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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 habitat characteristics and particularly such landscape attributes as forest fragmentation. I surveyed birds at 1,815 points along 121 transects that traversed ca. 400 km of forest. I also made 12,705 habitat measurements at survey points and computed areas of forest, non-forest, core forest and perimeter/area ratios of forest for 31,550 ha of study area. 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. Based on observations of 36,702 summering individuals of 123 species and 13,742 wintering individuals of 63 species, declines in community density occurred with increasing fragmentation although species richness was often more closely associated with habitat measures. Among landscape measures, forest fragmentation had the closest association with summer community measures 81% of the time, strongly suggesting that fragmentation effects were the predominant driver of such community patterns. However, short-distance migrant density and richness, foraging generalist density and richness, edge/successional species density and richness, habitat generalist density and Brown-headed Cowbird density showed little relationship to landscape measures. The effects of fragmentation appeared 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. Despite the importance of fragmentation effects, community and individual species measures often tended to be more closely associated with habitat measures than with those of fragmentation. In addition, few summer or winter community measures or species patterns showed any significant relationship to natural forest breaks. Winter community and species density patterns showed a limited relationship to landscape measures, although increasing fragmentation showed some association with increasing species richness and community density.

Investigation of the effects of forest fragmentation on natural 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). A recent review of global forest studies revealed that, for a range of community types and organisms, species richness, immigration rates and ecosystem function measures

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tended to decline over time with increased fragmentation. Among the strongest of these effects was that of the temporal decline in species richness experienced by terrestrial birds (Haddad et al. 2015). Indeed, birds have proven to be among the best studied and most useful in terms of understanding the effects of fragmentation on communities. Forest interior-breeding species that migrate to the neotropics have appeared to be 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. Hence, there appear to be significant gaps in our actual understanding of how fragmentation affects the functioning of bird communities. For example, 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. Indeed, we may expect that at this season of limited resources and energetically stressful conditions that the comparatively few species present will be primarily opportunistic, ecological generalists that can tolerate a variety of conditions. Yahner (1993) did find, however, that richness increased in heavily logged areas. Moreover, in experiments to get wintering birds to cross forest breaks, Black-capped Chickadees (*Parus 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 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 phe-

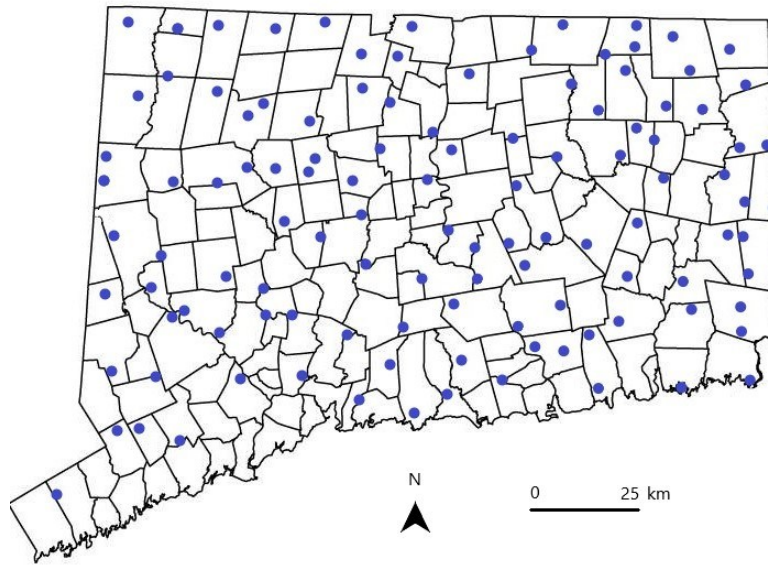


FIG. 1. Location of 121 study sites across Connecticut.

nomenon. Hence, forest fragmentation may further be described as a combination of forest loss (conversion of forest to non-forest) and a decrease in size and isolation of the remnant forest patches.

As noted by D'Eon (2002), landscape-scale empirical data are needed to evaluate hypotheses concerning the effects of fragmentation. As such, and to help distinguish among the various conflicting views on the effects of fragmentation on forest bird communities, 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 the breeding forest bird communities of this study, as well as their 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, resident, foraging generalist, 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 13,183 km<sup>2</sup>. Of this population, 26.6% is in the southwestern Connecticut portion of the 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. Overall, the wildland-urban interface, that land in which houses and wildlands meet, occurs at 72% of the total land area in Connecticut—the greatest of any state (Radeloff et al. 2005, 2018)—making examination of fragmentation issues particularly pertinent for this region. 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 bed-rock 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), with a 4.7% increase in developed land occurring from 1985 to 2015 (Arnold et al. 2020).

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. Moreover, it is in line with the distances employed in a number of other investigations that use the same survey protocol (e.g., Scott et al. 1986, Camp et al. 2009, Camp et al. 2015). 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  $-26^{\circ}\text{C}$ . 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 birds at each point. 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 al. 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, 2008, 2023a, Craig et al. 2022). 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.

It should be noted that distance sampling is not without sources of error, although analytic advances (e.g., Camp et al. 2009) continue to improve the reliability of results. Still, such factors as the statistical independence of sampling points and variability among observers in experience and perceptual abilities can cause differences in population density estimates (Craig 2023a, Craig and Pyle 2024). Hence, the employment of a single observer in this study and use of extended distances between sampling points has the advantage of minimizing these sources of variance.

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 2001) 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 this latter category 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 charac-



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.

teristics 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 latter 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 12,705 measurements. Beginning in 2001 and repeated each year 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 evaluated 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 1:20,000 black-and-white pre-growing season images covering 4.6 km<sup>2</sup> each and, depending on the year of the bird survey, either 2006 or 2008 1:25,000 color growing season images covering 36.0 km<sup>2</sup> 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 31,550 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  $\geq 100$  m from an exterior forest 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 non-forest and combined this area with all other non-forest 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., Kroodsmas 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

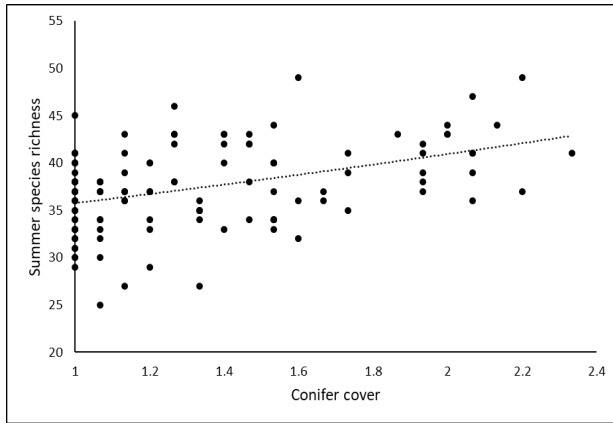


FIG. 3. Summer species richness increases with increasing conifer cover 1) deciduous: <10% evergreen conifers, 2) mixed: 20–60% evergreen coniferous, 3) coniferous:  $\geq 70\%$  evergreen conifers.

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 as the sum of all forest bird species encountered and community density as the sum of computed densities for all forest species encountered. To 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

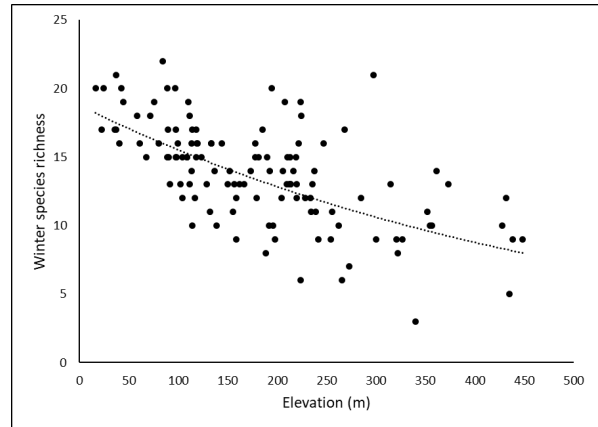


FIG. 4. Winter species richness declines with increasing elevation.

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 from tests with little predictive power as measured by standardized  $\beta$  coefficients, zero vs. part and partial correlations and tolerance values, 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



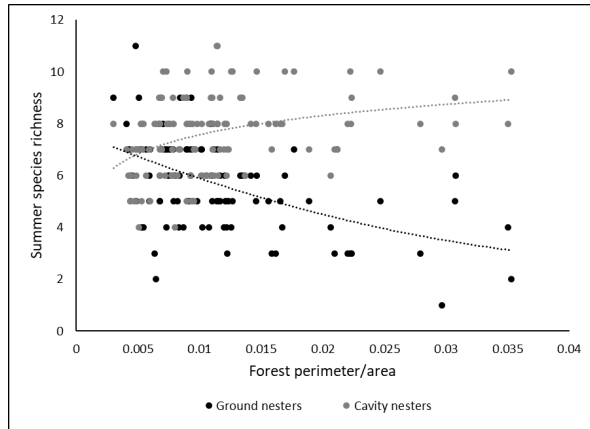


FIG. 5. Ground nester summer species richness declines with increasing forest perimeter/area whereas cavity nester richness increases.

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 indices (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  $\geq 90\%$  of study sites (Rasmussen et al. 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 and so that direct comparisons with study area-wide analyses could be made. 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 probab-

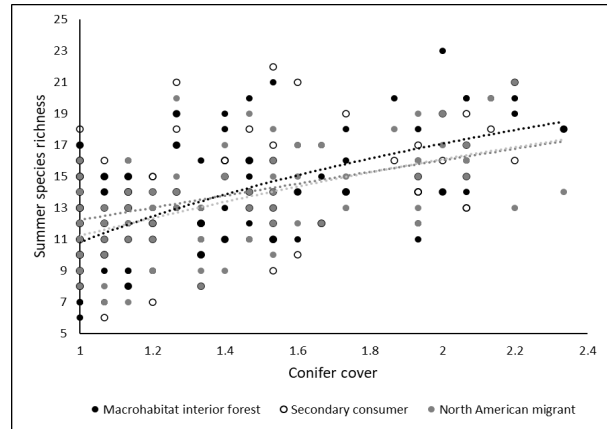


FIG. 6. Interior forest, secondary consumer and North American migrant summer species richness increase with increasing conifer cover.

ity 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 proportion 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 10 of the 32 models contained only significant habitat predictors. Of 15 examinations of winter community measures, 13 had the greatest  $r^2$  in models in which perimeter/area was included with habitat predictors. Another two had the greatest  $r^2$  in models in which proportion of human-associated habitats was included with habitat predictors. However, five of the 15 models contained only significant habitat predictors—particularly elevation (Table 1–3).

**Species richness.** Analysis of summer community richness (Table 1) showed that a model including human-associated 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, win-

TABLE 1. Multivariate regression analyses with highest adjusted  $r^2$  values for summer/winter community species richness and species classifications for nest site selection, macrohabitat use, microhabitat use, migration category and trophic category.

		$f$	$P$	Partial eta <sup>2</sup>	Adjusted $r^2$	$\beta$ coefficient	SE
Community richness							
Summer	Model	8.602	<0.001	0.312	0.275		
	Human-associated	2.938	0.089	0.025		-0.409	0.238
	Forest type	19.528	<0.001	0.146		0.527	0.119
	Moisture regime	2.062	0.154	0.018		-0.394	0.274
	Canopy cover	13.563	<0.001	0.106		-1.360	0.369
	Understory density	0.106	0.745	0.001		0.056	0.172
	Elevation	4.641	0.033	0.039		0.112	0.052
Winter	Model	15.048	<0.001	0.442	0.413		
	Perimeter/area	8.891	0.004	0.072		4.700	1.576
	Forest type	4.991	0.027	0.042		-0.342	0.153
	Moisture regime	0.577	0.449	0.005		-0.264	0.348
	Canopy cover	0.069	0.793	0.001		-0.123	0.469
	Understory density	0.042	0.838	0.000		-0.045	0.220
	Elevation	25.101	<0.001	0.180		-0.341	0.068
Nest site summer richness							
Ground	Model	14.911	<0.001	0.395	0.369		
	Perimeter/area	20.230	<0.001	0.151		-5.308	1.180
	Forest type	7.809	0.006	0.064		0.323	0.116
	Canopy cover	0.034	0.853	0.000		-0.066	0.355
	Understory density	3.311	0.071	0.028		0.297	0.163
	Elevation	8.014	0.005	0.066		0.146	0.051
Cavity	Model	8.152	<0.001	0.263	0.231		
	Core forest	19.839	<0.001	0.148		-0.510	0.115
	Forest type	0.839	0.362	0.007		-0.084	0.091
	Canopy cover	1.720	0.192	0.015		-0.378	0.288
	Understory density	12.841	0.001	0.101		-0.461	0.129
	Elevation	9.386	0.003	0.076		0.128	0.042
Canopy/understory	Model	9.081	<0.001	0.285	0.253		
	Human-associated	3.748	0.055	0.032		-0.457	0.236
	Forest type	22.989	<0.001	0.168		0.575	0.120
	Canopy cover	18.773	<0.001	0.141		-1.616	0.373
	Understory density	0.651	0.421	0.006		0.137	0.170
	Elevation	0.032	0.859	0.000		-0.009	0.052

## Macrohabitat summer richness

Interior forest	Model	34.673	<0.001	0.646	0.627		
	Human-associated	13.756	<0.001	0.108		-0.850	0.229
	Forest type	82.853	<0.001	0.421		1.021	0.112
	Moisture regime	7.265	0.008	0.060		-0.687	0.255
	Canopy cover	0.074	0.785	0.001		-0.094	0.345
	Elevation	27.037	<0.001	0.192		0.257	0.049
	Vertical	2.639	0.107	0.023		0.156	0.096
Edge/ successional	Model	6.088	<0.001	0.243	0.203		
	Core forest	1.824	0.180	0.016		-0.287	0.213
	Forest type	1.439	0.233	0.012		-0.182	0.151
	Moisture regime	0.893	0.347	0.008		0.320	0.338
	Canopy cover	15.945	<0.001	0.123		-1.847	0.463
	Elevation	1.271	0.262	0.011		-0.078	0.069
	Vertical	0.007	0.934	0.000		-0.011	0.127
Generalist	Model	3.764	0.002	0.165	0.121		
	Core forest	9.437	0.003	0.076		-0.303	0.099
	Forest type	0.041	0.839	0.000		-0.014	0.070
	Moisture regime	0.740	0.391	0.006		-0.135	0.157
	Canopy cover	0.083	0.774	0.001		-0.062	0.214
	Elevation	9.725	0.002	0.079		0.100	0.032
	Vertical	5.848	0.017	0.049		0.143	0.059
Foraging microhabitat summer richness							
Arboreal	Model	5.578	<0.001	0.195	0.160		
	Perimeter/area	7.006	0.009	0.057		-3.629	1.371
	Forest type	15.612	<0.001	0.120		0.533	0.135
	Canopy cover	5.602	0.020	0.046		-0.966	0.408
	Understory density	0.000	0.990	0.000		0.002	0.190
	Elevation	0.029	0.865	0.000		-0.010	0.060
Ground/shrub	Model	2.975	0.015	0.115	0.076		
	Core forest	4.104	0.045	0.034		-0.283	0.140
	Forest type	1.287	0.259	0.011		0.127	0.112
	Canopy cover	4.012	0.048	0.034		-0.697	0.348
	Understory density	0.448	0.504	0.004		-0.106	0.158
	Elevation	1.394	0.240	0.012		0.061	0.051
Generalist	Model	9.623	<0.001	0.295	0.264		
	Core forest	1.072	0.303	0.009		-0.115	0.111
	Forest type	8.518	0.004	0.069		0.260	0.089
	Canopy cover	4.091	0.045	0.034		-0.559	0.276
	Understory density	1.004	0.318	0.009		0.125	0.125
	Elevation	23.249	<0.001	0.168		0.197	0.041

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Migration summer richness							
Neotropical	Model	5.666	<0.001	0.198	0.163		
	Human-associated	16.361	<0.001	0.125		-1.677	0.415
	Forest type	3.711	0.057	0.031		0.260	0.135
	Canopy cover	8.108	0.005	0.066		-1.186	0.416
	Understory density	0.706	0.403	0.006		0.160	0.191
	Elevation	0.010	0.921	0.000		0.006	0.059
North American	Model	22.101	<0.001	0.490	0.468		
	Core forest	7.218	0.008	0.059		-0.379	0.141
	Forest type	54.450	<0.001	0.321		0.836	0.113
	Canopy cover	9.178	0.003	0.074		-1.063	0.351
	Understory density	0.067	0.796	0.001		0.041	0.159
	Elevation	18.730	<0.001	0.140		0.225	0.052
Resident	Model	8.687	<0.001	0.274	0.243		
	Core forest	8.476	0.004	0.069		-0.263	0.090
	Forest type	24.744	<0.001	0.177		-0.361	0.073
	Canopy cover	0.897	0.346	0.008		0.213	0.225
	Understory density	5.510	0.021	0.046		-0.239	0.102
	Elevation	0.029	0.865	0.000		-0.006	0.033
Trophic level summer richness							
Secondary consumer	Model	9.686	<0.001	0.296	0.266		
	Human-associated	6.889	0.010	0.057		-0.729	0.278
	Forest type	21.776	<0.001	0.159		0.661	0.142
	Canopy cover	10.470	0.002	0.083		-1.407	0.435
	Understory density	0.392	0.532	0.003		-0.125	0.200
	Elevation	1.668	0.199	0.014		0.080	0.062
Omnivore	Model	6.189	<0.001	0.212	0.178		
	Core forest	7.486	0.007	0.061		-0.279	0.102
	Forest type	2.836	0.095	0.024		0.138	0.082
	Canopy cover	6.051	0.015	0.050		-0.624	0.254
	Understory density	1.654	0.201	0.014		0.148	0.115
	Elevation	11.807	0.001	0.093		0.129	0.038
Herbivore	Model	0.946	0.454	0.039	0.002		
	Core forest	0.311	0.578	0.003		-0.037	0.065
	Forest type	0.769	0.382	0.007		0.046	0.053
	Canopy cover	1.077	0.302	0.009		0.169	0.163
	Understory density	0.071	0.790	0.001		-0.020	0.074
	Elevation	1.800	0.182	0.015		-0.032	0.024
Macrohabitat winter richness							
Interior forest	Model	5.918	<0.001	0.205	0.170		
	Human-associated	1.440	0.233	0.012		0.388	0.323
	Forest type	9.898	0.002	0.079		-0.519	0.165
	Canopy cover	3.279	0.073	0.028		0.916	0.506
	Understory density	1.507	0.222	0.013		-0.286	0.233
	Elevation	5.887	0.017	0.049		-0.175	0.072

Edge/successional	Model	15.656	<0.001	0.405	0.379		
	Perimeter/area	4.423	0.038	0.037		3.913	1.861
	Forest type	13.423	<0.001	0.105		-0.670	0.183
	Canopy cover	5.654	0.019	0.047		-1.318	0.554
	Understory density	0.049	0.824	0.000		0.057	0.258
	Elevation	12.715	0.001	0.100		-0.291	0.081
Generalist	Model	9.589	<0.001	0.294	0.264		
	Perimeter/area	9.578	0.002	0.077		3.347	1.081
	Forest type	0.110	0.741	0.001		0.035	0.106
	Canopy cover	0.256	0.614	0.002		0.163	0.322
	Understory density	0.152	0.697	0.001		0.058	0.150
	Elevation	13.956	<0.001	0.108		-0.177	0.047
Foraging microhabitat winter richness							
Arboreal	Model	14.224	<0.001	0.267	0.248		
	Perimeter/area	1.828	0.179	0.015		1.390	1.028
	Elevation	23.543	<0.001	0.168		-0.215	0.044
	dbh	0.019	0.890	0.000		0.113	0.820
Generalist	Model	3.444	0.019	0.081	0.058		
	Perimeter/area	2.275	0.134	0.019		1.763	1.169
	Elevation	0.861	0.355	0.007		-0.047	0.050
	dbh	3.592	0.061	0.030		-1.767	0.932
Trophic level winter richness							
Secondary consumer	Model	6.564	<0.001	0.185	0.156		
	Human-associated	1.169	0.282	0.010		0.318	0.294
	Forest type	4.584	0.034	0.038		0.328	0.153
	Elevation	13.873	<0.001	0.107		-0.248	0.067
	dbh	0.589	0.444	0.005		0.959	1.249
Omnivore	Model	15.741	<0.001	0.352	0.329		
	Perimeter/area	4.661	0.033	0.039		2.692	1.247
	Forest type	9.391	0.003	0.075		-0.385	0.126
	Elevation	15.016	<0.001	0.115		-0.215	0.055
	dbh	1.673	0.198	0.014		-1.302	1.007
Herbivore	Model	10.369	<0.001	0.263	0.238		
	Perimeter/area	6.995	0.009	0.057		5.251	1.985
	Forest type	0.157	0.693	0.001		-0.079	0.200
	Elevation	8.629	0.004	0.069		-0.259	0.088
	dbh	5.172	0.025	0.043		-3.645	1.603

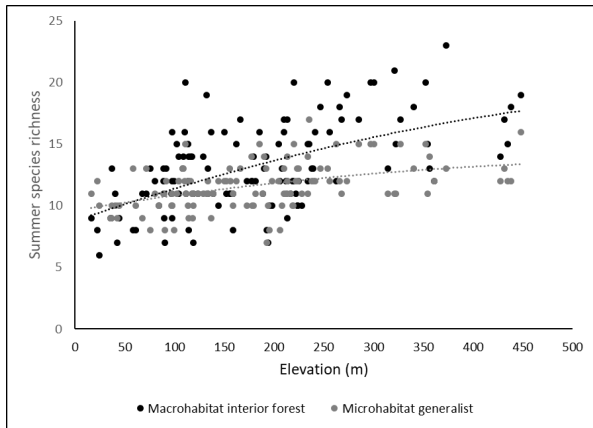


FIG.7. Interior forest and microhabitat summer species richness increase with increasing elevation.

ter 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).

*Nest site choice vs. summer richness.* 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 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.

*Macrohabitat associations vs. summer richness.* For macrohabitat associations vs. summer richness, the strongest relationships by far were for interior forest species. In this case, a model with human-associated 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

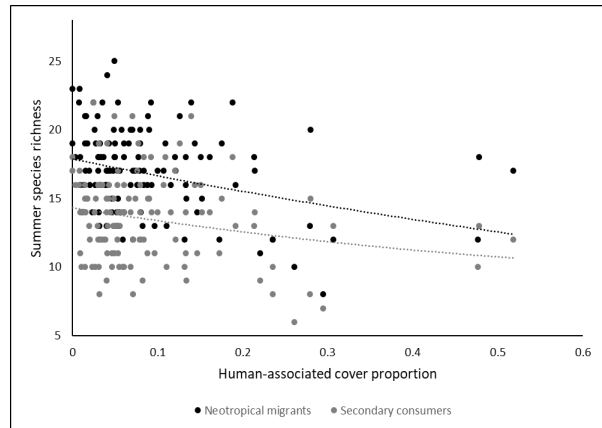


FIG.8. Neotropical migrant and secondary consumer summer species richness decline with increasing human-associated landscape cover.

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.

*Foraging microhabitat categories vs. summer richness.* For foraging 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 increasing elevation (Fig. 7) and secondarily increasing conifer cover. Arboreal forager richness showed the strongest relationship to a model including perimeter/area, with hierarchical analysis indicating 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.

*Migration categories vs. summer richness.* 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.



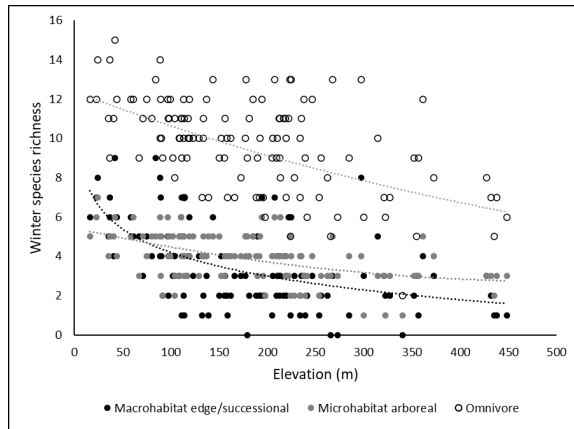


FIG. 9. Edge/successional, arboreal and omnivore winter species richness decline with elevation.

Neotropical migrant richness showed the weakest relationship to predictors, with the strongest association occurring for a model including human-associated forest breaks. Hierarchical analysis indicated that increasing richness was principally associated with only fewer human-associated forest breaks (Fig. 8).

*Trophic categories vs. summer richness.* For trophic categories vs. summer richness, the strongest relationships by far were for secondary consumers. In this case, a model with human-associated 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 associated with only decreasing canopy cover and increasing elevation. Herbivore richness showed no significant relationships with predictor variables.

*Macrohabitat categories vs. winter richness.* 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

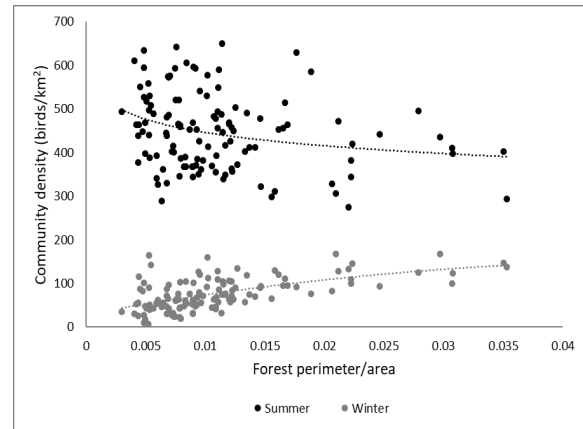


FIG. 10. Summer community density declines whereas winter community density increases with increasing forest perimeter/area.

including human-associated forest breaks. However, hierarchical analysis indicated that increasing richness was principally associated with only increasing deciduous cover and soil moisture and decreasing elevation (Fig. 9).

*Foraging microhabitat categories vs. winter richness.* For foraging 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 indicated 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.

*Trophic categories vs. winter richness.* 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 forest breaks, although hierarchical analysis indicated that increasing richness was principally associated with only decreasing deciduous cover and elevation.

TABLE 2. Multivariate regression analyses with highest adjusted  $r^2$  values for summer/winter community density and species classifications for nest site selection, macrohabitat use, microhabitat use, migration category and trophic category.

		$f$	$P$	Partial $\eta^2$	Adjusted $r^2$	$\beta$ coefficient	SE
Community density							
Summer	Model	10.694	<0.001	0.360	0.326		
	Perimeter/area	15.499	<0.001	0.120		-2.495	0.634
	Forest type	14.879	<0.001	0.115		0.237	0.061
	Moisture regime	17.949	<0.001	0.136		-0.593	0.140
	Canopy cover	4.934	0.028	0.041		-0.419	0.189
	Understory density	10.321	0.002	0.083		0.285	0.089
	Elevation	0.709	0.401	0.006		0.023	0.027
Winter	Model	17.182	<0.001	0.475	0.447		
	Perimeter/area	14.581	<0.001	0.113		6.423	1.682
	Forest type	0.005	0.944	0.000		-0.011	0.163
	Moisture regime	0.061	0.806	0.001		-0.091	0.371
	Canopy cover	0.188	0.666	0.002		0.217	0.501
	Understory density	0.524	0.470	0.005		0.170	0.235
	Elevation	33.964	<0.001	0.230		-0.423	0.073
Nest site summer density							
Ground	Model	28.003	<0.001	0.596	0.574		
	Perimeter/area	34.868	<0.001	0.234		-7.445	1.261
	Forest type	31.623	<0.001	0.217		0.688	0.122
	Moisture regime	0.232	0.631	0.002		-0.134	0.278
	Canopy cover	6.266	0.014	0.052		0.939	0.375
	Understory density	35.065	<0.001	0.235		1.043	0.176
	Elevation	5.078	0.026	0.043		0.123	0.054
Cavity	Model	7.272	<0.001	0.277	0.239		
	Core forest	20.190	<0.001	0.150		-0.631	0.141
	Forest type	3.372	0.069	0.029		-0.204	0.111
	Moisture regime	0.004	0.951	0.000		0.016	0.252
	Canopy cover	0.456	0.501	0.004		0.235	0.347
	Understory density	5.324	0.023	0.045		-0.368	0.159
	Elevation	0.120	0.729	0.001		-0.018	0.051
Canopy/understory	Model	7.086	<0.001	0.272	0.233		
	Perimeter/area	3.619	0.060	0.031		-1.596	0.839
	Forest type	3.753	0.055	0.032		0.158	0.081
	Moisture regime	19.573	<0.001	0.147		-0.819	0.185
	Canopy cover	10.944	0.001	0.088		-0.826	0.250
	Understory density	1.210	0.274	0.011		0.129	0.117
	Elevation	0.188	0.665	0.002		0.016	0.036

## Macrohabitat summer density

Interior forest	Model	40.295	<0.001	0.680	0.663		
	Core forest	33.869	<0.001	0.229		0.615	0.106
	Forest type	45.063	<0.001	0.283		0.561	0.083
	Moisture regime	9.072	0.003	0.074		-0.571	0.190
	Canopy cover	4.598	0.034	0.039		0.560	0.261
	Understory density	4.763	0.031	0.040		0.261	0.120
	Elevation	25.307	<0.001	0.182		0.192	0.038
Edge/ successional	Model	17.880	<0.001	0.526	0.496		
	Human-associated	0.159	0.691	0.001		-0.124	0.310
	Natural breaks	7.781	0.006	0.064		0.822	0.295
	Forest type	7.292	0.008	0.061		-0.414	0.153
	Moisture regime	0.826	0.365	0.007		-0.319	0.351
	Canopy cover	29.890	<0.001	0.209		-2.611	0.478
	Understory density	16.171	<0.001	0.125		0.908	0.226
	Elevation	5.981	0.016	0.050		-0.182	0.074
Generalist	Model	1.012	0.421	0.051	0.001		
	Perimeter/area	2.521	0.115	0.022		2.333	1.469
	Forest type	0.030	0.864	0.000		-0.025	0.143
	Moisture regime	0.003	0.956	0.000		0.018	0.324
	Canopy cover	0.130	0.720	0.001		0.157	0.437
	Understory density	0.192	0.662	0.002		-0.090	0.205
	Elevation	0.558	0.457	0.005		-0.047	0.063
Foraging microhabitat summer density							
Arboreal	Model	7.914	<0.001	0.294	0.257		
	Perimeter/area	13.440	<0.001	0.105		-3.693	1.007
	Forest type	5.785	0.018	0.048		0.235	0.098
	Moisture regime	9.005	0.003	0.073		-0.667	0.222
	Canopy cover	0.001	0.981	0.000		0.007	0.300
	Understory density	0.175	0.676	0.002		-0.059	0.141
	Elevation	3.010	0.085	0.026		0.075	0.043
Ground/shrub	Model	9.090	<0.001	0.324	0.288		
	Perimeter/area	17.565	<0.001	0.134		-3.879	0.926
	Forest type	17.474	<0.001	0.133		0.375	0.090
	Moisture regime	7.899	0.006	0.065		-0.574	0.204
	Canopy cover	0.542	0.463	0.005		-0.203	0.275
	Understory density	20.036	<0.001	0.149		0.579	0.129
	Elevation	0.861	0.355	0.007		-0.037	0.040
Generalist	Model	11.496	<0.001	0.377	0.344		
	Forest area	0.675	0.413	0.006		-0.161	0.196
	Forest type	1.900	0.171	0.016		0.136	0.099
	Moisture regime	6.411	0.013	0.053		-0.571	0.226
	Canopy cover	19.389	<0.001	0.145		-1.354	0.307
	Understory density	19.157	<0.001	0.144		0.626	0.143
	Elevation	0.164	0.686	0.001		-0.020	0.049

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Migration summer density							
Neotropical	Model	14.447	<0.001	0.432	0.402		
	Perimeter/area	33.155	<0.001	0.225		-4.556	0.791
	Forest type	3.724	0.056	0.032		0.148	0.077
	Moisture regime	29.347	<0.001	0.205		-0.946	0.175
	Canopy cover	0.842	0.361	0.007		-0.216	0.235
	Understory density	9.379	0.003	0.076		0.339	0.111
	Elevation	3.050	0.083	0.026		0.060	0.034
North American	Model	6.982	<0.001	0.269	0.230		
	Perimeter/area (tied)	0.291	0.590	0.003		0.829	1.535
	Forest type	24.560	<0.001	0.177		0.738	0.149
	Moisture regime	0.594	0.442	0.005		0.261	0.339
	Canopy cover	12.529	0.001	0.099		-1.617	0.457
	Understory density	1.276	0.261	0.011		0.242	0.215
	Elevation	0.155	0.695	0.001		-0.026	0.066
Resident	Model	7.782	<0.001	0.291	0.253		
	Perimeter/area	8.037	0.005	0.066		3.619	1.277
	Forest type	6.056	0.015	0.050		-0.305	0.124
	Moisture regime	0.176	0.676	0.002		0.118	0.282
	Canopy cover	1.750	0.189	0.015		0.503	0.380
	Understory density	1.130	0.290	0.010		-0.190	0.178
	Elevation	9.601	0.002	0.078		-0.171	0.055
Trophic level summer density							
Secondary consumer	Model	17.835	<0.001	0.484	0.457		
	Perimeter/area	18.951	<0.001	0.143		-5.467	1.256
	Forest type	39.946	<0.001	0.259		0.770	0.122
	Moisture regime	8.926	0.003	0.073		-0.828	0.277
	Canopy cover	0.923	0.339	0.008		0.359	0.374
	Understory density	4.039	0.047	0.034		0.353	0.175
	Elevation	4.094	0.045	0.035		0.110	0.054
Omnivore	Model	9.222	<0.001	0.327	0.291		
	Perimeter/area	3.176	0.077	0.027		-1.084	0.608
	Forest type	5.974	0.016	0.050		-0.144	0.059
	Moisture regime	7.593	0.007	0.062		-0.370	0.134
	Canopy cover	12.698	0.001	0.100		-0.645	0.181
	Understory density	11.648	0.001	0.093		0.290	0.085
	Elevation	2.437	0.121	0.021		-0.041	0.026
Herbivore	Model	4.241	0.001	0.182	0.139		
	Core forest	8.448	0.004	0.069		-0.840	0.289
	Forest type	1.917	0.169	0.017		0.316	0.229
	Moisture regime	0.049	0.825	0.000		0.115	0.519
	Canopy cover	1.062	0.305	0.009		0.736	0.714
	Understory density	0.695	0.406	0.006		-0.273	0.328
	Elevation	2.701	0.103	0.023		-0.172	0.105

## Macrohabitat winter density

Edge/ successional	Model	18.482	<0.001	0.446	0.421		
	Perimeter/area	1.983	0.162	0.017		11.139	7.909
	Canopy cover	7.948	0.006	0.065		-6.744	2.392
	Understory density	0.000	0.990	0.000		0.013	1.088
	Elevation	28.137	<0.001	0.197		-1.777	0.335
	dbh	10.701	0.001	0.085		-20.543	6.280
Generalist	Model	12.019	<0.001	0.343	0.315		
	Perimeter/area	24.627	<0.001	0.176		7.822	1.576
	Canopy cover	1.509	0.222	0.013		0.586	0.477
	Understory density	1.204	0.275	0.010		0.238	0.217
	Elevation	7.110	0.009	0.058		-0.178	0.067
	dbh	1.038	0.310	0.009		-1.275	1.251
Foraging microhabitat winter density							
Arboreal	Model	10.092	<0.001	0.305	0.275		
	Perimeter/area	5.383	0.022	0.045		5.425	2.338
	Canopy cover	0.163	0.688	0.001		-0.285	0.707
	Understory density	4.849	0.030	0.040		0.708	0.322
	Elevation	16.294	<0.001	0.124		-0.400	0.099
	dbh	2.678	0.104	0.023		3.038	1.856
Generalist	Model	12.554	<0.001	0.353	0.325		
	Perimeter/area	15.747	<0.001	0.12		7.383	1.860
	Canopy cover	5.544	0.020	0.046		1.325	0.563
	Understory density	0.142	0.707	0.001		-0.096	0.256
	Elevation	15.708	<0.001	0.12		-0.312	0.079
	dbh	4.035	0.047	0.034		-2.967	1.477
Trophic level winter density							
Omnivore	Model	38.637	<0.001	0.498	0.485		
	Perimeter/area	19.464	<0.001	0.143		7.803	1.769
	Forest type	11.416	0.001	0.089		-0.592	0.175
	Elevation	24.332	<0.001	0.172		-0.388	0.079

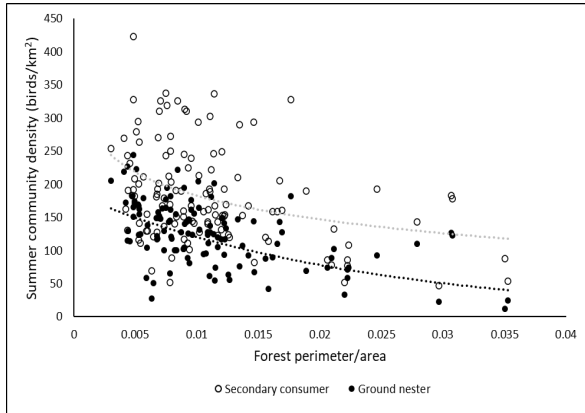


FIG. 11. Secondary consumer and ground nester summer density decline with increasing forest perimeter/area.

**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.

**Nest site choice vs. summer community 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 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).

**Macrohabitat associations vs. summer community density.** 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.

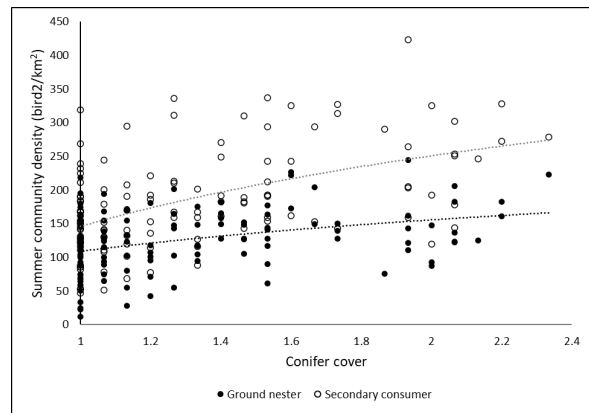


FIG. 12. Ground nester and secondary consumer summer density increase with increasing conifer cover.

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.

**Foraging microhabitat categories vs. summer community density.** A number of differences emerged between analyses of summer density and richness for foraging 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.

**Migration categories vs. summer community density.** A number of differences also emerged in analyses of summer richness vs. density with respect



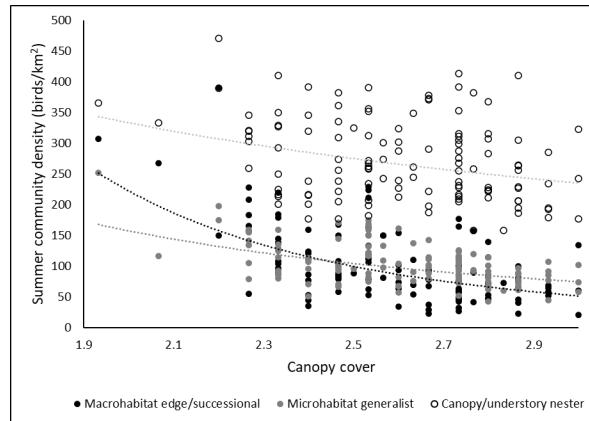


FIG. 13. Edge/successional, macrohabitat generalist and canopy/understory nester summer density decline with increasing canopy cover 1) open: <40% cover, 2) semi-open: 50–60% cover, and 3) closed: >70% cover.

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 either perimeter/area or core forest, 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.

*Trophic categories vs. summer community density.* 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  $r^2$  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

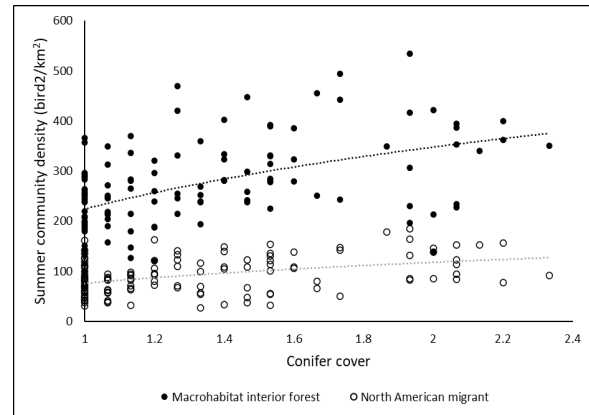


FIG. 14. Interior forest and North American migrant summer density increase with increasing conifer cover.

indicating that increasing density was principally associated with decreasing core forest.

*Macrohabitat categories vs. winter community density.* 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.

*Foraging microhabitat categories vs. winter community density.* As with winter richness, foraging 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.

*Trophic categories vs. winter community density.* For trophic categories vs. winter density, only omnivores occurred frequently enough for analysis. In this case, a model with perimeter/area had the

TABLE 3. Multivariate regression analyses with highest adjusted  $r^2$  values for summer/winter individual species relationships to landscape and habitat variables.

		$f$	$P$	Partial $\eta^2$	Adjusted $r^2$	$\beta$ coefficient	SE
Summer species							
Downy Woodpecker	Model	9.196	<0.001	0.241	0.215		
	Perimeter/area	2.306	0.132	0.019		3.385	1.519
	Forest type	26.530	<0.001	0.186		-1.861	0.361
	Canopy cover	3.435	0.066	0.029		-2.089	1.127
	Understory density	4.202	0.043	0.035		-1.083	0.528
Eastern Wood Pewee	Model	8.775	<0.001	0.316	0.280		
	Perimeter/area	0.044	0.835	0.000		0.772	3.697
	Forest type	13.179	<0.001	0.104		-1.302	0.359
	Moisture regime	4.985	0.028	0.042		1.822	0.816
	Canopy cover	11.266	0.001	0.090		3.692	1.100
	Understory density	9.857	0.002	0.080		-1.621	0.516
	Elevation	4.927	0.028	0.041		0.354	0.159
Blue Jay	Model	6.167	0.003	0.095	0.079		
	Perimeter/area	7.148	0.009	0.057		5.150	1.926
	Understory density	4.986	0.027	0.041		-0.687	0.308
Black-capped Chickadee	Model	10.313	<0.001	0.209	0.189		
	Human-associated	5.538	0.020	0.045		1.344	0.571
	Forest type	24.138	<0.001	0.171		1.546	0.315
	Moisture regime	8.396	0.004	0.067		2.120	0.732
Tufted Titmouse	Model	15.482	<0.001	0.348	0.326		
	Core forest	9.638	0.002	0.077		-1.487	0.479
	Forest type	6.243	0.014	0.051		-0.948	0.379
	Canopy cover	19.293	<0.001	0.143		5.170	1.177
	Elevation	12.200	0.001	0.095		-0.617	0.177
White-breasted Nuthatch	Model	1.137	0.344	0.075	0.009		
	Forest area	0.580	0.448	0.005		0.658	0.864
	Forest type	0.981	0.324	0.009		-0.433	0.438
	Moisture regime	2.032	0.157	0.018		1.414	0.992
	Canopy cover	0.045	0.832	0.000		0.289	1.356
	Understory density	2.565	0.112	0.022		-1.043	0.651
	Elevation	1.535	0.218	0.014		-0.265	0.214
	Model	10.914	<0.001	0.322	0.292		
Veery	Perimeter/area	5.190	0.025	0.043		-15.321	6.726
	Forest type	10.359	0.002	0.083		2.138	0.664
	Moisture regime	5.187	0.025	0.043		-3.391	1.489
	Understory density	27.819	<0.001	0.195		4.941	0.937
	Elevation	3.428	0.067	0.029		0.542	0.293

Wood Thrush	Model	10.972	<0.001	0.220	0.200		
	Human-associated	5.697	0.019	0.046		0.989	0.414
	Forest type	16.294	<0.001	0.122		-0.921	0.228
	Moisture regime	5.875	0.017	0.048		-1.286	0.530
American Robin	Model	18.535	<0.001	0.390	0.369		
	Human-associated	17.167	<0.001	0.129		4.247	1.025
	Forest type	10.010	0.002	0.079		-1.767	0.558
	Canopy cover	21.798	<0.001	0.158		-8.179	1.752
Red-eyed Vireo	Understory density	5.930	0.016	0.049		-1.977	0.812
	Model	17.190	<0.001	0.428	0.403		
	Perimeter/area	8.496	0.004	0.069		-4.271	1.465
	Forest type	8.381	0.005	0.068		-0.405	0.140
	Moisture regime	3.979	0.048	0.033		-0.629	0.316
	Canopy cover	8.427	0.004	0.068		1.240	0.427
	Elevation	23.151	<0.001	0.168		0.304	0.063
	Model	15.562	<0.001	0.450	0.421		
Ovenbird	Perimeter/area	13.172	<0.001	0.104		-23.408	6.450
	Forest type	14.701	<0.001	0.114		2.399	0.626
	Moisture regime	4.677	0.033	0.039		-3.078	1.424
	Canopy cover	6.170	0.014	0.051		4.768	1.919
	Understory density	12.671	0.001	0.100		3.208	0.901
	Elevation	8.754	0.004	0.071		0.823	0.278
	Model	16.013	<0.001	0.291	0.273		
	Forest area	40.993	<0.001	0.259		3.413	0.533
Scarlet Tanager	Understory density	10.216	0.002	0.080		-1.704	0.533
	Vertical	4.213	0.042	0.035		0.666	0.325
Brown-headed Cowbird	Model	6.137	0.001	0.136	0.114		
	Perimeter/area	9.557	0.002	0.076		-16.019	5.182
	Understory density	2.531	0.114	0.021		1.139	0.716
	Elevation	13.351	<0.001	0.102		-0.816	0.223
American Goldfinch	Model	8.961	<0.001	0.187	0.166		
	Human-associated	6.855	0.010	0.055		2.935	1.121
	Forest type	4.761	0.031	0.039		1.266	0.580
	Elevation	6.520	0.012	0.053		-0.654	0.256
Winter species							
Downy Woodpecker	Model	17.062	<0.001	0.304	0.287		
	Perimeter/area	5.445	0.021	0.044		10.924	4.682
	Forest type	11.068	0.001	0.086		-1.542	0.463
	Elevation	9.954	0.002	0.078		-0.658	0.208
Black-capped Chickadee	Model	10.794	<0.001	0.217	0.197		
	Perimeter/area	5.666	0.019	0.046		4.710	1.979
	Forest type	9.447	0.003	0.075		0.602	0.196
	Elevation	7.726	0.006	0.062		-0.245	0.088
White-breasted Nuthatch	Model	21.783	<0.001	0.270	0.257		
	Perimeter/area	28.189	<0.001	0.193		17.524	3.301
	Forest type	14.024	<0.001	0.106		-1.370	0.366

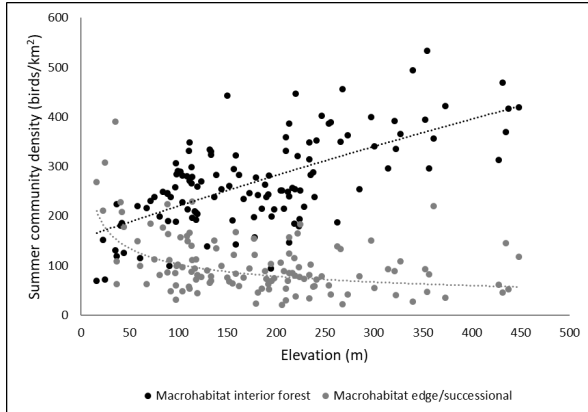


FIG. 15. Interior forest summer density increases whereas edge/successional density declines with increasing elevation.

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).

**Model assumptions.** In the cases of summer interior forest inhabitant, ground forager and herbivore densities, winter arboreal forager and secondary consumer densities, summer canopy nester richness and Ovenbird densities, regression diagnostics showed modest departures from model assumptions. In these instances, I also examined the strength of nonparametric Pearson correlations among variables, which for each of these categories strongly concurred with regression findings.

**Species composition.** In examining densities of the 14 summering species occurring at >90% of sites (Table 3), models with the greatest  $r^2$  included seven with perimeter/area, one with core forest, four with human-associated forest breaks, one with forest area 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 (Table 3).

**Summering species.** Increasing densities of the cavity nesting, resident, arboreal ecological generalist Downy Woodpecker (*Dryobates pubescens*) showed a slightly stronger relationship compared with other landscape models for one with perimeter/area, with hierarchical analysis indicating 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 (*Parus atricapillus*) showed a slightly stronger relationship to a model including human-associated cover, with hierarchical analysis indicating that

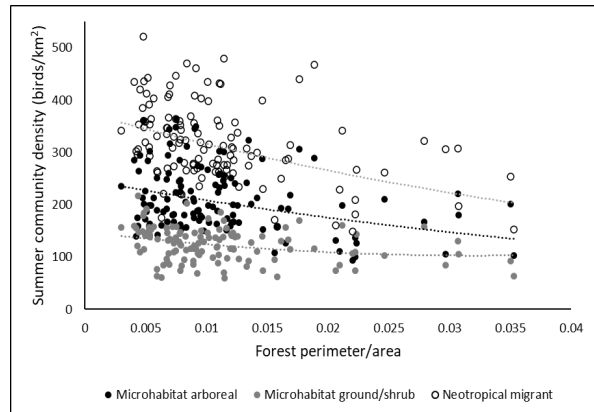


FIG. 16. Arboreal, ground/shrub and neotropical migrant density decline with increasing forest perimeter/area.

increasing densities were associated with primarily increasing conifer cover (Fig. 19) and secondarily increasing human 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 fuscescens*) 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 ustulata*) had a slightly stronger relationship to a model including human-associated cover, although hierarchical analysis indicated that increasing densities were associated only with primarily increasing deciduous cover (Fig. 19) and secondarily soil mois-

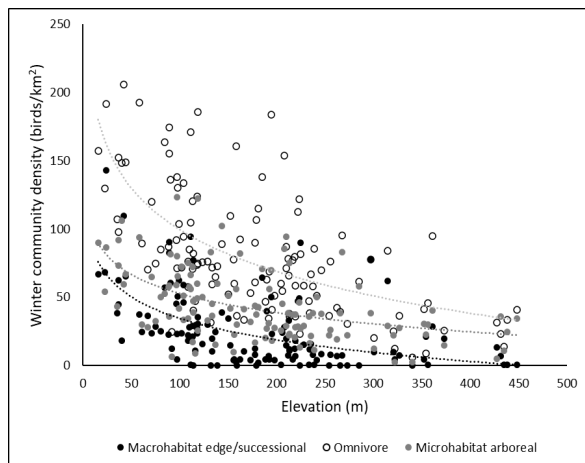


FIG. 17. Edge/successional, omnivore and arboreal winter density decline with increasing elevation.

ture. 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 forest area, with hierarchical analysis indicating that increasing densities were associated primarily with increasing forest area (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

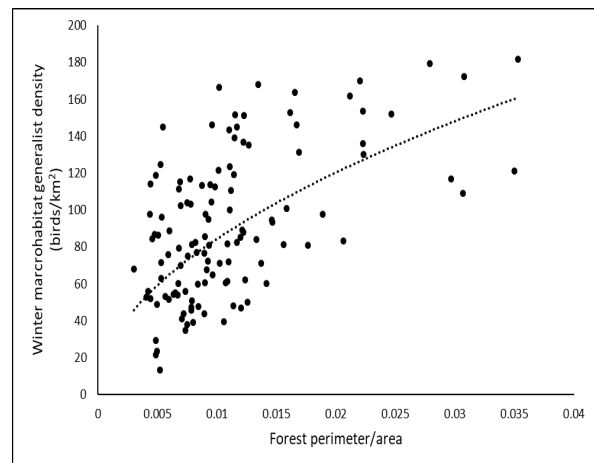


FIG. 18. Macrohabitat generalist winter density increases with increasing forest perimeter/area.

model including human-associated forest breaks, with hierarchical analysis indicating that increasing densities were weakly associated with increasing human-associated breaks and understory density.

**Wintering species.** 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  $t = -3.61$ ,  $df = 49$ ,  $P < 0.01$ ). Similarly, for summer community life history traits, species richness did not show overall differences between sampling periods in categories of nest site selection (ANOVA  $f = 0.62$ ,  $df = 1,294$ ,  $P =$

TABLE 4. Comparison of 2001 and 2004 regression analyses with highest adjusted  $r^2$  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.

		$f$	$P$	Partial $\eta^2$	Adjusted $r^2$	$\beta$ coefficient	SE
Community richness							
Summer							
2001	Model	1.574	0.209	0.093	0.034		
	Human-associated	0.000	0.986	0.000		0.007	0.410
	Forest type	2.531	0.118	0.052		0.290	0.182
	Canopy cover	2.234	0.142	0.046		-1.078	0.721
2004	Model	4.840	0.005	0.240	0.190		
	Human-associated	0.680	0.414	0.015		0.287	0.348
	Forest type	7.499	0.009	0.140		0.423	0.154
	Canopy cover	5.433	0.024	0.106		-1.425	0.611
Winter							
2001	Model	11.791	<0.001	0.334	0.306		
	Perimeter/area	1.025	0.317	0.021		2.806	2.772
	Elevation	17.172	<0.001	0.268		-0.457	0.110
2004	Model	24.595	<0.001	0.511	0.491		
	Perimeter/area	1.673	0.202	0.034		3.147	2.433
	Elevation	36.879	<0.001	0.440		-0.588	0.097
Nest site summer richness							
Ground							
2001	Model	4.561	0.007	0.229	0.179		
	Perimeter/area	8.567	0.005	0.157		-5.555	1.898
	Forest type	5.438	0.024	0.106		0.373	0.160
	Understory density	2.472	0.123	0.051		0.437	0.278
2004	Model	5.188	0.004	0.253	0.204		
	Perimeter/area	13.328	0.001	0.225		-5.985	1.639
	Forest type	4.036	0.050	0.081		0.278	0.138
	Understory density	0.167	0.685	0.004		0.098	0.240
Macrohabitat summer richness							
Interior forest							
2001	Model	30.246	<0.001	0.664	0.642		
	Human-associated	8.076	0.007	0.149		-0.877	0.309
	Forest type	46.050	<0.001	0.500		0.941	0.139
	Elevation	12.654	0.001	0.216		0.245	0.069
2004	Model	17.912	<0.001	0.539	0.509		
	Human-associated	2.883	0.096	0.059		-0.582	0.343
	Forest type	33.897	<0.001	0.424		0.896	0.154
	Elevation	4.724	0.035	0.093		0.166	0.076



## Foraging microhabitat summer richness

## Generalist

2001	Model	4.561	0.007	0.229	0.179		
	Core forest	0.941	0.337	0.020		-0.168	0.173
	Forest type	1.508	0.226	0.032		0.170	0.138
	Elevation	7.956	0.007	0.147		0.198	0.070
2004	Model	5.764	0.002	0.273	0.226		
	Core forest	3.494	0.068	0.071		-0.290	0.160
	Forest type	1.837	0.182	0.038		0.170	0.130
	Elevation	9.248	0.004	0.167		0.190	0.060

## Migration summer richness

## North American

2001	Model	9.878	<0.001	0.392	0.352		
	Core forest	0.740	0.394	0.016		-0.188	0.218
	Forest type	24.678	<0.001	0.349		0.885	0.178
	Canopy cover	1.459	0.233	0.031		-0.846	0.700
2004	Model	15.854	<0.001	0.508	0.476		
	Core forest	6.815	0.012	0.129		-0.443	0.170
	Forest type	29.183	<0.001	0.388		0.747	0.138
	Canopy cover	3.172	0.082	0.065		-0.968	0.544

## Trophic summer richness

## Secondary consumer

2001	Model	1.957	0.153	0.077	0.038		
	Human-associated	2.357	0.131	0.048		-0.592	0.386
	Forest type	1.940	0.170	0.040		0.241	0.173
2004	Model	1.891	0.162	0.074	0.035		
	Human-associated	0.005	0.944	0.000		0.032	0.445
	Forest type	3.713	0.060	0.073		0.385	0.200

## Macrohabitat winter richness

## Edge/successional

2001	Model	10.225	<0.001	0.400	0.361		
	Perimeter/area	1.752	0.192	0.037		3.704	2.799
	Forest type	2.490	0.121	0.051		-0.356	0.226
	Elevation	14.670	<0.001	0.242		-0.437	0.114
2004	Model	19.488	<0.001	0.560	0.531		
	Perimeter/area	2.344	0.133	0.048		4.961	3.240
	Forest type	14.504	<0.001	0.240		-0.996	0.261
	Elevation	19.727	<0.001	0.300		-0.586	0.132

## Foraging microhabitat winter richness

## Arboreal

2001	Model	2.990	0.060	0.113	0.075		
	Perimeter/area	0.630	0.431	0.013		1.360	1.713
	Elevation	3.680	0.061	0.073		-0.131	0.068
2004	Model	17.091	<0.001	0.421	0.396		
	Perimeter/area	0.180	0.674	0.004		0.629	1.485
	Elevation	28.726	<0.001	0.379		-0.317	0.059

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Trophic winter richness

Omnivore

2001	Model	8.370	0.001	0.263	0.231		
	Perimeter/area	0.036	0.850	0.001		-0.480	2.529
	Elevation	15.353	<0.001	0.246		-0.394	0.101
2004	Model	14.056	<0.001	0.374	0.348		
	Perimeter/area	0.048	0.827	0.001		0.478	2.175
	Elevation	24.246	<0.001	0.340		-0.426	0.087

Community density

Summer

2001	Model	2.367	0.083	0.134	0.077		
	Perimeter/area	5.354	0.025	0.104		-2.477	1.071
	Forest type	0.347	0.558	0.007		-0.052	0.088
	Moisture regime	0.539	0.467	0.012		-0.160	0.218
2004	Model	1.851	0.151	0.108	0.050		
	Perimeter/area	2.298	0.136	0.048		-1.439	0.949
	Forest type	1.419	0.240	0.030		0.093	0.078
	Moisture regime	1.865	0.179	0.039		-0.264	0.193

Winter

2001	Model	5.093	0.010	0.178	0.143		
	Perimeter/area	3.526	0.067	0.070		6.158	3.280
	Elevation	3.280	0.077	0.065		-0.236	0.131
2004	Model	19.168	<0.001	0.449	0.426		
	Perimeter/area	1.027	0.316	0.021		2.479	2.446
	Elevation	29.433	<0.001	0.385		-0.528	0.097

Nest site summer density

Ground

2001	Model	10.820	<0.001	0.414	0.375		
	Perimeter/area	18.205	<0.001	0.284		-9.050	2.121
	Forest type	8.048	0.007	0.149		0.508	0.179
	Understory density	11.965	0.001	0.206		1.075	0.311
2004	Model	24.073	<0.001	0.611	0.586		
	Perimeter/area	44.508	<0.001	0.492		-7.544	1.131
	Forest type	18.435	<0.001	0.286		0.410	0.095
	Understory density	22.047	<0.001	0.324		0.778	0.166

Macrohabitat summer density

Interior forest

2001	Model	14.540	<0.001	0.487	0.453		
	Core forest	15.095	<0.001	0.247		0.551	0.142
	Forest type	2.000	0.164	0.042		0.160	0.113
	Elevation	8.523	0.005	0.156		0.168	0.058
2004	Model	20.837	<0.001	0.576	0.548		
	Core forest	35.167	<0.001	0.433		0.686	0.116
	Forest type	15.165	<0.001	0.248		0.360	0.093
	Elevation	1.161	0.287	0.025		0.051	0.047

## Foraging microhabitat summer density

## Generalist

2001	Model	5.881	0.002	0.277	0.230		
	Forest area	0.498	0.484	0.011		-0.205	0.291
	Canopy cover	12.854	0.001	0.218		-2.319	0.647
	Understory density	0.877	0.354	0.019		0.264	0.282
2004	Model	7.429	<0.001	0.326	0.282		
	Forest area	3.659	0.062	0.074		-0.445	0.233
	Canopy cover	6.611	0.013	0.126		-1.332	0.518
	Understory density	6.954	0.011	0.131		0.595	0.226

## Migration summer density

## Neotropical

2001	Model	5.568	0.002	0.266	0.219		
	Perimeter/area	12.615	0.001	0.215		-4.446	1.252
	Moisture regime	1.858	0.179	0.039		-0.356	0.261
	Understory density	1.543	0.220	0.032		0.228	0.184
2004	Model	9.703	<0.001	0.388	0.348		
	Perimeter/area	15.954	<0.001	0.258		-3.894	0.975
	Moisture regime	9.730	0.003	0.175		-0.634	0.203
	Understory density	1.980	0.166	0.041		0.201	0.143

## Trophic summer density

## Secondary consumer

2001	Model	3.563	0.021	0.189	0.136		
	Perimeter/area	8.688	0.005	0.159		-5.104	1.732
	Forest type	2.828	0.099	0.058		0.240	0.143
	Moisture regime	0.141	0.709	0.003		-0.132	0.352
2004	Model	5.622	0.002	0.268	0.221		
	Perimeter/area	4.241	0.045	0.084		-3.177	1.543
	Forest type	9.986	0.003	0.178		0.401	0.127
	Moisture regime	3.405	0.071	0.069		-0.579	0.314

## Macrohabitat winter density

## Edge.successional

2001	Model	17.137	<0.001	0.422	0.497		
	Perimeter/area	1.220	0.275	0.025		13.084	11.848
	Elevation	25.569	<0.001	0.352		-2.384	0.471
2004	Model	17.758	<0.001	0.430	0.406		
	Perimeter/area	0.027	0.871	0.001		-2.268	13.923
	Elevation	32.187	<0.001	0.406		-3.143	0.554

## Foraging microhabitat winter density

## Generalist

2001	Model	0.483	0.620	0.020	-0.022		
	Perimeter/area	0.964	0.331	0.020		3.135	3.193
	Elevation	0.079	0.779	0.002		0.036	0.127
2004	Model	5.019	0.011	0.176	0.141		
	Perimeter/area	3.990	0.052	0.078		4.819	2.412
	Elevation	2.744	0.104	0.055		-0.159	0.096

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Trophic winter density

Omnivore

2001	Model	6.469	0.001	0.297	0.251		
	Core forest	1.775	0.189	0.037		-0.501	0.376
	Forest type	2.272	0.139	0.047		-0.453	0.301
	Elevation	7.147	0.010	0.134		-0.408	0.153
2004	Model	12.888	<0.001	0.457	0.421		
	Core forest	2.122	0.152	0.044		-0.396	0.272
	Forest type	4.986	0.030	0.098		-0.486	0.217
	Elevation	15.518	<0.001	0.252		-0.435	0.110

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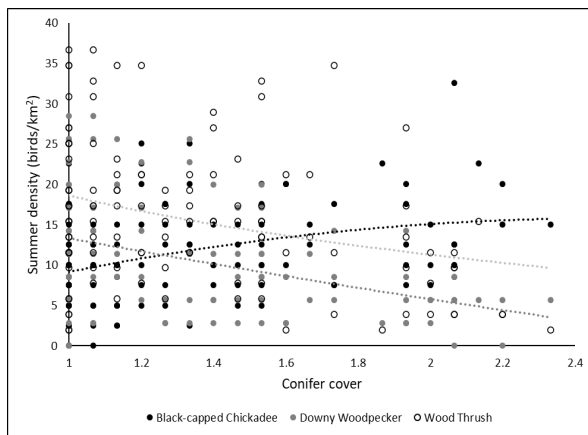


FIG. 19. Downy Woodpecker and Wood Thrush summer densities decline with conifer cover whereas Black-capped Chickadee densities increase.

0.43), macrohabitat choice ( $f = 0.03$ ,  $df = 1,294$ ,  $P = 0.87$ ), foraging microhabitat choice ( $f = 0.07$ ,  $df = 1,294$ ,  $P = 0.79$ ), migratory category ( $f < 0.01$ ,  $df = 1,294$ ,  $P = 0.97$ ) or trophic relationships ( $f = 0.04$ ,  $df = 1,294$ ,  $P = 0.85$ ). However, 2004–2006 had greater community density than 2001–2003 for nest site selection ( $f = 5.70$ ,  $df = 1,294$ ,  $P = 0.02$ ), macrohabitat choice ( $f = 4.91$ ,  $df = 1,294$ ,  $P = 0.03$ ), foraging microhabitat choice ( $f = 10.03$ ,  $df = 1,294$ ,  $P < 0.01$ ) and migratory category ( $f = 3.88$ ,  $df = 1,294$ ,  $P = 0.05$ ), although trophic relationships did not strongly differ ( $f = 2.82$ ,  $df = 1,294$ ,  $P = 0.09$ ). In winter, species richness also did not strongly differ overall for macrohabitat choice ( $f = 2.06$ ,  $df = 1,196$ ,  $P = 0.15$ ) or foraging microhabitat choice ( $f = 3.50$ ,  $df = 1,196$ ,  $P = 0.06$ ), although 2004–2006 had greater richness than 2001–2003 for omnivores (paired sample  $t = 2.20$ ,  $df = 49$ ,  $P = 0.03$ ). Moreover, 2004–2006 had greater community density than 2001–2003 for macrohabitat choice ( $f = 4.78$ ,  $df = 1,196$ ,  $P = 0.03$ ), foraging microhabitat choice ( $f = 3.76$ ,  $df = 1,196$ ,  $P < 0.01$ ) and omnivores (paired sample  $t = 4.06$ ,  $df = 49$ ,  $P < 0.01$ ).

Of 20 regression comparisons performed on community measures (Table 4), most were similar between sampling periods, although 12 showed at least some differences as measured by  $P \leq 0.05$  significance levels. Of eight comparisons with significant landscape results for at least one of the sampling periods, three showed differences and of 17 comparisons with significant habitat results for at least one of the sampling periods, nine showed differences. Specifically, as in the statewide analysis, increasing summer richness showed relationships with increasing conifer and decreasing canopy cover in 2004–2006, although these predictors were nonsignificant in 2001–2003. Also as in the

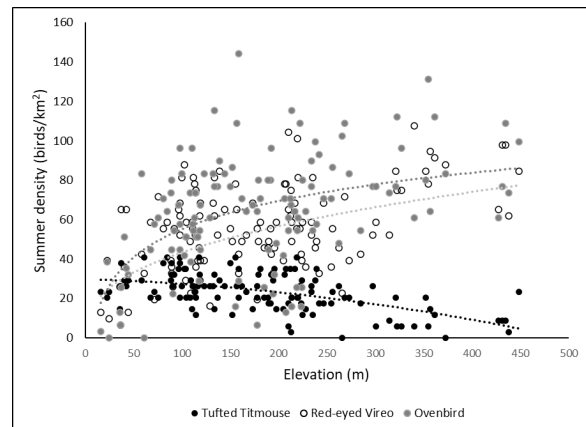


FIG. 20. Red-eyed Vireo and Ovenbird summer densities increase whereas Tufted Titmouse densities decline with increasing elevation.

statewide analysis, increasing winter richness was significantly associated with decreasing elevation during both periods. However, models were nonsignificant for summer community density in both sampling periods. In winter, as in the statewide analysis, increasing density was associated with decreasing elevation in 2004–2006, although elevation showed a weaker but similar relationship in 2001–2003.

*Temporal variation vs. community richness measures.* In the case of summer community richness measures, as with the statewide analysis more ground-nesting 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 significantly 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.

Winter community measures of increasing edge/successional richness showed, as in the statewide analysis, a significant relationship with

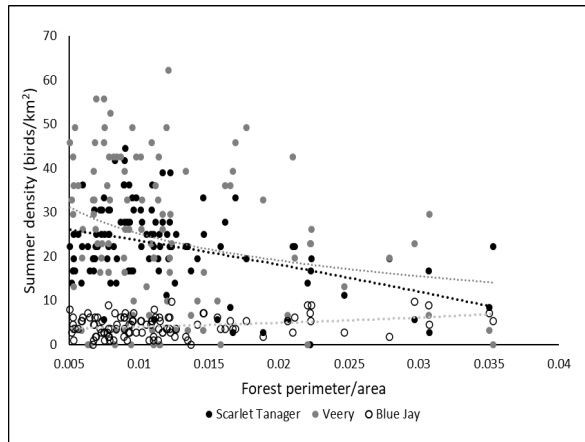


FIG. 21. Scarlet Tanager and Veery summer densities decline whereas Blue Jay densities increase with increasing forest perimeter/area.

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 relationship with declining elevation, although it was significant only in 2004–2006. As in the statewide analysis, increasing omnivore richness was significantly associated with decreasing elevation for both sampling periods.

*Temporal variation vs. community density measures.* 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 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 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 secondary consumer density was significantly associated with decreasing perimeter/areas, although increasing conifer cover was significantly related only in 2004–2006. Soil moisture was nonsignificant during both sampling periods.

Winter community density measures for forag-

ing microhabitat generalists showed no significant predictor 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 density in increasing deciduous cover was 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, multivariate regression showed that they had the closest association with these and other summer community measures 81% of the time, strongly suggesting that fragmentation effects are the underlying driver of such community patterns.

In the case of species richness, ground nester, arboreal forager and ground/shrub 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. 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 North American migrant, resident, foraging microhabitat generalist, edge/



successional and habitat generalist species, including the Brown-headed Cowbird (hypothesis 2), resident density and richness, short-distance migrant richness and habitat generalist richness did show significant increases with increasing fragmentation measures. However, short-distance migrant density, foraging generalist density and richness, edge/successional density and richness, habitat generalist density and Brown-headed Cowbird density showed no significant responses or responses opposite to these predictions. These findings are generally 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 and even in this instance the relationship was nonsignificant. 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, herbivores showed the strongest evidence of fragmentation predominating over habitat effects. In other instances, fragmentation and habitat effects were not clearly different. Similarly, of 16 tests concerning breeding richness, ground nesters and cavity nesters showed the best evidence of fragmentation predominating over habitat effects. Again, in other instances fragmentation and habitat effects were not clearly different. Moreover, 10 of the 14 breeding species examined had habitat effects principally influenced by them and three of these species had 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 one of 32 strongest summer models and none of 15 winter community measures showed a significant relationship to natural forest breaks, although even this effect disappeared with hierarchical analysis. Moreover, none of 14 strongest models for breeding species showed a relationship to natural forest breaks and 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). However, multivariate analyses showed a tendency for increasing richness and density to be associated with greater fragmentation. Of 13 additional winter community groups studied, hierarchical analysis showed that only habitat generalist density has a substantial increase with increasing perimeter/area, although multivariate analyses showed that seven others had a tendency to do the same. 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, hierarchical analysis showed that only one had a strong positive association with perimeter/area, although multivariate analyses showed that the other two also had a tendency to have the same relationship. Multivariate analysis also showed a negative relationship for two of the species with elevation. 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.

This study provides strong evidence that even in heavily forested Connecticut forest fragmentation is an important structuring feature for forest bird communities, with decreasing fragmentation associated with increases in such groups as neotropical migrants, forest interior species and ground nesters and increasing fragmentation associated with increases in such groups as short distance migrants, resident species, macrohabitat generalists and winter residents. Still, a number of expected community associations with fragmentation did not materialize. Moreover, habitat factors also played a large role in the occurrence of many species groups.

Because of the large samples of this study, the probability that these findings are due to chance is

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. This has led to a long-term increase in populations at this location (Craig et al. 2022) although the severe drought of 2000 (NIDIS 2024) also may have played a role in temporal shifts in densities. Despite this, over the wider area of northeastern Connecticut, populations have trended toward stable between 2004 and 2021 (Craig 2023b). 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 realized 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 winter severity that can drive species to change their winter distribution. 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 limited associations of winter species groups with predictor variables are not unexpected.

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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	Winter Microhabitat	Winter 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								
EWPW									
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
YSFL	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
EAWP		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
AMCR	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 consumer
CARW		edge/successional	ground/shrub	cavity	secondary consumer	resident	edge/successional	ground/shrub	secondary consumer
HOWR		edge/successional	generalist	cavity	secondary consumer	North American			
WIWR		forest interior	ground/shrub	cavity	secondary consumer	North American	forest interior	ground/shrub	secondary consumer
GCKI							generalist	generalist	secondary consumer
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
BTNW		forest interior	arboreal	canopy/understory	secondary consumer	neotropical			
BLBW		forest interior	arboreal	canopy/understory	secondary consumer	neotropical			
PIWA		forest interior	arboreal	canopy/understory	secondary consumer	North American			
PRAW		edge/successional	arboreal	canopy/understory	secondary consumer	neotropical			
CERW		forest interior	arboreal	canopy/understory	secondary consumer	neotropical			
BAWW		forest interior	arboreal	ground	secondary consumer	neotropical			

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			
CORE							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