety of terrains, has a well-developed theoretical underpinning that accounts for differential detectability of species (Buckland et al. 2001, Thomas et al. 2010, Research Unit for Population Assessment 2020) and has long been used for conducting large scale forest bird surveys (e.g., Scott et al. 1986, Camp et el. 2009, Linck et al. 2020). At each point, I estimated the horizontal distance at first detection to each bird encountered. To help calibrate distance estimates, before surveys I placed colored plastic flagging at 10 m intervals to 70 m from one point along each route and periodically walked from a point to detected birds to verify distance estimates. I also plotted on topographic maps the location of distant birds so that I could directly measure from the map their distance from the sampling point. Furthermore, I relied on my long experience with distance sampling of forest birds to record accurately distances of individuals encountered (e.g., Craig 1996). The vast majority of detections were aural, and I distinguished between detections of singing, territorial males and vocalizations by species not generally distinguishable to sex. I occasionally detected rarer bird species, particularly raptors, outside this sampling period. If I found no other individuals during the survey, I included the first of such detections in my survey, reasoning that doing so yielded a more accurate representation of species richness.

Although I recorded all birds encountered regardless of habitat affiliation, in analyses I considered only those species associated with forest, including earlier successional forest. I broadly defined such species as those that I observed to inhabit 1) unbroken forest, 2) forest openings caused by tree fall or selective logging, 3) closed to partly open swamps and 4) forested river banks. These constituted principal habitat patch types within the broader category of forest landscape, with the last three often referred to as forest gaps. I did not include in detailed analyses species that were associated primarily with marshes, shrub swamps, extensive fields, open water, or species detected flying high overhead, whose presence was unrelated with the forest environment. Hence, species like the Willow Flycatcher (*Empidonax traillii*) were associated exclusively with marsh shrubbery and were excluded from analyses.

Species classification. Various configurations of guild membership have sometimes been used in attempting to relate bird community patterns to forest fragmentation (e.g., Lindemayer et al. 2002). However, guild constructions (e.g., DeGraff et al. 1985, Gonzalez-Salazar et al. 2014) tend to combine separate measures of a species' ecology into a single metric. Much as use of the concept of species diversity resulted in a loss of information by combining separate measures (Hurlbert 1971), so the guild concept appears to do the same. As such, I used separate criteria in classifying species' ecological characteristics for analysis with fragmentation metrics, although I did so only in instances where I found information on species' ecology sufficient to make judgements (Appendix). For habitat relationships, I use my own quantitative analyses on Connecticut birds gathered concurrently with making population surveys. These analyses, generally based on large samples, examined the presence of individual birds with respect to habitat measures and also examined relationships of population densities to habitat measures (Craig 2017). In addition, I consulted species accounts in Billerman et al. (2022) and North American Breeding Bird Survey results (Sauer et al. 2017).

I first classified species into those associated with one of three macrohabitat categories: 1) forest interior, 2) forest edge and successional habitats and 3) generalists. I also classified with respect to principal foraging microhabitat: 1) ground/shrubs, 2) arboreal and 3) generalist. I did not subdivide arboreal foragers into those of the upper and mid-canopy, as I did not judge that quantitative data for many species were sufficient to make such distinctions. My own previous quantitative studies of foraging behavior and microhabitat selection of forest birds (e.g., Craig 1984, Craig and Beal 2002) have led me to conclude that many species are more versatile than generally assumed and that they may change their behavior within- and between-seasons, so without detailed quantitative investigations such distinctions cannot be made. I further classified species as to their nest site selection: 1) principally ground, 2) principally shrub and 3) cavity; their trophic relationship: 1) herbivore, 2) omnivore, 3) secondary consumer and 4) apex predator (although in practice I deleted these species from density analyses as they represented a nominal part of the community); and migratory group: 1) non-migratory or short-distance migrants in regions where they may be permanent residents, 2) North American to northern Mexico 3) neotropical, including South America, Caribbean, southern Mexico and central America. I did not classify species as to their foraging motion or area sensitivity, as I judged that many species have had such characteristics insufficiently quantified. I used all these categories in classifying breeding birds and all but nest site selection and migration for classifying wintering birds, although in these instances sufficient data for conducting statistical analyses did not exist for all categories.

Habitat evaluation for survey points. In addition to bird surveys, I measured seven habitat variables at each survey point, for a total of 12705 measurements. Beginning in 2001 and repeated each year

FIG 2. The Haddam, CT study site illustrates the delineation of habitats surrounding the survey transect. Pink = non-forest, purple = 100 m wide buffer surrounding non-forest, green = core forest over 100 m from non-forest, yellow surrounding line = 800 m wide buffer surrounding the yellow transect line, orange surrounding line = 100 m buffer beyond this for determining additional non-forest presence in computing core forest extent.

of the study thereafter, I visually evaluated habitat to a 70 m radius from each sampling station for: 1) forest type, 2) moisture regime, 3) diameter of canopy trees at breast height (dbh), 4) canopy cover, 5) understory density and 6) elevation at the location of the survey point. I also summed canopy and understory measures to provide a measure of 7) vertical vegetation complexity. Following bird surveys, I revisited each point each year of the study to verify these measurements.

Details of habitat evaluation procedures are in Craig (2017). Briefly, I recorded a numerical category for each habitat measure. Forest type consisted of three: 1) deciduous: <10% evergreen conifers, 2) mixed: 20−60% evergreen coniferous, 3) coniferous: >70% evergreen conifers. Moisture regimes were: 1) hydric, 2) mesic and 3) xeric. In practice, I distinguished swamp sites as hydric, dry ridges and sandy uplands as xeric and used mesic as a broader category describing intermediate situations. I divided prevailing canopy tree dbh into three categories: 1) young forest: <15 cm, 2) mature forest: >15−45 cm, and 3) old growth: >45 cm. I similarly divided canopy cover into three categories, estimating to the nearest 10%: 1) open: <40% cover, 2) semi-open: 50−60% cover, and 3) closed: >70% cover. I evalu-

ated understory density for larger shrubs and saplings ca. 1−4 m tall rather than for low ground covers and herbaceous growth: 1) open: <20% cover; 2) moderate: 30−60% cover, and 3) dense: >70% cover. I then computed the mean value for each of these measures for each transect, thereby converting them to continuous variables. In addition to these measures made at the study sites, I examined long-term USDA Forest Service data (Alerich 2000, Butler 2017) on tree volume and tree number for the state as a whole.

Landscape evaluation for survey points. To characterize the landscapes within which the survey transects were situated, I employed QGIS 3.16 geographic information systems software to analyze aerial orthophotos from the University of Connecticut Library Map and Geographic Information Center (http://magic.lib.uconn.edu/). For each transect, I overlaid two photos for analysis—2004 1:20000 black-and-white pre-growing season images covering 4.6 km^2 each and, depending on the year of the bird survey, either 2006 or 2008 1:25000 color growing season images covering 36.0 km^2 each. I georeferenced these to USGS topographic maps.

I plotted the survey points from each transect onto the photos and then constructed a 400 m wide

buffer around the transect, thereby producing an 800 m wide corridor (averaging 260.7 ha area and covering 31550 ha in sum for all transects) through which the transect passed. I chose this width because nearly all bird detections were within this corridor. In the corridor, I constructed polygons outlining each habitat present. Although pixel classification tools are frequently used for delineating habitats at this scale, I found that although doing so was more labor intensive, by visually comparing non-growing and growing season images and well as by relying on my familiarity with the study sites, I could construct digitized habitat polygons that maximized accuracy, precision and detail.

I distinguished the following habitat classes: 1) forest, including mature and earlier successional forest, 2) human-associated, including paved roads, residences and commercial development, 3) agricultural, including pastures, hayfields and cropland, 4) open water, including lakes and watercourses large enough to break the forest canopy, 5) marshes vegetated principally by perennial herbs and low shrubs and 6) beaches—non-vegetated sandy or gravelly coastal or lake shores. Once delineated, I used measurement tools to compute the area and perimeter of all habitat polygons. Using these, I computed perimeter/area ratios for forest polygons to provide a measure of forest fragmentation (McGarigal and Marks 1995). Moreover, to eliminate zeros from data and to focus analyses, I combined human-associated and agricultural measures into a single human-associated metric and combined open water, marshes and beaches into a natural breaks metric. I used the 2006 and 2008 images to update any changes that had occurred in landscapes since 2004 for those transects surveyed near those dates although, in practice, such updates were minimal.

I also computed the area of core forest in the corridor, which also may be considered as a forest fragmentation measure, as even if the total amount of forest in a location is great, if it is highly fragmented it will have little core forest. I defined core forest as that forest ≥ 100 m from an edge. I chose this distance based on my own long-term observations on the occurrence of forest birds and on observations like those of Robbins et al. (1988), Burke and Noll (1998), Jules (1998) and Lambert and Hannon (2000). Based in part on Vogt et al. (2007), it is also the measure used to compute core forest by the University of Connecticut Center for Land Use Education and Research (https://clear.uconn.edu/). To delineate core forest, I first constructed an additional 100 m buffer beyond the edge of the transect corridor so that I could assess which parts of the forest areas abutting the corridor edge could be included as core forest. Within the additional 100 m, I mapped nonforest and combined this area with all other nonforest areas into a new vector layer, constructed a 100 m buffer around it, and subtracted this sum from

the total forest area to yield a difference of core forest (Fig. 2).

In those few instances where lightly traveled dirt roads traversed forests, I chose to regard them as forest gaps and, thus, part of the forest ecosystem. Canopy generally closed over these roads and my observations of birds in their vicinity demonstrated the common occurrence of forest interior species in close proximity to them. Similarly, I took a different view from other researchers (e.g., Kroodsma 1984) concerning power line right-of-ways in that I considered them, with their early to mid-successional forest cover, as also part of the forest ecosystem. A mosaic of forest successional stages represents the pre-European landscape (Foster and O'Keefe 2000) in which forest bird species co-evolved. Indeed, the number of successional-associated bird species that are part of the forest community provides clear evidence of this. Not surprisingly, as noted, such forest variation does not have the type of impact on bird communities as human-associated development (Blake and Hoppes 1986, Drapeau et al. 2000, Thompson et al. 2002).

Analysis. I computed population densities with Distance 7.3 software (Thomas et al. 2010, Research Unit for Population Assessment 2020), consulting also the protocols of Buckland et al. (2001) in selecting detection functions. Based on initial plots of species detection probability vs. detection distances, I grouped similar observations, often into 5−10 categories, with interval cut points placed between favored rounding distances to minimize data "heaping" and to improve robustness of density estimation. I explored the fit of detection data to six models recommended by Buckland et al. (2001): uniform/cosine, uniform/simple polynomial, half normal/cosine, half normal/hermite polynomial, hazard rate/cosine and hazard rate/simple polynomial. As also recommended by Buckland et al. (2001), I explored truncating detection data for individual species to eliminate the largest 5−10% of values, which can facilitate model fitting by eliminating outliers. When doing so improved model fit, I employed this technique. I sought a conventional distance sampling model that yielded a smooth curve with near 100% detection probability at the left shoulder, evaluated fit by visual inspection of plotted data, with Akaike's Information Criterion and with chi-square goodness of fit tests and computed variance empirically. When species occurred in flocks, I performed analyses using clusters as the basis of density measurement. I used all distance measures obtained in this study (Craig 2017) in computing global detection functions, as large samples produce the most accurate detection functions and, thus, density estimates.

For each transect I computed the sampled species richness—the sum of all forest bird species encountered and community density—the sum of computed densities for all forest species encountered. To
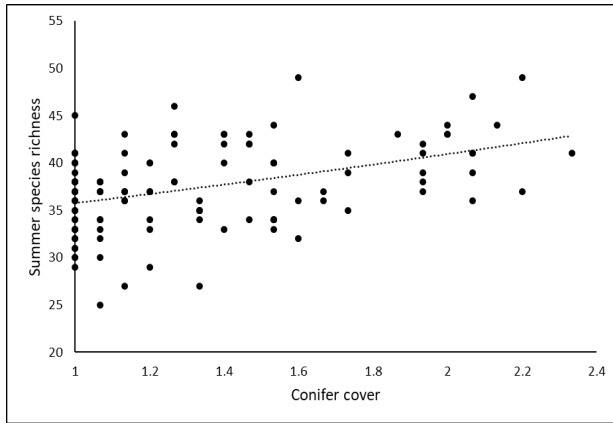
FIG. 3. Summer species richness increases with increasing conifer cover.

FIG. 4. Winter species richness declines with increasing elevation.

compute community density, I divided density estimates by two for species in which males and females were equally likely to be encountered before summing them with densities of those species represented by solely singing males. Doing so improved comparability among the study sites by accounting for any differences among them in densities represented by both sexes. In comparing bird community parameters with environmental factors, I used data from the contiguous years 2004−2009, as these were independent measures. I used the repeated measure 2001-2003 eastern Connecticut data to evaluate year to year variation in findings.

To investigate relationships among bird community vs. landscape and habitat effects, I first plotted community vs. predictor variables to examine the strength and shapes of their relationships. I then arcsine-square root transformed proportion, log transformed habitat and population density and square root transformed count variables to linearize their relationships. Although arcsine-square root transformations have been criticized because they can interfere with interpretability (Wharton and Hui 2011), in this instance I found the criticism to be overstated, as I discovered that their use had little effect on interpretations compared with results obtained when using untransformed proportions. Moreover, they provided modest improvements in meeting normality assumptions, although even untransformed proportions generally exhibited distributions that approximated normality. I next examined Pearson correlations among the predictors, which demonstrated that, as expected, most fragmentation and forest cover metrics were highly correlated, although habitat measures were not. Hence, I entered fragmentation variables into analyses separately, although human-associated and natural break habitats were not correlated, so I entered both into models as predictors.
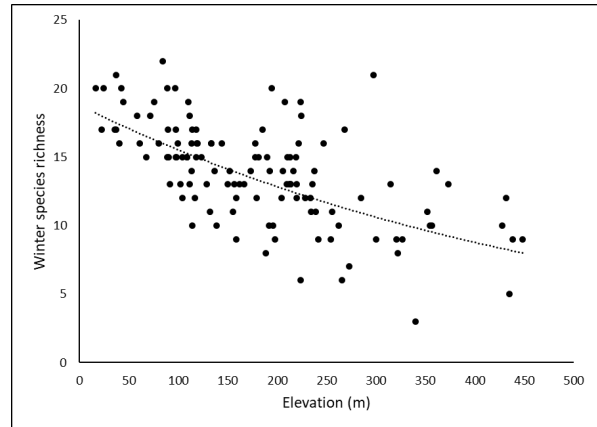
I performed analyses on classes of bird community measures vs. predictors with multivariate regression analysis. Geographically based data can exhibit spatial autocorrelation (Wimberly et al. 2009), although previous study had demonstrated that my community measures did not exhibit such autocorrelation (Craig and Klaver 2013), likely in large part because study sites were generally >8 km apart. Hence, ordinary least squares regressions were appropriate for analyses. For breeding birds, the classes included densities and richnesses within nest location, macrohabitat, microhabitat, migratory, and trophic categories. For wintering birds, they included densities and richnesses within macrohabitat, microhabitat and trophic categories, although in these instances there were some individual categories with insufficient data to warrant inclusion into models, as densities and species richness were, not surprisingly, much lower in winter. Following exploratory analyses, in all cases I dropped habitat variables with little predictive power from tests, particularly dbh and vertical vegetation complexity, to improve sample size with respect to number of variables entered into models.

To provide additional insights into results of community analyses, I employed hierarchical multiple regression analysis on individual community measures by successively entering into a model the predictor with the highest partial correlation until remaining predictors exhibited little improvement in model fit. I chose to include into final models predictors with condition indicies (measures of collinearity) below 30 and tolerance values (proportions of predictors not explained by other predictors) with values near or above 0.9. I performed multiple regressions on total community summer/winter species richness and summer/winter community density as well as widespread individual species which, to avoid analytic distortion, were those with populations present at ≥90% of study sites (Rasmussen et al.
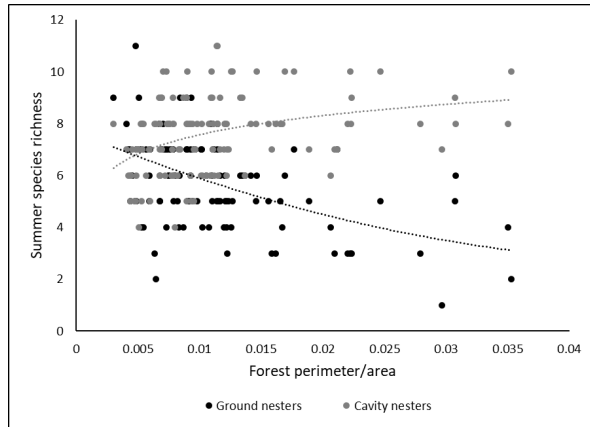
FIG. 5. Ground nester summer species richness declines with increasing forest perimeter/area whereas cavity nester richness increases.

FIG. 6. Interior forest, secondary consumer and North American migrant summer species richness increase with increasing conifer cover.

2020). In analyses, I evaluated the normality of error assumption with frequency histograms of standardized residuals and normal P-P plots of standardized residuals, the homoscedasticity assumption with scatterplots of residuals vs. predicted values and inspected data for multicollinearity by examining tolerance/variance inflation factors and condition indices.

To evaluate the extent of temporal variation in community relationships with respect to landscape and habitat variables, I compared summer/winter results of 2001−2003 surveys of eastern Connecticut with those from 2004−2006. Because sample size was smaller for eastern Connecticut compared with the study as a whole (50 vs. 121), I minimized the number of predictors entered into regression models, using the results of study area-wide analyses to guide variable selection. For each class of community measure, I entered the landscape variable with the strongest relationship as well as a maximum of two habitat variables showing the strongest relationship. I chose to analyze only the characteristic from each community class that exhibited the strongest relationship with predictors, reasoning that this one would have the greatest probability of uncovering temporal change in bird community response.

RESULTS

Bird community trends. From 2001 to 2009, I recorded 36,702 summering individuals of 123 species and 13,742 wintering individuals of 63 species. Of the species, 88 summering and 51 wintering ones classified as forest-associated (Appendix). Of 32 examinations of summer community measures, 11 had the greatest r^2 in models in which perimeter/area, a measure of forest fragmentation, was included with habitat predictor variables. Another 11 had proportion of core forest, six had proportion of human-associated and natural forest breaks and one had pro-

portion of total forest cover in models yielding the greatest r^2. In one instance, perimeter/area and core forest tied for greatest r^2 and in two instances no model yielded any significant relationships. Moreover, natural forest breaks alone yielded only one significant result and nine of the 32 models contained only significant habitat predictors. Of 15 examinations of winter community measures, 12 had the greatest r^2 in models in which perimeter/area was included with habitat predictors. Another three had the greatest r^2 in models in which proportion of human-associated habitats was included with habitat predictors. However, seven of the 15 models contained only significant habitat predictors—particularly elevation.
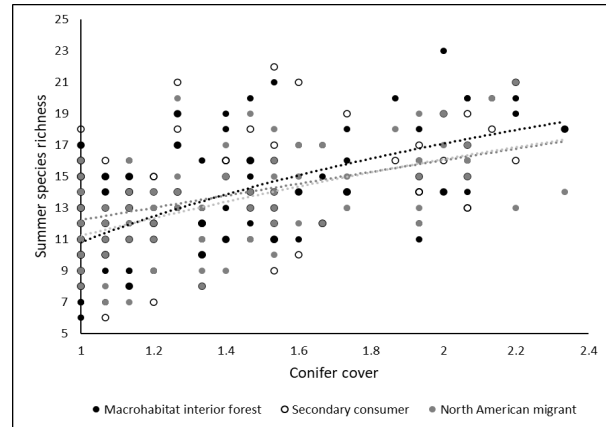
Species richness. Analysis of summer community richness (Table 1) showed that a model including human-associated and natural forest breaks and habitat predictors had a slightly greater r^2 than other landscape measures, although only habitat predictors had significant effects. Hierarchical analysis indicated that increasing richness was principally associated with primarily increasing conifer cover (Fig. 3) and secondarily decreasing canopy cover. In contrast, winter community richness had a slightly stronger relationship to a model including perimeter/area, although hierarchical analysis showed that only decreasing elevation contributed substantially to increasing richness (Fig. 4).

For nest site categories vs. summer richness, the strongest relationships by far were for ground nesters. In this case, a model with perimeter/area showed a slightly greater r^2 compared with other landscape measures, with hierarchical analysis indicating that increasing richness was associated with primarily decreasing perimeter/area (Fig. 5) and secondarily increasing conifer cover and understory density. Cavity nester richness showed a slightly stronger relationship to a model including core forest than to perimeter/area (Fig. 5), with hierarchical analysis

TABLE 1. Multivariate regression analyses' statistically significant ($P < 0.05$) r^2 values for summer/winter community species richness and species classifications for nest site selection, macrohabitat use, microhabitat use, migration category and trophic category.

			Landscape measures				Habitat measures						
		Total	Perimeter/ area	Forest area	Core forest	Human-associated	Conifer cover	Moisture regime	dbh	Canopy cover	Understory density	Elevation	Vertical complexity
Community richness													
Summer	Perimeter/area	0.301					0.148			0.097		0.044	
	Forest area	0.298					0.146			0.095			
	Core forest	0.294					0.139			0.081		0.062	
	Human-associated/ natural breaks	0.312					0.146			0.106		0.039	
Winter	Perimeter/area	0.442	0.072				0.042					0.18	
	Forest area	0.415					0.037					0.151	
	Core forest	0.424			0.042		0.042					0.175	
	Human-associated/ natural breaks	0.427				0.048	0.033					0.207	
Nest site summer richness													
Ground	Perimeter/area	0.395	0.151				0.064					0.066	
	Forest area	0.342		0.076			0.055					0.047	
	Core forest	0.364			0.107		0.064					0.061	
	Human-associated/ natural breaks	0.355				0.094	0.047					0.093	
Cavity	Perimeter/area	0.261	0.145								0.106	0.066	
	Forest area	0.213		0.090							0.084	0.062	
	Core forest	0.263			0.148						0.101	0.076	
	Human-associated/ natural breaks	0.232				0.111					0.109	0.048	
Canopy/understory	Perimeter/area	0.272					0.169			0.129			
	Forest area	0.268					0.167			0.124			
	Core forest	0.261					0.159			0.106			
	Human-associated/ natural breaks	0.285					0.168			0.141			
Macrohabitat summer richness													
Interior forest	Perimeter/area	0.637	0.085				0.425	0.051				0.180	
	Forest area	0.644		0.102			0.435	0.060				0.108	
	Core forest	0.635			0.079		0.430	0.051				0.163	
	Human-associated/ natural breaks	0.646				0.108	0.421	0.060				0.192	
Edge/successional	Perimeter/area	0.231								0.145			
	Forest area	0.232								0.135			
	Core forest	0.243								0.123			
	Human-associated/ natural breaks	0.232								0.147		0.037	
Generalist	Perimeter/area	0.144	0.053									0.062	0.055
	Forest area	0.131		0.039								0.061	0.052
	Core forest	0.165			0.076							0.079	0.049
	Human-associated/ natural breaks	0.116										0.044	0.047
Microhabitat summer richness													
Arboreal	Perimeter/area	0.195	0.057				0.120			0.046			
	Forest area	0.161					0.110			0.038			
	Core forest	0.162					0.112			0.039			
	Human-associated/ natural breaks	0.164				0.044	0.108			0.045			
Ground	Perimeter/area	0.098								0.047			
	Forest area									0.510			
	Core forest	0.115			0.034					0.034			
	Human-associated/ natural breaks	0.093								0.047			
Generalist	Perimeter/area	0.292					0.073			0.042		0.165	
	Forest area	0.289					0.074			0.043		0.132	
	Core forest	0.295					0.069			0.034		0.168	
	Human-associated/ natural breaks	0.294					0.078			0.057		0.130	

Migration summer richness

Category	Metric	V1	V2	V3	V4	V5	V6	V7	V8	V9
Neotropical	Perimeter/area	0.185	0.111				0.037	0.055		
	Forest area	0.135		0.057				0.049		
	Core forest	0.133			0.053		0.035	0.050		
	Human-associated/ natural breaks	0.198				0.125		0.066		
North American	Perimeter/area	0.482	0.044				0.329	0.094		0.126
	Forest area	0.472					0.327	0.089		0.109
	Core forest	0.490			0.059		0.321	0.074		0.140
	Human-associated/ natural breaks	0.464					0.334	0.098		0.096
Resident	Perimeter/area	0.256	0.046				0.165		0.048	
	Forest area	0.233					0.156		0.043	
	Core forest	0.274			0.069		0.177		0.046	
	Human-associated/ natural breaks	0.244					0.155		0.051	

Trophic level summer richness

Category	Metric	V1	V2	V3	V4	V5	V6	V7	V8	V9
Secondary consumer	Perimeter/area	0.290	0.047				0.167	0.077		
	Forest area	0.279		0.033			0.163	0.076		
	Core forest	0.272					0.162	0.073		
	Human-associated/ natural breaks	0.296				0.057	0.159	0.083		
Omnivore	Perimeter/area	0.171						0.076		0.055
	Forest area	0.176						0.067		0.061
	Core forest	0.212			0.061			0.050		0.093
	Human-associated/ natural breaks	0.162					0.034	0.081		0.042
Herbivore	Perimeter/area									
	Forest area									
	Core forest									
	Human-associated/ natural breaks									

Macrohabitat winter richness

Category	Metric	V1	V2	V3	V4	V5	V6	V7	V8	V9
Interior forest	Perimeter/area	0.203					0.082			0.045
	Forest area	0.195					0.077			0.048
	Core forest	0.200					0.082			0.045
	Human-associated/ natural breaks	0.205					0.079			0.049
Edge/successional	Perimeter/area	0.405	0.037				0.105	0.047		0.1
	Forest area	0.402					0.104	0.041		0.069
	Core forest	0.400					0.105	0.039		0.092
	Human-associated/ natural breaks	0.398					0.096	0.046		0.116
Generalist	Perimeter/area	0.294	0.077							0.108
	Forest area	0.257								0.093
	Core forest	0.266			0.041					0.110
	Human-associated/ natural breaks	0.277				0.054				0.131

Microhabitat winter richness

Category	Metric	V1	V2	V3	V4	V5	V6	V7	V8	V9
Arboreal	Perimeter/area	0.267								0.168
	Forest area	0.256								0.175
	Core forest	0.259								0.173
	Human-associated/ natural breaks	0.260								0.186
Generalist	Perimeter/area	0.081								
	Forest area	0.065								
	Core forest	0.065								
	Human-associated/ natural breaks	0.071								

Trophic level winter richness

Category	Metric	V1	V2	V3	V4	V5	V6	V7	V8	V9
Secondary consumer	Perimeter/area	0.183					0.036			0.102
	Forest area	0.177					0.040			0.111
	Core forest	0.177					0.038			0.114
	Human-associated/ natural breaks	0.185					0.038			0.107
Omnivore	Perimeter/area	0.352					0.075			0.115
	Forest area	0.339					0.072			0.091
	Core forest	0.343					0.075			0.108
	Human-associated/ natural breaks	0.345					0.068			0.131
Herbivore	perimeterarea f	0.263						0.043		0.069
	propforest	0.241						0.038		0.055
	propcoref	0.253						0.041		0.063
	prophuman/natural	0.238						0.037		0.095
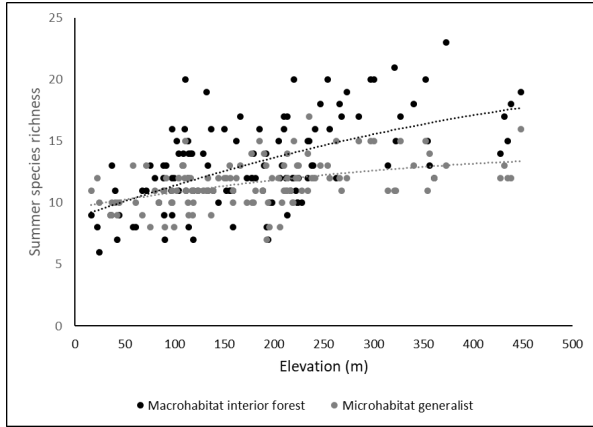
FIG.7. Interior forest and microhabitat summer species richness increase with increasing elevation.

FIG.8. Neotropical migrant and secondary consumer summer species richness decline with increasing human-associated landscape cover.

indicating that increasing richness was associated with primarily decreasing core forest and secondarily decreasing conifer cover and understory density. Canopy/understory nester richness showed a slightly stronger relationship to a model including human-associated and natural forest breaks than to perimeter/area, although hierarchical analysis indicated that increasing richness was principally associated with only increasing soil moisture and decreasing canopy cover.

For macrohabitat associations vs. summer richness, the strongest relationships by far were for interior forest species. In this case, a model with human-associated and natural forest breaks showed a slightly greater r^2 compared with other landscape measures. However, hierarchical analysis indicated that increasing richness was associated with primarily increasing conifer cover (Fig. 6) and secondarily elevation (Fig. 7). Edge/successional richness showed the strongest relationship to a model including core forest, although hierarchical analysis indicated that increasing richness was principally associated with only decreasing canopy cover and elevation. Generalist richness showed the weakest relationship to predictors, with a model again including core forest showing the greatest r^2. Hierarchical analysis indicated that increasing richness was primarily associated with only decreasing core forest and increasing vertical vegetation complexity.

For microhabitat categories vs. summer richness, the strongest relationships by far were for ecological generalists. In this case, a model with core forest showed a slightly greater r^2 compared with other landscape measures, although hierarchical analysis indicated that increasing richness was associated with primarily elevation (Fig. 7) and secondarily increasing conifer cover. Arboreal forager richness showed the strongest relationship to a model including perimeter/area, with hierarchical analysis indicat-
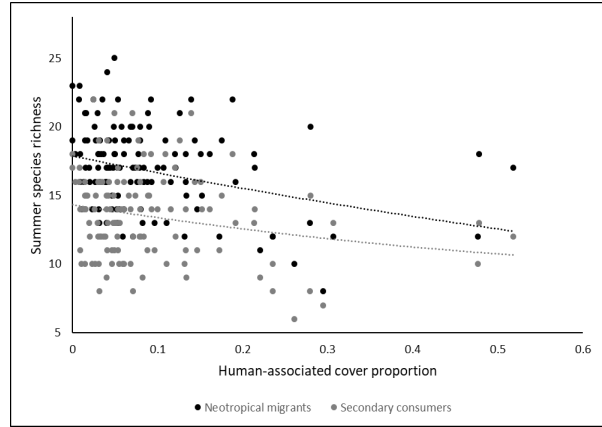
ing that increasing richness was principally associated with only decreasing perimeter/area and increasing conifer cover. Ground/shrub forager richness showed the weakest relationship to predictors, with the strongest relationship occurring for a model including core forest, although hierarchical analysis indicated that increasing richness was principally associated with only decreasing canopy cover.

For migration categories vs. summer richness, the strongest relationships by far were for North American migrants. In this case, a model with core forest showed a slightly greater r^2 compared with other landscape measures, although hierarchical analysis indicated that increasing richness was principally associated with only decreasing deciduous and canopy cover (Fig. 7). Resident richness showed the strongest relationship to a model including core forest, with hierarchical analysis indicating that increasing richness was principally associated with decreasing core forest, conifer cover and understory density. Neotropical migrant richness showed the weakest relationship to predictors, with the strongest association occurring for a model including human-associated and natural forest breaks. Hierarchical analysis indicated that increasing richness was principally associated with only fewer human-associated forest breaks (Fig. 8).

For trophic categories vs. summer richness, the strongest relationships by far were for secondary consumers. In this case, a model with human-associated and natural forest breaks showed a slightly greater r^2 compared with other landscape measures, with hierarchical analysis indicating that increasing richness was associated with primarily increasing conifer cover (Fig. 6) and secondarily decreasing human-associated forest breaks (Fig. 8). Omnivore richness showed the strongest relationship to a model including core forest, although hierarchical analysis indicated that increasing richness was principally
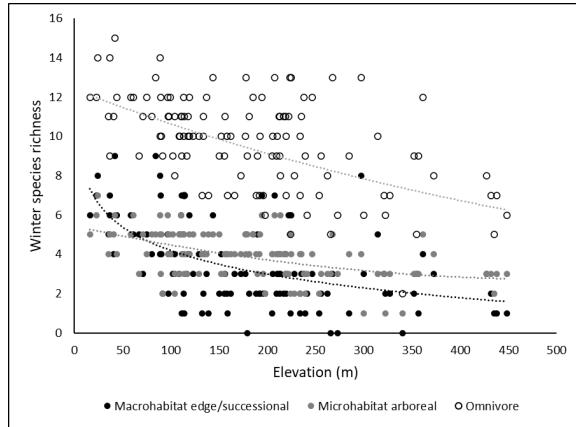
FIG. 9. Edge/successional, arboreal and omnivore winter species richness decline with elevation.

FIG. 10. Summer community density declines whereas winter community density increases with increasing forest perimeter/area.

associated with only decreasing canopy cover and increasing elevation. Herbivore richness showed no significant relationships with predictor variables.

For macrohabitat categories vs. winter richness, the strongest relationships by far were for edge/successional species. In this case, a model with perimeter/area showed a slightly greater r^2 compared with other landscape measures, although hierarchical analysis indicated that increasing richness was principally associated with only decreasing conifer cover and elevation (Fig. 9). Habitat generalist species richness also showed the strongest relationship to a model including perimeter/area, although hierarchical analysis indicated that increasing richness was principally associated with only decreasing elevation. Interior forest species richness showed the weakest relationship to predictors, with the strongest one occurring for a model including human-associated and natural forest breaks. However, hierarchical analysis indicated that increasing richness was principally associated with only increasing conifer cover and soil moisture and decreasing elevation.

For microhabitat categories vs. winter richness, the strongest relationships by far were for arboreal species. In this case, a model with perimeter/area showed a slightly greater r^2 compared with other landscape measures, although hierarchical analysis indicating that increasing richness was principally associated with only decreasing elevation (Fig. 9). Foraging generalist species richness also showed the strongest relationship to a model including perimeter/area, with hierarchical analysis indicating that increasing richness was principally associated with increasing perimeter/area. Ground/shrub foraging species occurred with insufficient frequency for an analysis to be conducted.
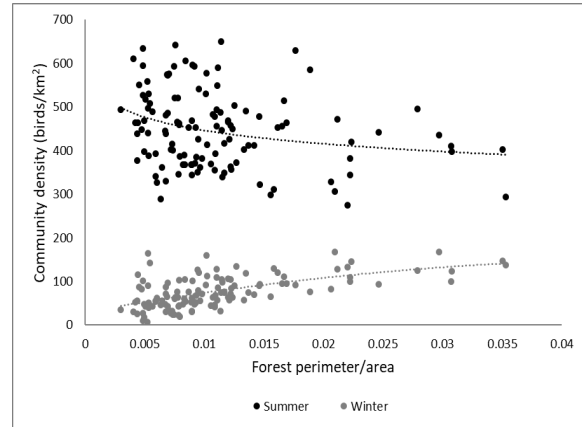
For trophic categories vs. winter richness, the strongest relationships by far were for omnivore species. In this case, a model with perimeter/area showed a slightly greater r^2 compared with other landscape measures, although hierarchical analysis indicated that increasing richness was principally associated with only decreasing conifer cover and elevation (Fig. 9). Herbivore species richness showed the strongest relationship to a model including perimeter/area, although hierarchical analysis indicated that increasing richness was principally associated with only decreasing elevation. Secondary consumer richness showed the weakest relationship to predictors, with the strongest relationship occurring for a model including human-associated and natural forest breaks, although hierarchical analysis indicated that increasing richness was principally associated with only decreasing deciduous cover and elevation.

Community density . Analysis of summer community density (Table 2) showed that a model including perimeter/area and habitat predictors had the greatest r^2, with hierarchical analysis indicating that increasing density was principally associated with decreasing perimeter/area (Fig. 10) and increasing conifer cover, soil moisture and understory density. Winter community density also had the strongest relationship to a model including perimeter/area (Fig. 10), although in this case hierarchical analysis showed, as with winter richness, that only decreasing elevation contributed substantially to increasing density.

Density responses of summer nest site categories to predictors were generally similar to those of richness for all categories. Categories vs. density showed that the strongest relationships by far were for ground nesters. For ground nesters, a model with perimeter/area showed a slightly greater r^2 value compared with other landscape measures, with

TABLE 2. Multivariate regression analyses' statistically significant ($P < 0.05$) r^2 values for summer/winter community density and species classifications for nest site selection, macrohabitat use, microhabitat use, migration category and trophic category.

		Landscape measures						Habitat measures					
		Total	Perimeter/ area	Forest area	Core forest	Human-associated	Natural breaks	Conifer cover	Moisture regime	dbh	Canopy cover	Understory density	Elevation
Community density													
Summer	Perimeter/area	0.360	0.120					0.115	0.136		0.041	0.083	
	Forest area	0.327		0.074				0.108	0.125		0.040	0.066	
	Core forest	0.347			0.102			0.119	0.133		0.050	0.078	
	Human-associated/ natural breaks	0.345				0.099		0.098	0.135		0.042	0.088	
Winter	Perimeter/area	0.475	0.113										0.230
	Forest area	0.419											0.215
	Core forest	0.444			0.061								0.224
	Human-associated/ natural breaks	0.455				0.079							0.259
Nest site summer density													
Ground	Perimeter/area	0.596	0.234					0.217			0.052	0.235	0.043
	Forest area	0.538		0.125				0.189			0.045	0.188	
	Core forest	0.568			0.182			0.214			0.034	0.218	0.036
	Human-associated/ natural breaks	0.571				0.188		0.182			0.047	0.237	0.065
Cavity	Perimeter/area	0.268	0.141									0.048	
	Forest area	0.202		0.062								0.035	
	Core forest	0.277			0.150							0.045	
	Human-associated/ natural breaks	0.255				0.125						0.053	
Canopy/understory	Perimeter/area	0.272							0.147		0.088		
	Forest area	0.258							0.138		0.082		
	Core forest	0.266							0.144		0.089		
	Human-associated/ natural breaks	0.269							0.147		0.088		
Macrohabitat summer density													
Interior forest	Perimeter/area	0.671	0.208					0.263	0.066		0.064	0.043	0.219
	Forest area	0.668		0.202				0.264	0.070		0.048		0.128
	Core forest	0.680			0.229			0.283	0.074		0.039	0.040	0.182
	Human-associated/ natural breaks	0.677				0.191	0.088	0.262	0.073		0.045		0.141
Edge/successional	Perimeter/area	0.494						0.043			0.228	0.091	0.125
	Forest area	0.494						0.049			0.196	0.095	0.057
	Core forest	0.490						0.047			0.200	0.091	0.083
	Human-associated/ natural breaks	0.526					0.064	0.061			0.209	0.125	0.050
Generalist	Perimeter/area												
	Forest area												
	Core forest												
	Human-associated/ natural breaks												
Microhabitat summer density													
Arboreal	Perimeter/area	0.294	0.105					0.048	0.073				
	Forest area	0.256		0.057				0.043	0.055				
	Core forest	0.281			0.090			0.052	0.072				
	Human-associated/ natural breaks	0.277				0.084		0.037	0.073				0.038
Ground	Perimeter/area	0.324	0.134					0.133	0.065			0.149	
	Forest area	0.284		0.082				0.123	0.058			0.125	
	Core forest	0.294			0.096			0.132	0.059			0.140	
	Human-associated/ natural breaks	0.279				0.076		0.109	0.058			0.148	
Generalist	Perimeter/area	0.373							0.061		0.162	0.140	
	Forest area	0.377							0.053		0.145	0.144	
	Core forest	0.374							0.057		0.149	0.140	
	Human-associated/ natural breaks	0.373							0.058		0.156	0.139	

Migration summer density												
Neotropical	Perimeter/area	0.432	0.225					0.205			0.076	
	Forest area	0.340		0.100				0.167			0.052	
	Core forest	0.400			0.182		0.035	0.194			0.068	
	Human-associated/ natural breaks	0.392				0.170		0.195			0.080	0.046
North American	Perimeter/area	0.269					0.177			0.099		
	Forest area	0.267					0.181			0.105		
	Core forest	0.269					0.174			0.092		
	Human-associated/ natural breaks	0.268					0.181			0.099		
Resident	Perimeter/area	0.291	0.066				0.050					0.078
	Forest area	0.249					0.043					0.080
	Core forest	0.287	0.061				0.054					0.066
	Human-associated/ natural breaks	0.281				0.054	0.042					0.093
Trophic level summer density												
Secondary consumer	Perimeter/area	0.484	0.143				0.259	0.073			0.034	0.035
	Forest area	0.456		0.095			0.246	0.066				
	Core forest	0.474			0.126		0.263	0.072				
	Human-associated/ natural breaks	0.480				0.136	0.239	0.077			0.039	0.046
Omnivore	Perimeter/area	0.327					0.050	0.062		0.100	0.093	
	Forest area	0.316					0.051	0.057		0.094	0.086	
	Core forest	0.320					0.048	0.060		0.099	0.090	
	Human-associated/ natural breaks	0.312					0.055	0.055		0.089	0.093	
Herbivore	Perimeter/area	0.163	0.047									0.037
	Forest area	0.155		0.038								
	Core forest	0.182			0.069							
	Human-associated/ natural breaks	0.175				0.060						0.040
Macrohabitat winter density												
edge/successional	Perimeter/area	0.446							0.065	0.065		0.197
	Forest area	0.442							0.081	0.062		0.157
	Core forest	0.439							0.085	0.063		0.201
	Human-associated/ natural breaks	0.440							0.079	0.067		0.215
generalist	Perimeter/area	0.343	0.176									0.058
	Forest area	0.223										0.073
	Core forest	0.271			0.086							0.068
	Human-associated/ natural breaks	0.268				0.082						0.090
Microhabitat winter density												
Arboreal	Perimeter/area	0.305	0.045								0.040	0.124
	Forest area	0.273										0.157
	Core forest	0.284									0.039	0.133
	Human-associated/ natural breaks	0.294									0.037	0.140
Generalist	Perimeter/area	0.353	0.120						0.034	0.046		0.120
	Forest area	0.280										0.120
	Core forest	0.312			0.065					0.043		0.124
	Human-associated/ natural breaks	0.316				0.069				0.038		0.146
Trophic level winter density												
Omnivore	Perimeter/area	0.498	0.143				0.089					0.172
	Forest area	0.434		0.034			0.071					0.161
	Core forest	0.462			0.063		0.084					0.167
	Human-associated/ natural breaks	0.472				0.099	0.069					0.204
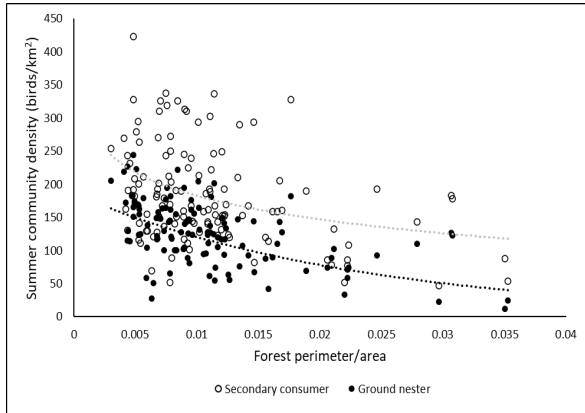
FIG. 11. Secondary consumer and ground nester summer density decline with increasing forest perimeter/area.

FIG. 12. Ground nester and secondary consumer summer density increase with increasing conifer cover.

hierarchical analysis indicating that increasing density was principally associated with decreasing perimeter/area (Fig. 11) and increasing conifer cover (Fig. 12) and understory density. Cavity nester density showed the strongest relationship to a model including core forest, with hierarchical analysis indicating that increasing density was principally associated with decreasing core forest and understory density. Canopy/understory nester density showed the strongest relationship to a model including perimeter/area, although hierarchical analysis indicated that increasing density was principally associated with only increasing soil moisture and decreasing canopy cover (Fig. 13).

Density responses of summer macrohabitat categories to predictors were also generally similar to those of richness for all categories. Categories vs. bird density showed that the strongest relationships by far were for interior forest species. In this case, a model with core forest showed a slightly greater r^2 compared with other landscape measures. However, hierarchical analysis indicated that increasing density was principally associated with only increasing conifer cover (Fig. 14) and elevation (Fig. 15). Edge/successional density showed the strongest relationship to a model including human-associated and natural forest breaks, although hierarchical analysis indicated that increasing density was principally associated with only decreasing canopy cover (Fig. 13) and elevation (Fig. 15). Generalist density showed no significant relationships.

A number of differences emerged between analyses of summer density and richness for microhabitat categories. As with summer richness, analysis of categories vs. density showed that the strongest relationships by far were for ecological generalists. However, in this case a model with proportion of forest cover showed a slightly greater r^2 compared with other landscape measures, although hierarchical analysis indicated that increasing density
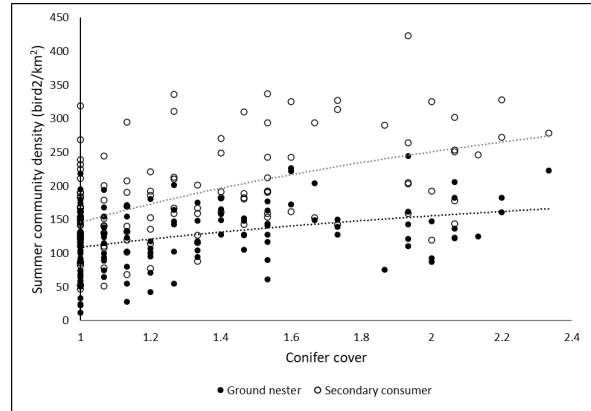
was principally associated with only decreasing canopy cover (Fig. 13) and increasing understory density. Arboreal forager density showed the strongest relationship to a model including perimeter/area, with hierarchical analysis indicating that increasing density was principally associated with decreasing perimeter/area (Fig. 16) and increasing conifer cover and soil moisture. Ground/shrub forager density showed the strongest relationship to a model including perimeter/area, with hierarchical analysis indicating that increasing density was principally associated with decreasing perimeter/area (Fig. 16) and increasing conifer cover, soil moisture and understory density.

A number of differences also emerged in analyses of summer richness vs. density with respect to migration categories. Analysis of these vs. density showed that the strongest relationships by far were for neotropical migrants. In this case, a model with perimeter/area showed a slightly greater r^2 compared with other landscape measures, with hierarchical analysis indicating that increasing density was principally associated with decreasing perimeter/area (Fig. 16) and increasing soil moisture and understory density. North American migrant density showed the strongest relationship to a model also including perimeter/area, although hierarchical analysis indicated that increasing density was principally associated with only decreasing deciduous (Fig. 14) and canopy cover. Resident density also showed the strongest relationship to a model including perimeter/area, with hierarchical analysis indicating that increasing density was principally associated with decreasing perimeter/area and elevation.

As with summer richness, analysis of trophic categories vs. summer density showed that the strongest relationships by far were for secondary consumers. Otherwise, some differences emerged among responses to predictors. In this case, a model with perimeter/area showed a slightly greater r^2
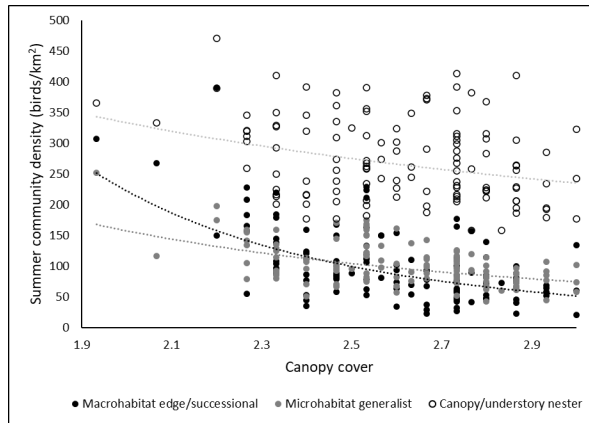
FIG. 13. Edge/successional, macrohabitat generalist and canopy/understory nester summer density decline with increasing canopy cover.

FIG. 14. Interior forest and North American migrant summer density increase with increasing conifer cover.

compared with other landscape measures, with hierarchical analysis indicating that increasing density was principally associated with decreasing perimeter/area (Fig. 11) and increasing conifer cover (Fig. 12) and soil moisture. Omnivore density also showed the strongest relationship to a model including perimeter/area, although hierarchical analysis indicated that increasing density was principally associated with only decreasing canopy cover and increasing understory density. Herbivore density showed the strongest relationship to a model including core forest, with hierarchical analysis indicating that increasing density was principally associated with decreasing core forest.

Because of the low density of wintering birds present in forests, only several community density categories had measures at >90% of sites. As with winter richness, macrohabitat categories vs. winter density showed that the strongest relationships by far were for edge/successional species. In this case, a model with perimeter/area showed a slightly greater r^2 compared with other landscape measures, although hierarchical analysis indicated that increasing density was principally associated with only decreasing elevation (Fig. 17). Habitat generalist density showed the strongest relationship with a model including perimeter/area, with hierarchical analysis indicating that increasing density was principally associated with increasing perimeter/area (Fig. 18). Species that specialized in interior forest use occurred with insufficient frequency for analysis.

As with winter richness, microhabitat categories vs. winter density showed that arboreal species had the strongest relationship with a model including perimeter/area, although hierarchical analysis indicated that increasing density was principally associated with only decreasing elevation (Fig. 17). Foraging generalist density also showed the strongest relationship with a model including perimeter/
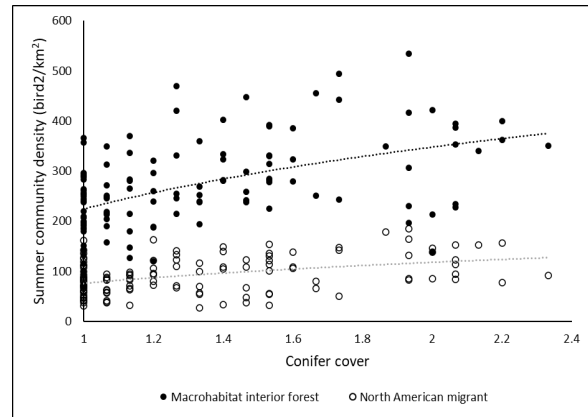
area, although hierarchical analysis again indicated that increasing density was principally associated with only decreasing elevation. Ground/shrub foragers occurred with insufficient frequency for an analysis to be conducted.

For trophic categories vs. winter richness, only omnivores occurred frequently enough for analysis. In this case, a model with perimeter/area had the greatest r^2. However, as with richness analysis, hierarchical analysis indicated that increasing density was principally associated with only decreasing conifer cover and elevation (Fig. 17).

Species composition. In examining densities of the 14 summering species occurring at >90% of sites (Table 3), models with the greatest r^2 included six with perimeter/area, one with core forest, five with human-associated and natural forest breaks, one with no difference among landscape predictors and one with no significant associations with any predictors. Moreover, two species had significant associations only with habitat predictors (Table 3). For densities of three widespread wintering species, all had the greatest r^2 for models in which perimeter/area was included with habitat measures.

Increasing densities of the cavity nesting, resident, arboreal ecological generalist Downy Woodpecker (*Drybates pubescens*) showed a slightly stronger relationship compared with other landscape models for one with perimeter/area, with hierarchical analysis indicated that increasing density was associated with primarily increasing deciduous cover (Fig. 19) and secondarily with decreasing perimeter/area. In contrast, the also cavity-nesting, resident, northerly-distributed arboreal ecological generalist Black-capped Chickadee (*Poecile atricapillus*) showed a slightly stronger relationship to a model including human-associated cover, with hierarchical analysis indicating that increasing densities were associated with primarily increasing conifer cover (Fig. 19) and secondarily increasing human

TABLE 3. Multivariate regression analyses' statistically significant ($P < 0.05$) r^2 values for summer/winter community density and species classifications for nest site selection, macrohabitat use, microhabitat use, migration category and trophic category.

| | | | Landscape measures | | | | | Habitat measures | | | | | | |
		Total	Perimeter/area	Forest area	Core forest	Human-associated	Natural breaks	Conifer cover	Moisture regime	dbh	Canopy cover	Understory density	Elevation	Vertical complexity
Summer species														
Downy Woodpecker	Perimeter/area	0.241						0.186				0.034		
	Forest area	0.229						0.183			0.034	0.034		
	Core forest	0.235						0.187				0.034		
	Human-associated/ natural breaks	0.230						0.182			0.034	0.037		
Eastern Wood Pewee	Perimeter/area	0.316						0.104	0.042		0.090	0.080	0.041	
	Forest area	0.316						0.103	0.041		0.088	0.078	0.034	
	Core forest	0.316						0.102	0.041		0.085	0.080	0.036	
	Human-associated/ natural breaks	0.316						0.103	0.041		0.088	0.080	0.041	
Blue Jay	Perimeter/area	0.095	0.057									0.041		
	Forest area	0.083		0.045								0.035		
	Core forest	0.064										0.039		
	Human-associated/ natural breaks	0.084												
Black-capped Chickadee	Perimeter/area	0.184						0.157	0.053					
	Forest area	0.181						0.157	0.051					
	Core forest	0.193						0.158	0.059					
	Human-associated/ natural breaks	0.209				0.045		0.171	0.067					
Tufted Titmouse	Perimeter/area	0.344	0.071					0.045			0.130		0.115	
	Forest area	0.309						0.039			0.111		0.102	
	Core forest	0.348			0.077			0.051			0.143		0.095	
	Human-associated/ natural breaks	0.333				0.056		0.036			0.128		0.134	
Veery	Perimeter/area	0.322	0.043					0.083	0.043			0.195		
	Forest area	0.305						0.078	0.038			0.182		
	Core forest	0.317			0.036			0.085	0.043			0.193		
	Human-associated/ natural breaks	0.317				0.036		0.075	0.044			0.198	0.037	
Wood Thrush	Perimeter/area	0.190						0.131	0.062					
	Forest area	0.183						0.131	0.066					
	Core forest	0.187						0.133	0.063					
	Human-associated/ natural breaks	0.220				0.046		0.122	0.048					
American Robin	Perimeter/area	0.371	0.101					0.089			0.171	0.044		
	Forest area	0.357		0.082				0.082			0.154	0.034		
	Core forest	0.350			0.072			0.090			0.151	0.041		
	Human-associated/ natural breaks	0.390				0.129		0.079			0.158	0.049		
Red-eyed Vireo	Perimeter/area	0.428	0.069					0.068	0.033		0.068		0.168	
	Forest area	0.416		0.050				0.066	0.033		0.064		0.122	
	Core forest	0.425			0.065			0.062	0.034		0.054		0.149	
	Human-associated/ natural breaks	0.401						0.077			0.071		0.205	
Ovenbird	Perimeter/area	0.450	0.104					0.114	0.039		0.051	0.100	0.071	
	Forest area	0.449		0.101				0.115	0.042		0.041	0.083	0.034	
	Core forest	0.444			0.093			0.119	0.039		0.038	0.095	0.060	
	Human-associated/ natural breaks	0.418				0.051		0.095	0.034		0.053	0.100	0.101	
Scarlet Tanager	Perimeter/area	0.213	0.177									0.054		
	Forest area	0.291		0.259								0.080		0.035
	Core forest	0.255			0.222							0.062		
	Human-associated/ natural breaks	0.293				0.134	0.138					0.087		
Brown-headed Cowbird	Perimeter/area	0.136	0.076										0.102	
	Forest area	0.109		0.046									0.088	
	Core forest	0.115			0.053								0.091	
	Human-associated/ natural breaks	0.116				0.054							0.088	

American Goldfinch	Perimeter/area	0.173	0.039				0.033	0.053
	Forest area	0.169		0.035				0.037
	Core forest	0.184			0.052			0.037
	Human-associated/ natural breaks	0.187				0.055	0.039	0.053
Winter species								
Downy Woodpecker	Perimeter/area	0.304	0.044				0.086	0.078
	Forest area	0.272					0.069	0.118
	Core forest	0.278					0.078	0.096
	Human-associated/ natural breaks	0.29					0.078	0.096
Black-capped Chickadee	Perimeter/area	0.217	0.046				0.075	0.062
	Forest area	0.181					0.08	0.079
	Core forest	0.206			0.033		0.071	0.058
	Human-associated/ natural breaks	0.208				0.035	0.084	0.076
White-breasted Nuthatch	Perimeter/area	0.27	0.193				0.106	
	Forest area	0.183		0.097			0.094	
	Core forest	0.245			0.165		0.109	
	Human-associated/ natural breaks	0.232				0.151	0.089	
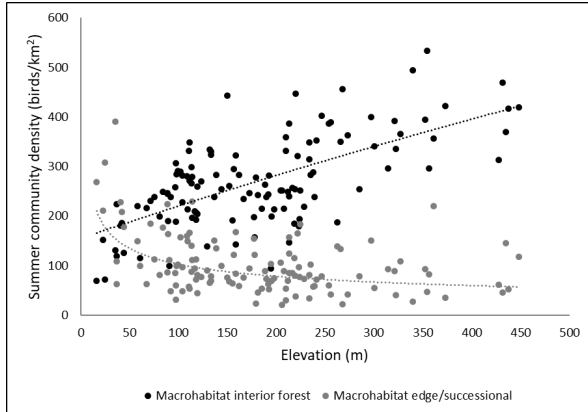
FIG. 15. Interior forest summer density increases whereas edge/successional density declines with increasing elevation.

FIG. 16. Arboreal, ground/shrub and neotropical migrant density decline with increasing forest perimeter/area.

cover and soil moisture. The ecologically similar but southerly-distributed Tufted Titmouse (*Baeolophus bicolor*) showed a slightly stronger relationship to a model including core forest cover, with hierarchical analysis indicating that increasing densities were associated with primarily decreasing elevation (Fig. 20) and secondarily increasing canopy cover. The also similar White-breasted Nuthatch (*Sitta carolinensis*) showed no significant relationships to any models. The ecological generalist, North American migrant Blue Jay (*Cyanocitta cristata*) showed weak associations with landscape and habitat variables, with hierarchical analysis demonstrating the strongest relationship to a model including increasing perimeter/area (Fig. 21) and decreasing understory density.

The tree-nesting, arboreal, interior forest-associated neotropical migrant Eastern Wood Pewee (*Contopus virens*) showed no significant relationships to landscape variables although hierarchical analysis indicated that increasing densities were most closely associated with increasing canopy and deciduous cover. The ground-nesting, interior forest-associated, northerly-distributed neotropical migrant Veery (*Catharus fuscesens*) showed a slightly stronger relationship to a model including perimeter/area, with hierarchical analysis indicating that increasing densities were associated with primarily increasing understory density and secondarily increasing conifer cover and perimeter/area (Fig. 21). The ecologically similar but tree and shrub-nesting, centrally-distributed Wood Thrush (*Hylocichla mustelina*) had a slightly stronger relationship to a model including human cover, although hierarchical analysis indicated that increasing densities were associated only with primarily increasing deciduous cover (Fig. 19) and secondarily soil moisture. The tree and shrub-nesting, edge/successional habitat-associated North American migrant American Robin (*Turdus migratorius*)
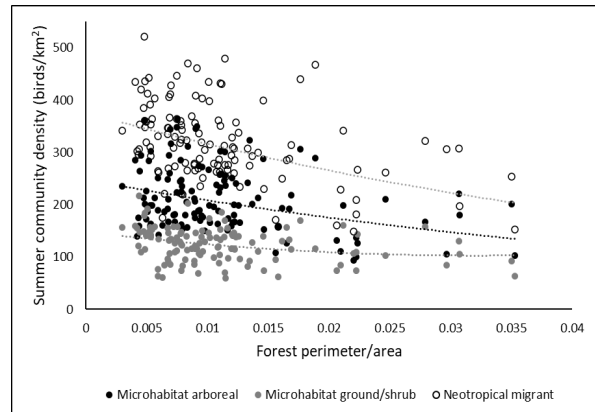
showed a slightly closer relationship to a model including human-associated cover, although hierarchical analysis indicated that increasing densities were principally associated only with decreasing canopy cover.

The tree-nesting, interior forest-associated, arboreal foraging, neotropical migrant Red-eyed Vireo (*Vireo olivaceus*) showed the closest relationship to a model including perimeter/area, although hierarchical analysis indicated that increasing densities were associated with primarily increasing elevation (Fig. 20) and, secondarily increasing canopy cover. The ecologically similar but ground-nesting, ground and shrub-foraging Ovenbird (*Seiurus aurocapilla*) also showed a slightly closer relationship to a model including perimeter/area, although hierarchical analysis indicated that increasing densities were principally associated only with increasing elevation (Fig. 20). The tree-nesting, interior forest-associated neotropical migrant Scarlet Tanager (*Piranga olivacea*) showed a slightly stronger relationship to a model including human-associated cover and natural forest breaks, with hierarchical analysis indicating that increasing densities were associated primarily with decreasing human-associated and natural forest breaks (Fig. 21) and secondarily with decreasing understory density.

The edge/successional-associated, ground and shrub-foraging, North American migrant Brown-headed Cowbird showed a slightly stronger relationship to a model including perimeter/area, although hierarchical analysis showed that increasing densities were weakly associated only with decreasing elevation. The ecological generalist, North American migrant American Goldfinch (*Spinus tristis*) showed a slightly stronger relationship to a model including human-associated forest breaks, with hierarchical analysis indicting that increasing densities
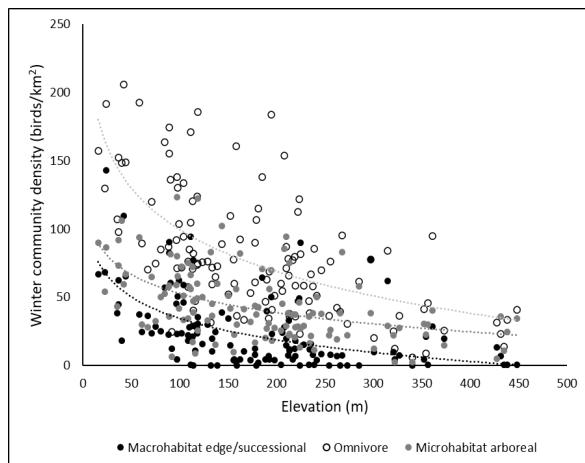
FIG. 17. Edge/successional, omnivore and arboreal winter density decline with increasing elevation.

FIG. 18. Macrohabitat generalist winter density increases with increasing forest perimeter/area.

were weakly associated with increasing human-associated breaks and understory density.

For the three widespread wintering species, the generalist Downy Woodpecker showed a slightly stronger relationship to a model including perimeter/area, with hierarchical analysis indicating that increasing densities were primarily associated with declining conifer cover and elevation. The generalist Black-capped Chickadee also showed a slightly stronger relationship to a model including perimeter/area, with hierarchical analysis indicating that increasing densities were weakly associated with increasing perimeter/area and conifer cover. Increasing densities of the generalist White-breasted Nuthatch again showed a stronger relationship to a model including perimeter/area, with hierarchical analysis indicating that increasing densities were associated with primarily increasing perimeter/area and secondarily increasing deciduous cover.

Temporal variation. Species richness in eastern Connecticut did not significantly vary between the 2001–2003 and 2004–2006 sampling periods for either summer (Wilcoxon $Z = -0.72$, N = 50, $P = 0.47$) or winter (paired sample $t = -1.82$, df = 49, $P = 0.08$). However, summer community density was significantly greater in 2004–2006 than in 2001–2003 (Wilcoxon $Z = -4.01$, $n = 50$, $P < 0.01$). Moreover, winter density was also greater in 2004–2006 (paired sample $t = -3.61$, df = 49, $P < 0.01$).

Of 20 tests performed on community measures (Table 4), 11 showed at least some differences between sampling periods. Of seven significant landscape results, two showed differences and of 17 significant habitat results, nine showed at least some differences. Specifically, as in the statewide analysis, increasing summer richness showed sig-
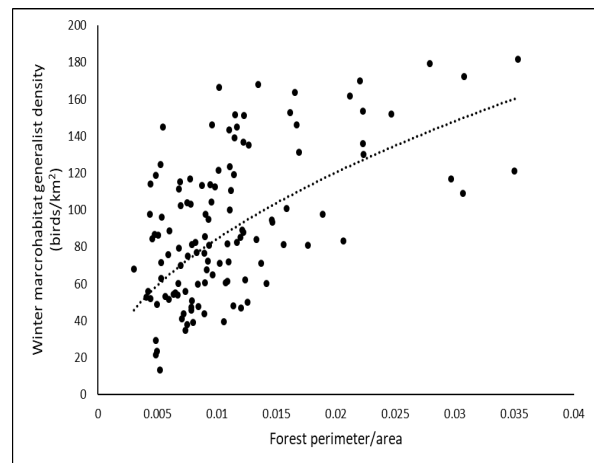
nificant relationships with increasing conifer and decreasing canopy cover in 2004–2006, although these predictors were nonsignificant in 2001–2003. Also as in the statewide analysis, increasing winter richness was significantly associated with decreasing elevation during both periods. However, there were no significant relationships for summer community density in either sampling period. In winter, as in the statewide analysis, increasing density was associated with decreasing elevation in 2004–2006, although there were no significant results in 2001–2003.

In the case of classes of summer community richness measures, as with the statewide analysis more ground nester species were significantly associated with decreasing perimeter/area and increasing conifer cover during both sampling periods, although there was no significant relationship with understory density. Also as with the statewide analysis, increasing interior forest richness was significantly associated with increasing conifer cover and elevation during both sampling periods, although it was related to decreasing human cover only in 2001–2003. As in the statewide analysis, increasing microhabitat generalist richness was significantly associated with increasing elevation for both sampling periods, although conifer cover was nonsignificant for both periods. As in the statewide analysis, increasing North American migrant richness was significantly associated with increasing conifer cover during both sampling periods, although increasing core forest was significant only in 2004–2006 and canopy cover had nonsignificant effects. Secondary consumers showed no significant relationships with human-associated cover or conifer cover, unlike in the statewide analysis.

TABLE 4. Comparison of 2001 and 2004 regression analyses' statistically significant (P < 0.05) r^2 values for summer/winter eastern Connecticut community species richness and species classifications for nest site selection, macrohabitat use, microhabitat use, migration category and trophic category. n/s = nonsignificant.

| | Year | Total | Landscape measures | | | | Habitat measures | | | | |
---	---	---	Perimeter/area	Forest area	Core forest	Human-associated	Conifer cover	Moisture regime	Canopy cover	Understory density	Elevation
Community richness											
Summer	2001	n/s									
	2004	0.240					0.140		0.106		
Winter	2001	0.334									0.268
	2004	0.511									0.440
Nest site summer richness											
Ground	2001	0.229	0.157				0.106				
	2004	0.253	0.225				0.081				
Macrohabitat summer richness											
Interior forest	2001	0.664				0.216	0.500				0.216
	2004	0.539					0.424				0.093
Microhabitat summer richness											
Arboreal	2001	0.229									0.147
	2004	0.273									0.167
Migration summer richness											
North American	2001	0.392					0.349				
	2004	0.508			0.129		0.388				
Trophic summer richness											
Secondary consumer	2001	n/s									
	2004	n/s									
Macrohabitat winter richness											
Edge/successional	2001	0.400									0.242
	2004	0.560					0.240				0.300
Microhabitat winter richness											
Arboreal	2001	n/s									
	2004	0.421									0.379
Trophic winter richness											
Omnivore	2001	0.263									0.246
	2004	0.374									0.340
Community density											
Summer	2001	n/s									
	2004	n/s									
Winter	2001	0.178									
	2004	0.449									0.385
Nest site summer density											
Ground	2001	0.414	0.284				0.149			0.206	
	2004	0.611	0.492				0.286			0.324	
Macrohabitat summer density											
Interior forest	2001	0.487			0.247						0.156
	2004	0.576			0.433		0.248				
Microhabitat summer density											
Generalist	2001	0.277							0.218		
	2004	0.326							0.126	0.131	
Migration summer density											
Neotropical	2001	0.266	0.215								
	2004	0.388	0.258					0.175			
Trophic summer density											
Secondary consumer	2001	0.189	0.159								
	2004	0.268	0.084				0.178				
Macrohabitat winter density											
Edge.successional	2001	0.422									0.352
	2004	0.430									0.406
Microhabitat winter density											
Generalist	2001	2001	0.192								0.181
	2004	n/s									
Trophic winter density											
Omnivore	2001	0.297									0.134
	2004	0.457					0.098				0.252
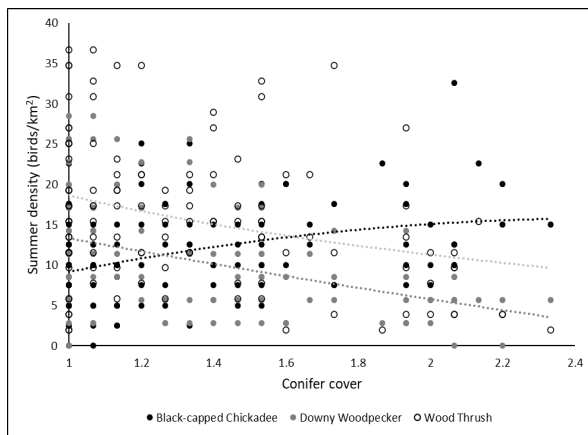
FIG. 19. Downy Woodpecker and Wood Thrush summer densities decline with conifer cover whereas Black-capped Chickadee densities increase.

FIG. 20. Red-eyed Vireo and Ovenbird summer densities increase whereas Tufted Titmouse densities decline with increasing elevation.

Winter community measures of increasing edge/successional richness showed, as in the statewide analysis, a significant relationship with decreasing elevation for both sampling periods, although decreasing conifer cover was significant only in 2004−2006. In the case of increasing arboreal richness, as in the statewide analysis, there was a significant relationship with declining elevation, although only in 2004−2006. As in the statewide analysis, increasing omnivore richness was significantly associated with decreasing elevation for both sampling periods, although conifer cover was nonsignificant.

In the case of classes of summer community density measures, increasing ground nester density was significantly associated with decreasing perimeter/area, increasing conifer cover and understory density during both sampling periods, as also observed in the statewide analysis. Much as in the statewide analysis, increasing interior forest bird density was significantly associated with increasing core forest during both sampling periods, although increasing conifer cover was significant in only 2004−2006 and increasing elevation was significant only in 2001−2003. As in the statewide analysis, increasing neotropical migrant density was significantly associated with decreasing perimeter/area, although increasing soil moisture was significant only in 2004−2006. Conifer cover and understory density were nonsignificant factors, however. As in the statewide analysis, increasing microhabitat generalist density was significantly associated with decreasing canopy cover, although increasing understory density was significant only in 2004−2006. As in the statewide analysis, increasing secondary consumer density was significantly associated with decreasing perimeter/areas, although increasing
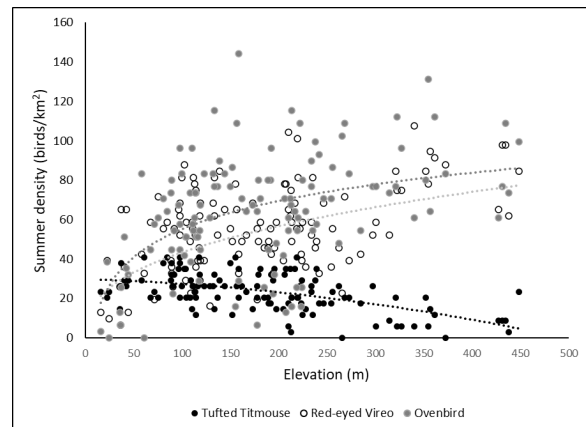
conifer cover was related only in 2004−2006. Soil moisture was nonsignificant during both sampling periods.

Winter community density measures for microhabitat generalists showed no significant relationships, although in the statewide analysis increasing density was significantly associated with declining elevation. As in the statewide analysis, increasing density of edge/successional habitat specialists was associated with declining elevation for both sampling periods. Also as in the statewide analysis, increasing omnivore density was significantly associated with declining elevation during both sampling periods, although increasing densities in increasing deciduous cover were significant only in 2004−2006.

DISCUSSION

The first hypothesis tested, that the richness and density of breeding communities as well as the richness and density of neotropical migrant, ground nesting, interior forest-dwelling, arboreal foraging and ground/shrub foraging birds would decline with increasing fragmentation, was supported in each instance by population density results. These findings are consistent with the contentions of George et al. (2002), Manolis et al. (2002) and Hoover et al. (2006). Summer community density, neotropical migrant, ground nester, interior forest-dwelling, arboreal forager and ground/shrub forager densities were most closely associated, albeit often only slightly, with models that included either perimeter/area or core forest. Despite the small improvement in model fit offered by fragmentation measures compared with the other highly correlated landscape measures, they had the closest association with these
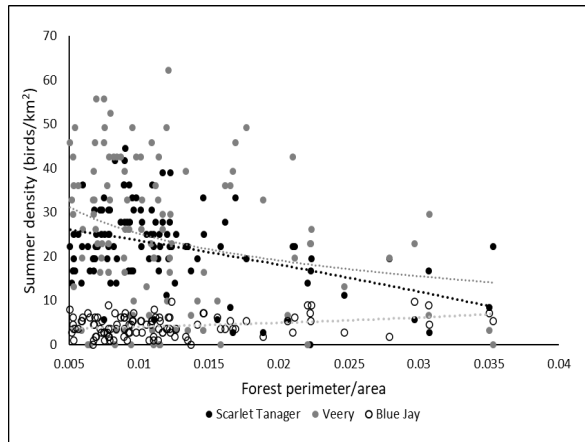
FIG. 21. Scarlet Tanager and Veery summer densities decline whereas Blue Jay densities increase with increasing forest perimeter/area.

and other summer community measures 67% of the time, strongly suggesting that fragmentation effects are the underlying driver of such community patterns.

In the case of species richness, only ground nester and arboreal forager richness were most closely associated with fragmentation measures. Summer community, neotropical migrant and interior forest-associated richness were instead associated with the proportion of human-associated forest breaks and ground/shrub forager richness showed a weak to no significant relationship with landscape measures. These richness findings are at least in part at odds with the assertions of such researchers as Ambuel and Temple (1983), Robbins et al. (1989), Lynch et al. (2003) and Zipkin et al. (2009), although they show consistency with those of Hawrot and Niemi (1996), Drapeau et al. (2000) and Manuwal et al. (2002). Moreover, in most instances habitat factors also appeared to exert substantial influence on richness and density, in agreement with the findings of Lynch and Whigham (1984) and Dorazio et al. (2015).

In the case of richness and community density showing increases with increasing fragmentation for breeding short-distance migrant, resident, foraging generalist, edge/successional and habitat generalist species, including the Brown-headed Cowbird (hypothesis 2), resident density and richness and habitat generalist richness did show increases with increasing fragmentation measures. However, short-distance migrant density and richness, foraging generalist density and richness, edge/successional density and richness, habitat generalist density and Brown-headed Cowbird density showed no likely significant response to landscape measures, although short distance migrant richness showed a possible weak increase with increasing core forest, in contrast to prediction. These findings are general-

ly consistent with those of Lynch and Whigham (1984), Telleria and Santos (1994) and Hobson and Bayne (2000). The findings for the brood parasitic cowbird contrast with those of Robinson et al. (1995), Donovan (1997) and Hobson and Bayne (2000), although they are consistent with the findings of Askins and Philbrick (1987), Fauth (2000) and Morimoto et al. (2012) likely because, as noted by Hanski et al. (1996), parasitism levels are related to geographic differences in density and densities in Connecticut are comparatively low (Sauer et al. 2017).

In the case of forest area effects predominating over fragmentation effects (hypothesis 3), this study provides, in contrast to the opinion of D'Eon (2002), evidence that the effects of fragmentation appear to predominate over those of simply forest extent in predicting summer and winter bird community characteristics even in the comparatively extensive forests of southern New England. Indeed, forest extent was the best predictor in only one of 32 instances of summer community measures and in none of 15 winter measures. Although this more heavily forested landscape may ameliorate some effects of fragmentation (Rosenberg et al. 1999, Thompson et al. 2002, Rittenhouse et al. 2010), it does not appear to eliminate them.

In the case of fragmentation effects predominating over local habitat effects (hypothesis 4), of 16 tests concerning breeding density only three, for cavity nesting birds, arboreal foragers and herbivores, showed limited signs of predominating over habitat effects. Similarly, of 16 tests concerning breeding richness, only three, for neotropical migrants, ground nesters and cavity nesters, showed limited signs of predominating over habitat effects. Moreover, eight of the 14 breeding species examined showed habitat effects greatly predominating over landscape effects, with three of these species showing no significant relationships with landscape measures. Hence, evidence supporting this hypothesis is weak, which is consistent with the views of Lynch and Whigham (1984), Dorazio et al. (2015) and Craig et al. (2022).

In the case of natural forest breaks having fewer community effects than human-associated ones (hypothesis 5), only two of 32 summer and none of 15 winter community measures showed any significant relationship to natural forest breaks, although even these effects disappeared with hierarchical analysis. Moreover, only one of 14 breeding species, the Scarlet Tanager, showed a relationship to natural forest breaks, with the Scarlet Tanager showing increased densities with declining natural breaks. None of the three wintering species studied showed such a relationship. Hence, this evidence supports Drapeau et al.'s (2000) assertion that the effects of natural forest breaks on bird communities

are limited.

In the case of fragmentation showing little community consequence in winter (hypothesis 6), winter richness and community density showed, based on hierarchical analysis, no likely relationship to any landscape measures, much as Hamel et al. (1993) and Yahner (1993) found, although this contrasted with results of Doherty and Grubb (2000). Moreover, of 13 additional winter community groups studied, 10 showed weak to no relationships with any landscape measures, with hierarchical analysis showing that only habitat generalist density has a substantial increase with increasing perimeter/area. These results are not surprising in light of the prevalence of ecological generalist species at this season (Appendix). In addition, of the three species occurring frequently enough for analysis, only one showed a strong positive association with perimeter/area, whereas the remaining two showed a weak positive association. In most cases, the habitat variable of overriding importance to winter community groups was elevation, including for two of the three species. Craig (2012) similarly found that six of 10 resident species concentrated at lower elevations in winter, with winter movements to lower elevations likely related to populations seeking less metabolically costly landscapes.

Because of the large samples of this study, the probability that findings are due to chance seems low. However, duplicate observations for eastern Connecticut, still with a substantial sample size, do show that temporal variation occurs in some ecological relationships, much as Wiens (1981) reported for shrubsteppe birds. The increase in breeding community density observed from 2001−2003 to 2004−2006 in part may be explained by the intensive management for earlier successional growth occurring in the 3213 ha Yale-Myers Forest in northeastern Connecticut that has led to a long-term increase in populations at this location (Craig et al. 2022). However, over the wider area of northeastern Connecticut, populations have trended toward stable between 2004 and 2021 (Craig in press). Notably, some significant community group observations occurred only during 2004−2006, when community density was higher. This could mean that the lower densities observed during 2001−2003 led to species expanding their niche width at a time when fewer competitors were present. Other consistent differences occurring among community groups in eastern Connecticut vs. the entire study area could reflect environmental differences of eastern Connecticut leading to habitat use differences. The more extensive, xeric moraine-derived soils of this region is one possible driver of such differences.

We might expect that particularly in winter there will be annual variation in observed ecological relationships, as species composition and population densities change annually due to changing resource availability driving species' range irruptions, such as occur with boreal finches, or annual shifts in weather patterns driving species near their northern range limit to move further south. Indeed, during the study period, boreal finches were nearly absent during some years but abundant during others (Craig 2017). Hence, my observations of temporal changes in population density and the occurrence of few consistent associations of species groups with predictor variables are not unexpected.

ACKNOWLEDGEMENTS

LITERATURE CITED

ALERICH, C.L. 1999. Forest Statistics for Connecticut. USDA Forest Service, Northeastern Research Station Resource Bulletin NE−147.

ASKINS R.A. and M.J. PHILBRICK. 1987. Effect of changes in regional forest abundance on the decline and recovery of a forest bird community. Wilson Bulletin 99:7−21.

AMBUEL, B. and S.A. TEMPLE. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. Ecology 64:1057−1068.

BILLERMAN, S.M., B.K. KEENEY, P.G. RODEWALD and T.S. SCHULENBERG, Editors. 2022. Birds of the World. Cornell Laboratory of Ornithology, Ithaca, NY. https://birdsoftheworld.org/bow/home

BLAKE, J.G. and W.G. HOPPES. 1986. Influence of resource abundance on use of tree-fall gaps by birds in an isolated woodlot. The Auk 103:328−340.

BLAKE, J.G. and J.R. KARR. 1987. Breeding birds of isolated woodlots: area and habitat relationships. Ecology 68:1724−1734.

BOULINIER, T., J.D. NICHOLS, J.E. HINES, J.R. SAUER, C.H. FLATHER and K.H. POLLOCKS. 2001. Forest fragmentation and bird community dynamics: inferences at regional scales. Ecology 82:1159−1169.

BRAWN, J.D. and S.K. ROBINSON. 1996. Source-sink population dynamic may complicate the inter-

pretation of long-term census data. Ecology 77:3−12.

BUCKLAND, S.T., D.R. ANDERSON, K.P BURNHAM, J.L. LAAKE, D.L. BORCHERS and L. THOMAS. 2001. Introduction to distance sampling. Oxford University Press, Oxford, UK.

BURKE, D.M. and E. NOLL. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. The Auk 115:96−104.

BUTLER, B..J. 2017. Forests of Connecticut, 2016. USDA Forest Service, Northeast Research Station Update FS−130.

CAMP, R.J., T.K. PRATT, A.P. MARSHALL, F. AMIDON and L.L. WILLIAMS. 2009. Recent status and trends of the land bird avifauna on Saipan, Mariana Islands, with emphasis on the endangered Nightingale Reed-warbler *Acrocephalus luscinia.* Bird Conservation International 19:323–337.

[CLEAR] CENTER FOR LAND USE EDUCATION AND RESEARCH. 2020. Connecticut forest fragmentation. University of Connecticut, Storrs, CT. https://clear.uconn.edu/projects/landscape/ct-forestfrag/.

CRAIG, R.J. 1984. Comparative foraging ecology of Louisiana and Northern waterthrushes. Wilson Bulletin 96:173−185.

CRAIG, R.J. 1996. Seasonal population surveys and natural history of a Micronesian bird community. Wilson Bulletin 108:246–267.

CRAIG, R.J. 2012. Seasonal shifts in population distributions and habitat use by permanent resident forest birds in eastern Connecticut. Bird Conservation Research Contribution 17.

CRAIG, R.J. 2017. Forest birds of Connecticut and Rhode Island. Bird Conservation Research Contribution 23.

CRAIG, R.J. [in press]. Temporal change in the forest birds of northeastern Connecticut shows partial concordance with predicted effects of climate and habitat change. Wilson Journal of Ornithology.

CRAIG, R.J. and K.G. BEAL. 2002. Microhabitat partitioning among surviving members of a Pacific island bird community. Wilson Bulletin 114:102-116.

CRAIG, R.J., M.C. DUGUID and M.S. ASHTON. 2022. Breeding forest birds in northeastern Connecticut show a long-term population increase and high species turnover. Wilson Journal of Ornithology 134:27−42.

CRAIG, R.J. and R.W. KLAVER. 2013. Factors influencing geographic patterns in diversity of forest bird communities of eastern Connecticut, USA. Ecography 36:599-609.

D'EON, R.G. 2002. Forest fragmentation and forest management: A plea for empirical data. The Forestry Chronicle 78:686-689.

DEGRAAF, R.M., T.J. MAIER and T. FULLER. 1999. Predation of small eggs in artificial nests: effects of nest position edge and potential predator abundance in extensive forest. Wilson Bulletin 111:236−242.

DEGRAAF, R.M., N. G. TILGHMAN AND S. H. ANDERSON. 1985. Foraging guilds of North American birds. Environmental Management 9:493−536.

DOHERTY, P.F. and T.C. GRUBB JR. 2000. Habitat and landscape correlates of presence density and species richness of birds wintering in forest fragments in Ohio. Wilson Bulletin 112:388−394.

DONOVAN T.M., P.W. JONES, E.M. ANNAND and F.R. THOMPSON III. 1997. Variation in local-scale edge effects: mechanism and landscape context. Ecology 78:2064−2075.

DORAZIO, R.M., E.F. CONNOR and R.A. ASKINS. 2015. Estimating the effects of habitat and biological interactions in an avian community. PLoS ONE 10:e0135987.

DOWHAN, J.J. and R.J. CRAIG. 1976. Rare and Endangered Species of Connecticut and Their Habitats. Connecticut Geological and Natural History Survey Report of Investigations 6.

DRAPEAU, P., A. LEDUC, J.F. GIROUX, J.P.L. SAVARD, Y. BERGERON and W.L. VICKERY. 2000. Landscape-scale disturbances and changes in bird communities of boreal mixed-wood forests. Ecological Monographs 70:423−444.

FAUTH, P.T. 2000. Reproductive success of Wood Thrushes in forest fragments in northern Indiana. The Auk 117:194−204.

FOSTER DR AND JF O'KEEFE. 2000. New England forests through time. Harvard University Press, Cambridge, MA.

GALLI, A.E., C.F. LECK and R.T.T. FORMAN. 1976. Avian distribution patterns in forest islands of different sizes in central New Jersey. The Auk 93:356−364.

GEORGE, T.L. and L.A. BRAND. 2002. The effects of habitat fragmentation on birds in coast redwood forests. Studies in Avian Biology 25:92−102.

GIBBS, J.P. and J. FAABORG. 1990. Estimating the viability of Ovenbird and Kentucky Warbler populations in forest fragments. Conservation Biology 4:193−196.

GONZÁLEZ-SALAZAR, C.G., E. MARTÍNEZ-MEYER and G. LÓPEZ-SANTIAGO. 2014. A hierarchical classification of trophic guilds for North American birds and mammals. Mexicana de Biodiversidad 85:931−941.

HAMEL, P.B., W.P. SMITH and J.W. WAHL. 1993. Wintering bird populations of fragmented forest habitat in the central basin, Tennessee. Biological Conservation 66:107−115.

Hames R.S., K. Rosenberg and A.A. Dhondt. 2001. Site reoccupation in fragmented landscapes: testing predictions of metapopulation theory. Journal of Animal Ecology 70:182−190.

Hanski I.K., T.J. Fenske and G.J. Niemi. 1996. Lack of edge effect in nesting success of breeding birds of managed forest landscapes. The Auk 113:578−585.

Hawrot, R. and G.J. Nemi. 1996. Effects of edge type and patch shape on avian communities in a mixed conifer-hardwood forest. The Auk 113:586−598.

Hobson, K.A. and E. Bayne. 2000. Effects of forest fragmentation by agriculture on avian communities in the southern boreal mixed woods of western Canada. Wilson Bulletin 112:373−387.

Hoover, J.P., T.H. Tear and M.E. Baltz. 2006. Edge effects reduce the nesting success of Acadian Flycatchers in a moderately fragmented forest. Journal of Field Ornithology 77:425–436.

Hurlbert, S.H. 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52:577-586.

Ilgen, L.W., A.W. Benton, K.C. Stevens, Jr. and A.E. Shearin. 1966. Soil survey of Tolland County, Connecticut. U.S. Soil Conservation Service, Series 1961, no. 35.

Jules, E.S. 1998. Habitat fragmentation and demographic change for a common plant: trillium in old-growth forests. Ecology 79:1645-1656.

King, D.I., C.R. Griffin and R.M. DeGraaf. 1997. Effect of clear-cut borders on distribution and abundance of forest birds in northern New Hampshire. Wilson Bulletin 109:239-245.

Kroodsma, R.L. 1984. Effects of edge on breeding forest bird species. Wilson Bulletin 96:426-436.

Lambert, J.D. and S.J. Hannon. 2000. Short-term effects of timber harvest on abundance, territory characteristics, and pairing success of ovenbirds in riparian buffer strips. The Auk 117:687-698.

Linck, E.B., E.C. Fricke and H.S. Rogers. 2020. Varied abundance and functional diversity across native forest bird communities in the Mariana Islands. Wilson Journal of Ornithology 132:22–28.

Lindemayer, D.B., R.B. Cunningham, C.F. Donnelly, H. Nix and B.D. Lindemayer. 2002. Effects of forest fragmentation on bird assemblages in a novel landscape context. Ecological Monographs 72:1–18.

Lynch, J.F. and D.F. Whigham. 1984. Effects of forest fragmentation on breeding bird communities in Maryland, USA. Biological Conservation 28: 287–324.

Manolis, J.C., D.E. Anderson and F. Cuthbert. 2002. Edge effect on nesting success of ground nesting birds near regenerating clearcuts in a forest-dominated landscape. The Auk 119:955–970.

Manuwal, D.A. and N.J. Manuwal. 2002. Effects of habitat fragmentation of birds in the coastal coniferous forests of the Pacific northwest. Studies in Avian Biology 25:103−112.

Matthysen, E. and F. Adriaensen. 1998. Forest size and isolation have no effect on reproductive success of Eurasian nuthatches (*Sitta europaea*). The Auk 115:955−963.

McGarigal, K and B.J. Marks. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. Gen. Tech. Rep. PNW-GTR-351. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Morimoto, D.C., M.A. Frankel, M. Hersek and F.E. Wasserman. 2012. Forest fragmentation effects on Ovenbird populations in the urban region of eastern Massachusetts, USA. Urban Habitats https://urbanhabitats.org/v07n01/forestfragmentation_full.html.

[NOAA] National Oceanic and Atmospheric Administration. 2020. State climate summaries: Connecticut. https://statesummaries.ncics.org/chapter/ct/.

Pearson, S.M. 1993. The spatial extent and relative influence of landscape-level factors on wintering bird populations. Landscape Ecology 8:3−8.

Rasmussen, C.L., J. Palarea-Albaladejo, M.K. Johansson, P. Crowley, M.L. Stevens, N. Gupta, K. Karstad and A. Holtermann. 2020. Zero problems with compositional data of physical behaviors: a comparison of three zero replacement methods. International Journal of Behavioral Nutrition and Physical Activity. 17:126.

Research Unit for Wildlife Population Assessment. 2020. Distance 7.3 Release 2 Users Guide. Research Unit for Population Assessment, St. Andrews, UK.

Rittenhouse, C.D., A.M. Pidgeon, T.P. Albright, P.D. Culbert, M.K. Clayton, C.H. Flather, C. Huang, J.G. Masek, S.I. Stewart and V.C. Radeloff. 2010. Conservation of Forest Birds: Evidence of a Shifting Baseline in Community Structure. PLoS ONE 5(8) e11938.

Robbins, C.S. 1988. Forest fragmentation and its effects on birds. in: Managing north-central forests for non-timber valves: proceedings of the fourth Society of American Foresters Region V Technical Conference, Duluth, Minne-

sota, November 29-December 1, 1988. Society of American Foresters, Bethesda, MD.

ROBBINS, C.S., D.K. DAWSON and B.A. DOWELL. 1989. Habitat area requirements of breeding forest birds of the Middle Atlantic states. Wildlife Monographs 103.

ROBERTS, A. 1981. Soil survey of Windham County, Connecticut. U.S. Soil Conservation Service.

ROBINSON, S.K., F.R. THOMPSON III, T.M. DONOVAN, D.R. WHITEHEAD and J. FAABORG. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987−1990.

RODEWALD, A.D., L.J. KEARNS and D.P. SHUSTACK. 2012. Consequences of urbanizing landscapes to reproductive performance. Biological Conservation 160:32−39.

ROSENBERG, K.V., J.D. LOWE and A.A. DHONDT. 1999. Effects of forest fragmentation on breeding tanagers: a continental perspective. Conservation Biology 13:568–583.

SAUER, J.R., D.K. NIVEN, J.E. HINES, D.J. ZIOLKOWSKI, JR, K.L. PARDIECK, J.E. FALLON and W.A. LINK. 2017. The North American Breeding Bird Survey, Results and Analysis 1966−2015. Version 2.07.2017 USGS Patuxent Wildlife Research Center, Laurel, MD.

SCOTT, J.M., S. MOUNTAINSPRING, F.L. RAMSEY and C.B. KEPLER. 1986. Forest bird communities of the Hawaiian Islands: their dynamics, ecology and conservation. Studies in Avian Biology 9.

SKIRVEN, A.A. 1981. Effects of time of day and time of seasons on the number of observations and density estimates of breeding birds. Pages 271−274. In: C. J. Ralph and J. M Scott, Editors. Estimating numbers of terrestrial birds. Studies in Avian Biology 6.

ST. CLAIR, C.C., M. BÉLISLE, A. DESROCHERS and S. HANNON. 1998. Winter responses of forest birds to habitat corridors and gaps. Conservation Ecology 2(2):13. http://www.consecol.org/vol2/iss2/art13/

STONE, J.R., J.P. SCHAFER, E.H. LONDON, M. DiGIACOMO-COHEN, R.S. LEWIS and W.B. THOMPSON. 1999. Quarternary geologic map of Connecticut and Long Island Sound. U.S. Geological Survey Open-file Report 98-371.

TELLERIA, J.L. and T. SANTOS. 1994. Effects of forest fragmentation on a guild of wintering passerines: the role of habitat selection. Biological Conservation 71:61−67.

THOMAS, L, S.T. BUCKLAND, E.A. REXSTAD, J.L. LAAKE, S. STRINDBERG, S.L. HEDLEY, J.R. BISHOP, T.A. MARQUES and K.P. BURNHAM. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

TITTLER, R., L. FAHIG and M. VILLARD. 2006. Evidence of large-scale source-sink dynamics and long-distance dispersal among Wood Thrush populations. Ecology 87: 3029–3036.

THOMPSON, F.R. III, T.M. DONOVAN, R.M. DEGRAFF, J. FAABORG and S.K. ROBINSON. 2002. A multi-scale perspective of the effects of forest fragmentation on birds in eastern forests. In Effects of habitat fragmentation on birds in western landscapes: contrasts with paradigms from the eastern United States (T.L. George and DS Dobkin, Editors). Studies in Avian Biology 25:8−19.

U.S. CENSUS BUREAU. 2020. 2020 census results. https://www.census.gov/programs-surveys/decennial-census/decade/2020/2020-census-results.html.

VILLARD, M. 1998. On forest-interior species, edge avoidance, area sensitivity, and dogmas in avian conservation. The Auk 115:801−805.

VOGT, P., K.H. RIITTERS, C. ESTREGUIL, J. KOZAK, T.G. WADE and J.D. WICKHAM. 2007. Mapping spatial patterns with morphological image processing. Landscape Ecology 22:71−177.

WHARTON, D.I. and F.K.C. HUI. 2011. The arcsine is asinine: the analysis of proportions in ecology. Ecology 92:3-10.

WIENS, J.A. 1981. Scale problems in avian censusing. Studies in Avian Biology 6:513−521.

WILCOVE, D.S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211−1214.

YAHNER, R.S. 1993. Effects of long-term forest clear-cutting on wintering and breeding birds. Wilson Bulletin 105:239−255.

ZIPKIN, E.F., A. DEWAN and J.A. ROYLE. 2009. Impacts of forest fragmentation on species richness: a hierarchical approach to community modelling. Journal of Applied Ecology 46:815–822.

Appendix. Summer/winter classifications of species and summer density corrections (density/2). Species with no data were either not present or too rare for analysis.

Species	Summer density correction	Macrohabitat	Microhabitat	Nest site	Trophic	Migration	Winter Macrohabitat	Microhabitat	Trophic
SSHA							generalist	generalist	apex
COHA	2.00	edge/successional	ground/shrub	canopy/understory		North American	generalist	ground/shrub	apex
NOGO	2.00	forest interior	ground/shrub	canopy/understory		North American	forest interior	ground/shrub	apex
RSHA	2.00	forest interior	ground/shrub	canopy/understory		North American	generalist	ground/shrub	apex
BWHA	2.00	forest interior	ground/shrub	canopy/understory		neotropical			
RTHA	2.00	generalist	ground/shrub	canopy/understory		North American	generalist	ground/shrub	apex
RUGR	2.00	edge/successional	generalist	ground	herbivore	resident	edge/successional	generalist	herbivore
WITU	2.00	edge/successional	ground/shrub	ground	omnivore	resident	edge/successional	ground/shrub	omnivore
AMWO									
MODO		edge/successional	ground/shrub	canopy/understory	herbivore	North American	edge/successional	generalist	herbivore
BBCU	2.00	edge/successional	arboreal	canopy/understory	secondary consumer	neotropical			
YBCU		edge/successional	arboreal	canopy/understory	secondary consumer	neotropical			
GHOW	2.00								
BAOW	2.00								
WHIP									
RTHU	2.00	generalist	generalist	canopy/understory	omnivore	North American			
RBWO	2.00	forest interior	arboreal	cavity	omnivore	resident	forest interior	arboreal	omnivore
YBSA	2.00	generalist	arboreal	cavity	omnivore	North American			
DOWO	2.00	generalist	arboreal	cavity	omnivore	resident	generalist	arboreal	omnivore
HAWO	2.00	generalist	arboreal	cavity	omnivore	resident	generalist	arboreal	omnivore
COFL	2.00	generalist	ground/shrub	cavity	secondary consumer	North American	generalist	ground/shrub	omnivore
PIWO	2.00	forest interior	generalist	cavity	omnivore	resident	forest interior	generalist	omnivore
EWPE		forest interior	arboreal	canopy/understory	secondary consumer	neotropical			
ACFL		forest interior	arboreal	canopy/understory	secondary consumer	neotropical			
LEFL		edge/successional	arboreal	canopy/understory	secondary consumer	neotropical			
EAPH		generalist	generalist		omnivore	North American			
GCFL	2.00	generalist	generalist	canopy/understory	secondary consumer	neotropical			
EAKI	2.00	edge/successional	generalist	canopy/understory	omnivore	neotropical			
BLJA	2.00	generalist	generalist	canopy/understory	omnivore	North American	generalist	generalist	omnivore
COCR	2.00	edge/successional	generalist	canopy/understory	omnivore	North American	edge/successional	generalist	omnivore
CORA	2.00	generalist	generalist		omnivore	resident	generalist	generalist	omnivore
BCCH	2.00	generalist	arboreal	cavity	omnivore	resident	generalist	arboreal	omnivore
TUTI	2.00	generalist	generalist	cavity	omnivore	resident	generalist	generalist	omnivore
RBNU	2.00	forest interior	generalist	cavity	omnivore	North American	generalist	generalist	omnivore
WBNU	2.00	generalist	generalist	cavity	omnivore	resident	generalist	generalist	omnivore
BRCR		forest interior	arboreal	cavity	secondary consumer	North American	forest interior	arboreal	secondary
CAWR		edge/successional	ground/shrub	cavity	secondary consumer	resident	edge/successional	ground/shrub	secondary
HOWR		edge/successional	generalist	cavity	secondary consumer	North American			
WIWR		forest interior	ground/shrub	cavity	secondary consumer	North American	forest interior	ground/shrub	secondary
GCKI							generalist	generalist	secondary
BGGN	2.00	generalist	arboreal	canopy/understory	secondary consumer	North American			
EABL	2.00	edge/successional	ground/shrub	cavity	omnivore	North American	edge/successional	ground/shrub	omnivore
VEER		forest interior	generalist	ground	omnivore	neotropical			
HETH		forest interior	generalist	ground	secondary consumer	North American	forest interior	generalist	omnivore
WOTH		forest interior	ground/shrub	canopy/understory	omnivore	neotropical			
AMRO	2.00	edge/successional	generalist	canopy/understory	omnivore	North American	generalist	generalist	omnivore
GRCA		edge/successional	generalist	canopy/understory	omnivore	neotropical	edge/successional	generalist	omnivore
CEDW	2.00	edge/successional	arboreal	canopy/understory	omnivore	North American	edge/successional	arboreal	herbivore
WEVI		edge/successional	arboreal	canopy/understory	secondary consumer	North American			
SOVI		forest interior	arboreal	canopy/understory	secondary consumer	North American			
YTVI		generalist	arboreal	canopy/understory	secondary consumer	neotropical			
WAVI		edge/successional	arboreal	canopy/understory	secondary consumer	neotropical			
REVI		forest interior	arboreal	canopy/understory	omnivore	neotropical			
BWWA		edge/successional	arboreal	ground	secondary consumer	neotropical			
NAWA									
CSWA		edge/successional	generalist	canopy/understory	secondary consumer	neotropical			
MAWA		generalist	arboreal	canopy/understory	secondary consumer	neotropical			
BTBW		forest interior	generalist	canopy/understory	secondary consumer	neotropical			
YRWA		forest interior	arboreal	canopy/understory	omnivore	North American	edge/successional	arboreal	omnivore
BTGW		forest interior	arboreal	canopy/understory	secondary consumer	neotropical			
BLWA		forest interior	arboreal	canopy/understory	secondary consumer	neotropical			
PIWA		forest interior	arboreal	canopy/understory	secondary consumer	North American			
PRWA		edge/successional	arboreal	canopy/understory	secondary consumer	neotropical			
CEWA		forest interior	arboreal	canopy/understory	secondary consumer	neotropical			
BAWA		forest interior	arboreal	ground	secondary consumer	neotropical			

Code		Habitat	Substrate	Foraging	Trophic	Migratory	Habitat	Substrate	Trophic
AMRE		edge/successional	arboreal	canopy/understory	secondary consumer	neotropical			
WEWA		forest interior	arboreal	ground	secondary consumer	neotropical			
OVEN		forest interior	ground/shrub	ground	secondary consumer	neotropical			
NOWA		forest interior	ground/shrub	ground	secondary consumer	neotropical			
LOWA		forest interior	ground/shrub	ground	secondary consumer	neotropical			
COYE		edge/successional	ground/shrub	canopy/understory	secondary consumer	neotropical			
HOWA		edge/successional	arboreal	canopy/understory	secondary consumer	neotropical			
CAWA		forest interior	ground/shrub	ground	secondary consumer	neotropical			
SCTA		forest interior	arboreal	canopy/understory	omnivore	neotropical			
NOCA	2.00	edge/successional	ground/shrub	canopy/understory	omnivore	resident	edge/successional	ground/shrub	omnivore
RBGR		edge/successional	arboreal	canopy/understory	omnivore	neotropical			
INBU		edge/successional	generalist	canopy/understory	omnivore	neotropical			
RSTO		edge/successional	ground/shrub	ground	omnivore	North American	edge/successional	ground/shrub	omnivore
CHSP		edge/successional	ground/shrub	canopy/understory	omnivore	North American			
SOSP		edge/successional	ground/shrub	canopy/understory	omnivore	North American	edge/successional	ground/shrub	omnivore
DEJU		forest interior	ground/shrub	ground	omnivore	North American	edge/successional	ground/shrub	herbivore
BHCO	2.00	edge/successional	ground/shrub		omnivore	North American			
NOOR		edge/successional	arboreal	canopy/understory	omnivore	neotropical			
PUFI		edge/successional	arboreal	canopy/understory	omnivore	North American			
REDP							edge/successional	generalist	herbivore
PISI							generalist	generalist	omnivore
AMGO	2.00	generalist	generalist	canopy/understory	herbivore	North American	generalist	generalist	herbivore
WTSP							edge/successional	ground/shrub	herbivore
TRSP							edge/successional	ground/shrub	herbivore
RECR							generalist	arboreal	herbivore
FICR	2.00	edge/successional	generalist	canopy/understory	omnivore	North American			
PIGR							generalist	generalist	herbivore