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Robert J. Craig
Bird Conservation Research, Inc.

Robert W. Klaver
United States Geological Survey, bkklaver@iastate.edu

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Abstract

At regional scales, the most important variables associated with diversity are latitudinally-based temperature and net primary productivity, although diversity is also influenced by habitat. We examined bird species richness, community density and community evenness in forests of eastern Connecticut to determine whether: 1) spatial and seasonal patterns exist in diversity, 2) energy explains the greatest proportion of variation in diversity parameters, 3) variation in habitat explains remaining diversity variance, and 4) seasonal shifts in diversity provide clues about how environmental variables shape communities. We sought to discover if our data supported predictions of the species–energy hypothesis. We used the variable circular plot technique to estimate bird populations and quantified the location, elevation, forest type, vegetation type, canopy cover, moisture regime, understory density and primary production for the study sites. We found that 1) summer richness and population densities are roughly equal in northeastern and southeastern Connecticut, whereas in winter both concentrate toward the coast, 2) variables linked with temperature explained much of the patterns in winter diversity, but energy-related variables showed little relationship to summer diversity, 3) the effect of habitat variables on diversity parameters predominated in summer, although their effect was weak, 4) contrary to theory, evenness increased from summer to winter, and 5) support for predictions of species–energy theory was primarily restricted to winter data. Although energy and habitat played a role in explaining community patterns, they left much of the variance in regional diversity unexplained, suggesting that a large stochastic component to diversity also may exist.

Disciplines

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Comments

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Factors influencing geographic patterns in diversity of forest bird communities of eastern Connecticut, USA

Robert J. Craig and Robert W. Klaver

R. J. Craig (mail@birdconservationresearch.org), Bird Conservation Research, Inc., 90 Liberty Highway, Putnam, CT 06260, USA. – R. W. Klaver, U. S. Geological Survey, Iowa Cooperative Fish and Wildlife Research Unit, 342 Science II, Iowa State Univ., Ames, IA 50011-3221, USA.

At regional scales, the most important variables associated with diversity are latitudinally-based temperature and net primary productivity, although diversity is also influenced by habitat. We examined bird species richness, community density and community evenness in forests of eastern Connecticut to determine whether: 1) spatial and seasonal patterns exist in diversity, 2) energy explains the greatest proportion of variation in diversity parameters, 3) variation in habitat explains remaining diversity variance, and 4) seasonal shifts in diversity provide clues about how environmental variables shape communities. We sought to discover if our data supported predictions of the species–energy hypothesis. We used the variable circular plot technique to estimate bird populations and quantified the location, elevation, forest type, vegetation type, canopy cover, moisture regime, understory density and primary production for the study sites. We found that 1) summer richness and population densities are roughly equal in northeastern and southeastern Connecticut, whereas in winter both concentrate toward the coast, 2) variables linked with temperature explained much of the patterns in winter diversity, but energy-related variables showed little relationship to summer diversity, 3) the effect of habitat variables on diversity parameters predominated in summer, although their effect was weak, 4) contrary to theory, evenness increased from summer to winter, and 5) support for predictions of species–energy theory was primarily restricted to winter data. Although energy and habitat played a role in explaining community patterns, they left much of the variance in regional diversity unexplained, suggesting that a large stochastic component to diversity also may exist.

An important goal of ecology has been to elucidate the mechanisms that produce geographic patterns in diversity (MacArthur 1972, Rosenzweig 1995). Wright et al.'s (1993) review showed that aside from the species–area effects of local habitat patches, the most important variable associated with diversity is energy availability and its surrogates, particularly latitudinally-based temperature variation (thermal kinetic energy), although net primary productivity (chemical potential energy) has been related to diversity as well (Hurlbert and Haskell 2003, Evans et al. 2006).

Factors controlling diversity may vary seasonally, with compelling evidence for regional temperature driving temperate bird diversity coming particularly from winter studies (Bock and Lepthein 1974, Root 1988, Evans et al. 2006). Winter species richness grows southward with increasing winter temperatures toward regions with 245 frost-free days (Bock and Lepthein 1974, Hawkins et al. 2007). Little productivity occurs at this season, so temperature assumes a central role in energy budgets (Stalmaster 1983) in a season when physical factors exert the greatest effect on community organization (Rotenberry et al. 1979). Compared to summer, winter species richness is also thought to be reduced and evenness at its lowest (Holmes and Sturges

1973) because the winter environment is less predictable (Tramer 1969), leading to a few common species being present and more species being represented by only few individuals.

Summer bird diversity has shown patterns related to energy that differ from those of winter. Bird species richness declines to the north of the northeastern United States and southern maritime Canada as well as to the south of this region (MacArthur and Wilson 1967, Robbins et al. 1986, O'Connor et al. 1996). Rabenold (1979) hypothesized that this was related to a concentrated pulse of summer production in the northeast. There is indeed a positive relationship between primary productivity and summer bird diversity at the continental scale (Hurlbert and Haskell 2003, Evans et al. 2006).

Regardless of the specific seasonal pattern, the positive relationship between diversity and energy has led to development of a 'species–energy' hypothesis (Wright 1983), which postulates that increased energy supports more individuals, which in turn yields the presence of more species. This process may occur through expanding food supplies (Currie 1991) or reducing metabolic costs (Lennon et al. 2000), which reduce local extinction probability,

particularly by the rarest community members (Evans et al. 2006), although greater numbers of individuals may simply increase the random probability that more species are present (Hubbell 2001, Currie et al. 2004).

Despite evidence supporting the role of energy in influencing bird diversity and the underlying distributions of individual species (Root 1988, Hitch and Leberg 2007), patterns emerging at multiple scales may be complex (Wiens 1989), in part because habitat variables may contribute to such patterns. Flather and Sauer (1996) and Hurlbert and Haskell (2003) report positive relationships between habitat variables and diversity in summer and Pearson (1993) and Doherty and Grubb (2000) report them in winter.

Bird diversity has been studied at scales ranging from local to continental. At the largest scales, data from the Breeding Bird Survey (Sauer et al. 2005) and Christmas Bird Count (National Audubon Society 2009) have proven useful for identifying patterns in North American bird diversity (Bock and Lepthein 1974, Root 1988, Hurlbert and Haskell 2003, Evans et al. 2006) even though they have weaknesses in quality and interpretation (James et al. 1996, Thomas 1996). Such databases are, however, insufficiently systematic and quantitative for more detailed regional studies. At regional scales, state breeding bird atlases (Enser 1992, Bevier 1994) have provided a measure of systematic coverage for a single season, but patterns reported are difficult to interpret because data gathered are variable in terms of the intensity of coverage, use of untrained observers of differing ability and sampling that does not clearly relate diversity to habitats.

To conduct a finer grained examination of seasonal patterns in regional diversity with systematically collected, habitat-specific, quantitative data, we surveyed birds in extensively forested eastern Connecticut, USA. Community parameters studied at this scale show less population variation than do local studies (Fahrig and Merriam 1994), which assists with elucidation of community organizing principles (Bart 2005). In this study, we map for eastern Connecticut both winter and summer components of forest species diversity: richness, evenness and population density (Tramer 1969). We test if 1) spatial and seasonal patterns exist in regional diversity, 2) energy explains the greatest proportion of variation in diversity parameters, with effects of chemical potential energy predominating in summer and thermal kinetic energy predominating in winter, 3) variation in habitat explains the bulk of remaining diversity variance, and 4) seasonal shifts in diversity patterns provide additional clues about how environmental variables shape community patterns.

Understanding the mechanisms that shape large-scale patterns in bird diversity may improve decision-making in regional conservation planning. We further test if our data provide empirical support for the species–energy hypothesis. Currie et al. (2004) developed a series of predictions for the hypothesis that are relevant to the scale of this investigation: 1) density and energy positively co-vary, 2) density and richness co-vary with a log-log slope of 0.26 based on the canonical log-normal frequency distribution, 3) richness and energy positively co-vary, 4) covariance should be strongest between energy–density, followed by density and species and weakest between energy and species,

- 5) changes in energy lead to changes in density and species,
- 6) energy and individuals/species positively co-vary.

Methods

Study areas

The northern half of eastern Connecticut has lower mean annual temperatures (8.6°C), shorter frost-free growing season and steeply hilly topography reaching elevations to 400 m, whereas the southern half, especially near the coast and along major rivers, has higher mean annual temperatures (10.0°C), up to 20 d longer frost-free growing season and lower lying topography, with elevations below 120 m (Brumbach 1965, Dowhan and Craig 1976).

The region is largely forested, with cover varying from 69% in the north to 63% in the south (Alerich 1999). Its most widespread forest associations are those dominated by oaks and hickories, although conifer–hardwood associations are present to the north. On mesic soils, maples, beeches and ashes often predominate, in hydric situations hardwoods occur separately or with conifers, and in xeric areas pine–oak associations occur, particularly in glacially deposited sands (Alerich 1999, Craig et al. 2003).

For analyses, we divided eastern Connecticut into northeastern and southeastern portions, with the boundary between them coincident with their Connecticut ecoregional boundaries (Dowhan and Craig 1976). Based on the size of the regions and their extent of forest cover, we surveyed 26 sites in northeastern and 24 sites in southeastern Connecticut to provide similar levels of sampling intensity (Fig. 1). The source pool of sites was public access

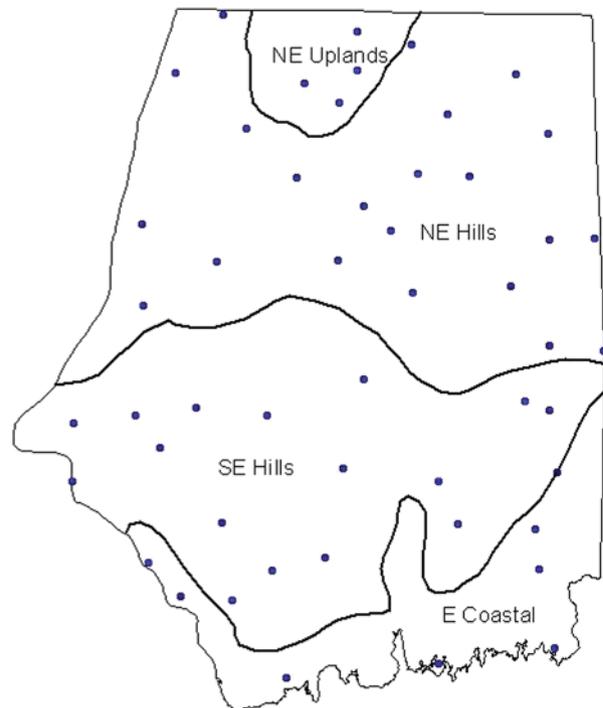


Figure 1. The distribution of the center points of study areas in eastern Connecticut with respect to ecoregions (Dowhan and Craig 1976).

parcels of extensive, unfragmented forest (over 200 ha). We surveyed northeastern Connecticut in the summers of 2001 and 2004 and winters of 2001–2002 and 2004–2005, and southeastern Connecticut in the summers of 2002 and 2005 and winter of 2002–2003 and 2005–2006. Sampling one region per year provided a measure of annual within-region survey variance.

We sampled the two regions systematically by dividing them into ca 90 km² survey blocks with a sampling grid. We randomly chose one site per grid cell although, in practice, many cells contained only one available choice. At nearly all sites, we were able to establish routes through forests about which we had no a priori knowledge, thereby avoiding unconscious biasing of sampling results. In six cells with no sites available (e.g. urban areas), we sampled sites closest to cell boundaries or, in two instances, substituted parcels in regions with ca 90% forest cover to sample more equitably the forests in those regions.

Bird surveys

We used the variable circular plot (VCP) technique to survey bird populations. It has wide utility in evaluating populations over a variety of terrains (Scott et al. 1986) and has a well-developed theoretical underpinning that accounts for differential detectability of species (Buckland et al. 2001), key to producing precise density estimates (Simons et al. 2007). Survey routes began at first light (ca 05:15 in summer, 07:00 in winter) and lasted about 3.5 h. Because observer differences in perception can be great (McDonald 1981) and temporal improvements in observer ability may occur (Norvell et al. 2003), the long experienced RJC made all observations (Davis 1981).

We established a line transect at each sampling location, with transects traversing about 3.2–4 km of forest depending upon terrain and other local conditions. Along each transect, we placed 15 points (750 total points), the maximum number we could survey during the peak of morning bird activity (before 09:00 in summer and 10:30 in winter), and recorded locations and elevations of points with a Garmin Etrex global positioning device (Garmin, Olathe, KS). Survey points were generally about 200 m apart, a distance empirically determined to minimize detecting the same birds from two successive points, and greater than that used in other studies (Scott et al. 1986). In instances where loudly vocal birds might be detected from two stations, we lengthened distances to ensure sampling individuals only once.

We sampled at each point for eight minutes, a time used frequently in VCP surveys because it approximates an instantaneous count yet is long enough to record adequately birds present (Scott et al. 1986). At points, we estimated the horizontal distance at first detection (usually aural) to each bird encountered. To maximize consistency in distance estimation, during every survey we directly measured with a tape or global positioning the distance to at least several vocalizing birds. Between sampling periods, we occasionally detected rarer bird species, particularly raptors. If we found no other individuals of these species at sampling points, we included the first of such detections in the survey at the point of observation.

Summer field observations occurred from mid-May to early July, the height of the local breeding season, and we made winter observations from mid-December to the end of February, the height of the local winter season (Craig unpubl.), to minimize alteration of survey results due to behavioral changes (Skirven 1981). We visited sites in random order and re-randomized the visitation order each season and year. Each year, we also duplicated a survey at one site in both winter and summer. Doing so over the course of the study gave us a series of measures on within-season variance. We recorded only forest-associated species, which we defined as those inhabiting unbroken forest, forest openings caused by tree fall or selective logging, closed to partly open swamps and forested river banks.

Habitat measurements

We visually evaluated habitat in a 70 m radius from each sampling station after each bird survey, verifying and refining these evaluations during summer and winter. Small changes in conditions that occurred after 2001–2003 (e.g. selective logging) necessitated that we update values in 2004–2006 surveys. To evaluate habitat, we used global positioning to walk a straight line beginning 70 m before to 70 m past a sample point, and observed in all directions to 70 m when at the sample point. While observing, we visually estimated to the nearest 10% a) forest type: 1) deciduous: $\leq 10\%$ evergreen conifers, 2) mixed: 20–60% evergreen coniferous, 3) coniferous: $\geq 70\%$ evergreen conifers; b) vegetation type (also generally arranged from deciduous to coniferous): 1) oak-dominated (oak, hickory, black birch *Betula lenta*), 2) mixed deciduous (e.g. red maple *Acer rubrum*, white ash *Fraxinus americana*, yellow poplar *Liriodendron tulipifera*), 3) conifer–hardwood (e.g. eastern hemlock *Tsuga canadensis*, eastern white pine *Pinus strobus*, northern red oak *Quercus rubra*, sugar maple *A. saccharum*, American beech *Fagus grandiflora*, yellow birch *B. alleghaniensis*), 4) pine–oak (e.g. eastern white pine, pitch pine *P. rigida*, scarlet oak *Q. coccinea*), 5) conifer (eastern hemlock, eastern white pine, plantation conifers), 6) mixed sites (e.g. half oak-dominated, half mixed deciduous); c) moisture regime: 1) hydric: poorly drained or muck and peat soils, 2) mesic: silt loam and sandy loam soils, 3) xeric: exposed bedrock and sandy, gravelly and rocky soils; d) prevailing canopy tree dbh: 1) young forest: ≤ 15 cm, 2) mature forest: > 15 –45 cm, 3) old growth: > 45 cm (see also Alerich 1999); e) canopy cover: 1) open: $\leq 40\%$ canopy cover, 2) semi-open: 50–60% cover, 3) closed: $\geq 70\%$ cover; f) understory density (1–4 m tall): 1) open: $\leq 20\%$ cover, 2) moderate: 30–60% cover, 3) dense: $\geq 70\%$ cover (Craig et al. 2003). We also summed canopy and understory measures to provide a measure of vertical vegetation complexity. We used these numeric values in analyzing habitat data from plots. When plots had intermediate characteristics (e.g. half of a plot was hydric and half mesic), we assigned them an intermediate value (e.g. 1.5). If, however, a plot was comprised of $\geq 70\%$ of a single category, we assigned the plot the value of that category.

Although we attempted to approximate random sampling of habitats, producing a truly random sample for a region where most land is in private ownership was impossible. Hence, we compared our observations with independently gathered U.S. Forest Service (USFS) data on forest vegetation (Alerich 1999) to evaluate further whether sampling was representative.

To provide a measure of chemical potential energy available at the study sites, we used normalized difference vegetative index (NDVI) readings from the National Oceanic and Atmospheric Administration Advanced Very High Resolution satellite, which provide a reasonable measure of net primary production (Parelo et al. 1997). We constructed a 400 m perimeter around each transect (the zone in which most all bird observations were made) and computed for each transect the median annual NDVI value for the year in which the transect was run. Using median values prevented data skewing from aberrant NDVI readings. Our three coastal transects failed to produce NDVI readings, so we estimated missing values with averages from the three nearest transects. Doing so permitted all other habitat data to be entered for these transects in analyses with no loss of sample size. Exploratory analyses with the three transects deleted yielded results nearly identical to those with the transects included. We chose to enter summer data only into models, reasoning that summer production is most likely to influence diversity in summer and winter, especially in that winter production is minimal in southern New England.

Statistical analyses

We computed for our 15 samples per transect proportionate cover by the six vegetation types and mean transect values for forest type, vegetation type, elevation, latitude, moisture regime, dbh, canopy cover, understory density and vertical vegetation complexity. Because latitude and particularly elevation are both related to local temperature regimes in Connecticut (Brumbach 1965), we divided elevation by latitude for each transect to provide a measure related to regional temperature regimes (elevation latitude⁻¹). The resulting measure scaled the effects of elevation with respect to latitude, making it a location vector in that it contains information on magnitude and direction. In exploratory analyses it better predicted diversity than its component variables. To determine the closeness of the location-temperature relationship, we also estimated regional temperature at study sites by first regressing 30-yr mean May–July and December–February temperatures from 19 southern New England weather stations (NOAA 2004) with their location vectors.

We evaluated collinearity among habitat variables by examining data plots, correlation matrices and collinearity diagnostics in SPSS ver. 15.0 software (SPSS 2006). Forest and vegetation type proved strongly correlated, so we dropped forest type from further consideration in diversity–habitat analyses because vegetation type yielded a more detailed view forest composition. Vertical vegetation complexity also was correlated with understory cover, as was NDVI and vegetation type, with greater NDVI related

to greater deciduous cover. When examining these variables versus diversity parameters, we entered them into separate models and evaluated comparative model fit with the corrected Akaike's information criterion (AIC_c).

In examining species richness for each transect we computed, using the methods of Burnham and Overton (1979), estimates of total richness with SPECRICH (< www.mbr-pwrc.usgs.gov/software/comdyn.html >) to account for the differential detection probabilities of species. However, exploratory analyses revealed that estimated and directly measured richness were highly correlated (2001–2003: Pearson correlation = 0.91, $p < 0.001$; 2004–2006: Pearson correlation = 0.92, $p < 0.001$). Furthermore, estimated richnesses were in some cases greater than the region's entire species pool or less than the actual number of species detected, which indicated that the estimates added unrealistic variance to our data. Hence, we used our original data as measures of richness in analyses.

To calculate population densities at each transect for each bird species, we determined the species' winter and summer detection functions by using the techniques of Buckland et al. (2001), as described in detail by Craig et al. (2003), with Distance 5.0 software (Thomas et al. 2006). We chose best fitting functions by plotting data, with Akaike's information criterion and with chi-square goodness of fit tests. When species occurred in flocks, we performed analyses with flocks as the basis of measurement (Buckland et al. 2001). Because our sample sizes were very large, virtually all species had detection frequencies adequate for conducting Distance analyses. In those few instances where species were encountered rarely (e.g. American woodcock *Scolopax minor*), we computed community densities with these species omitted.

We characterized species evenness for each transect with the coefficient of variation for species densities, which increases as evenness declines. When we performed exploratory analyses with evenness indices described by Smith and Wilson (1996), the coefficient of variation performed similarly.

To test for spatial and seasonal patterns in our data, we analyzed species richness and community density data versus region and season, with year as a repeated measure in analyses of variance. Although seasonal differences in richness and density are expected, testing in this manner permitted examination of geographic diversity patterns with variance due to seasonal change accounted for. Exploratory examination of evenness data showed, however, that seasonal data had unequal variances that could not be eliminated by transformations. We therefore analyzed seasonal trends in evenness, which were of themselves of interest, with unequal variance t-tests and regional trends within seasons with repeated measures analysis of variance. We checked fit to model assumptions with Levene's test for equality of error variances, Kolmogorov–Smirnov and Shapiro–Wilk normality tests, Durbin–Watson test for serial correlation of residuals and residual plots (SPSS 2006).

Because habitat conditions changed at study sites between sets of bird surveys, we examined the role of energy and habitat in shaping diversity by conducting an analysis of variance with year of observation as a factor and habitat variables as covariates. Doing so permitted the effects of

habitat to be considered in light of temporal variation in diversity. In assessing test results, we considered the significance of parameter estimates and η^2 (partial eta-squared – an estimate of effect sizes; SPSS 2006). We examined partial correlation plots to determine if diversity parameters and habitat variables exhibited nonlinearity.

To further assess our findings in light of temporal variation in richness and density, we calculated species turnover for each site as the sum of species found in a single year only divided by the total species found in both years of study combined. We calculated the annual change in population density for each site by dividing the absolute value of the difference in density between years by the average density. We similarly computed change in within-season duplicate surveys to examine within-year variance in richness and density. To search for significant annual changes in turnover, we used a factorial analysis of variance on species data vs season and region. In the case of density turnover, we found that seasonal error variances were significantly different, so we performed separate seasonal t-tests on data. For seasonal differences in density turnover, we performed a Mann–Whitney U test. All result means are reported \pm SE.

Because our data were geographically based, they had the potential to exhibit spatial autocorrelation. Spatial autocorrelation may be viewed as a missing variable problem where the errors represent one or more spatially structured independent variables that are missing from the regression model (Ver Hoef et al. 2001, Wimberly et al. 2009). We evaluated spatial autocorrelation by comparing ordinary least-squares regression (OLS) and simultaneous autoregression (SAR) models (Wimberly et al. 2009). Analyses were carried out in program R ver. 2.12.2 (R Development Core Team). The spatial autoregressive models were fitted using spautolm function in the spdep spatial analysis package of R (Bivand 2002). We compared OLS and SAR model by evaluating the significance of the maximum likelihood autoregressive coefficient (λ). If λ was significant, we concluded that the SAR model was appropriate.

Results

Habitat

Our 750 plots sampled an area of 1154.5 ha in eastern Connecticut, compared with 451 USFS plots covering 30.3 ha for the entire state (Alerich 1999). Estimates of vegetation cover were within standard errors of USFS estimates, and standard errors showed that our data had greater precision and likely greater accuracy than those of USFS. Hence, our data appeared to approximate a random sample of available habitats. Moreover, average seasonal temperature and elevation latitude⁻¹ of weather stations showed a strong negative linear relationship in both summer ($r^2_{1,17} = 0.63$, $p = 0.000$) and winter ($r^2_{1,17} = 0.68$, $p = 0.000$). Habitat findings match descriptions of regional habitats reported by Dowhan and Craig (1976), Alerich (1999) and Stone et al. (1999). With the exception of NDVI, habitat variables underwent little change during the study period (Table 1).

Table 1. Mean (\pm SD) habitat measures for study sites in northeast and southeast Connecticut. Elevation latitude⁻¹: 7.50 = maximum – 0.55 = minimum; median normalized difference vegetative index (NDVI): 71.00 = maximum – 31.00 = minimum; forest type: (1) deciduous – (3) coniferous; moisture regime: xeric (1) – hydric (3); canopy cover: open (1) – closed (3); understory density: open (1) – dense (3); dbh: (1) < 15 cm – (3) > 45 cm; vegetation complexity: 5.60 maximum – 4.00 minimum.

	Northeast	Southeast
Elevation latitude ⁻¹	4.86 \pm 1.34	2.50 \pm 1.09
Median NDVI		
2001–2002	54.77 \pm 11.68	58.81 \pm 9.00
2004–2005	61.06 \pm 3.75	55.00 \pm 4.44
Forest type	1.58 \pm 0.41	1.21 \pm 0.27
Moisture regime	2.28 \pm 0.23	2.25 \pm 0.27
Canopy cover	2.65 \pm 0.20	2.65 \pm 0.16
Understory density	2.26 \pm 0.03	2.35 \pm 0.43
Diameter at breast height	2.00 \pm 0.05	2.00 \pm 0.09
Vegetation complexity	4.91 \pm 0.26	4.99 \pm 0.44
Vegetation type (%):		
Oak-dominated	36.41 \pm 1.07	57.22 \pm 1.05
Mixed deciduous	12.05 \pm 0.50	24.44 \pm 0.84
Conifer–hardwood	16.41 \pm 0.95	5.56 \pm 0.45
Pine–oak	15.38 \pm 0.74	4.72 \pm 0.39
Conifer	10.26 \pm 0.48	3.33 \pm 0.26
Mixed categories	5.64 \pm 0.41	4.72 \pm 0.34

Bird communities

The 50 survey routes covered about 180 km of forest habitat. Computations of richness and density are based on the 30926 individuals of 87 species recorded during the study. Summer communities were dominated in descending order by the ovenbird *Seiurus aurocapillus*, red-eyed vireo *Vireo olivaceus*, tufted titmouse *Baeolophus bicolor* and veery *Catharus fuscescens*, which alone comprised 39% of birds present. In contrast, winter communities were dominated by the golden-crowned kinglet *Regulus satrapa*, black-capped chickadee *Poecile atricapillus*, tufted titmouse and American goldfinch *Carduelis tristis*, which comprised 65% of birds present. Craig et al. (2003) report seasonal density estimates for individual species.

Not surprisingly, species richness (Table 2) significantly decreased from summer to winter ($F_{1,96} = 1483.9$, $p < 0.001$). There was a significant difference between regions ($F_{1,96} = 13.6$, $p < 0.001$) and a significant season-region interaction ($F_{1,96} = 19.2$, $p < 0.001$), because regional summer richness was nearly equal, whereas in winter it

Table 2. Mean (\pm SE) diversity values for study sites in northeastern and southeastern Connecticut.

	Northeastern Connecticut	Southeastern Connecticut
Species richness (species/transect):		
Summer	38.27 \pm 0.65	37.67 \pm 0.56
Winter	11.44 \pm 0.43	15.21 \pm 0.43
Community density (birds km ⁻²):		
Summer	175.52 \pm 2.65	180.63 \pm 2.58
Winter	48.98 \pm 3.07	74.19 \pm 4.60
Evenness		
Summer	1.06 \pm 0.02	1.04 \pm 0.02
Winter	0.97 \pm 0.03	1.00 \pm 0.03

was highest in the southeast. There was no significant difference between years ($F_{1,96} = 2.4$, $p = 0.13$) or in other interaction terms.

Community density estimates (Table 2) significantly decreased from summer to winter ($F_{1,96} = 974.2$, $p < 0.001$). There was a significant difference between regions ($F_{1,96} = 20.0$, $p < 0.001$), with northeastern Connecticut having lower densities, particularly in winter. There was also a significant difference between years ($F_{1,96} = 33.2$, $p < 0.001$) but not in any interaction terms.

Evenness (Table 2) was significantly lower in summer than winter during 2004–2006 (unequal variance $t_{91,43} = 4.2$, $p < 0.001$) but not 2001–2003 (unequal variance $t_{85,26} = 1.1$, $p = 0.278$). Though far more species were present in summer, especially the red-eyed vireo and ovenbird tended to dominate numerically so that they had reduced evenness compared with winter, when usually no species was overwhelmingly abundant (except during the winter of 2001–2002, when golden-crowned kinglets made a major winter incursion into northeastern Connecticut). Evenness showed little difference between regions (summer $F_{1,96} = 0.4$, $p = 0.539$, winter $F_{1,96} = 2.36$, $p = 0.131$), although they differed among years in winter (summer $F_{1,96} = 0.2$, $p = 0.627$, winter $F_{1,96} = 4.7$, $p = 0.036$), and showed a significant winter interaction between regions and years (summer $F_{1,96} = 0.3$, $p = 0.616$, winter $F_{1,96} = 12.4$, $p = 0.001$), with evenness increasing in northeastern Connecticut and decreasing in southeastern Connecticut from 2001–2002 to 2004–2005. The interaction was largely attributable to the winter, 2001–2002 incursion by golden-crowned kinglets.

Annual variation in species richness was significantly lower in summer ($29 \pm 1\%$) than winter ($44 \pm 1\%$; $F_{1,96} = 89.7$, $p < 0.001$). The difference between regions was non-significant ($F_{1,96} = 1.8$, $p = 0.18$), and no significant

interaction occurred between regions and seasons ($F_{1,96} = 1.0$, $p = 0.32$). In contrast, daily variation in richness was 16% in summer and 34% in winter, in both cases about a third less than annual variation. Annual variation in density was significantly lower in summer ($12 \pm 1\%$) than winter ($38 \pm 4\%$; $t_{98} = 6.7$, $p < 0.001$). The difference between regions was non-significant for both summer ($t_{48} = 0.6$, $p = 0.57$) and winter ($t_{48} = 0.5$, $p = 0.64$; inequality of seasonal variances precluded entering season into an analysis of variance). Daily variation in density also was roughly a third less than annual variation (summer: 5%, winter: 25%).

Diversity–habitat

No significant spatial autocorrelations existed for summer or winter species richness (Table 3). Hence, we used a regression model with elevation latitude^{-1} , moisture regime, canopy cover and dbh all entered into analyses of diversity vs habitat. A model that also contained vegetation type and vertical vegetation complexity best predicted summer species richness, although not greatly better than models with understory density or NDVI. A model with NDVI and understory density best predicted winter species richness, although again very similarly to models with vertical vegetation complexity (Table 4).

No significant spatial autocorrelation existed for summer density data (Table 3). A model with vegetation type and understory density best predicted summer community density, although almost identically to models with vertical vegetation complexity or NDVI (Table 4). In winter, a significant spatial autocorrelation existed for density, with year, dbh and elevation latitude^{-1} being added to the SAR model (Table 3).

Table 3. Best fitting models for simultaneous autoregression analyses of diversity–habitat analyses. VT = vegetation type, CC = canopy cover, UD = understory density, MR = moisture regime, DBH = tree diameter, EL = elevation latitude^{-1} . Evidence ratio compares the best fitting with the next best model.

	Model and significant factors	lambda	z	p	Delta AIC	Evidence ratio
Richness						
Summer	VT + CC	0.200		0.758	2.60	3.67
	VT		4.568	<0.001		
	CC		-2.965	0.003		
Winter	DBH + EL + Year	0.118		0.879	5.64	16.77
	DBH		-2.211	0.027		
	EL		-9.003	<0.001		
Density						
Summer	CC + MR + EL + Year	0.383		0.610	4.00	7.39
	CC		-3.240	0.001		
	MR		-2.685	0.007		
	EL		-2.297	0.022		
	Year		3.091	0.002		
Winter	VT + MR + DBH + EL + Year	-1.000		0.043	3.50	5.75
	VT		2.434	0.015		
	DBH		-2.147	0.032		
	EL		-7.387	<0.001		
	Year		2.779	0.005		
Evenness						
Summer	EL	-0.769		0.478	3.22	5.00
	EL		3.590	<0.001		
Winter	VT + Year	-0.362		0.618	8.35	65.11
	VT		3.058	0.002		
	Year		-2.415	0.016		

Table 4. Best fitting models, as determined by delta AIC with the next best model, for diversity–habitat analyses. VT = vegetation type, VC = vegetation complexity, CC = canopy cover, UD = understory density, MR = moisture regime, DBH = tree diameter, NDVI = normalized difference vegetative index, EL = elevation latitude⁻¹.

Model and significant factors		F _{1,92}	n ²	p	Delta AIC	Evidence ratio
Richness						
Summer	VT + MR + DBH + CC + EL + VC + Year				0.042	1.021
	VT	16.3	0.150	<0.001		
	CC	5.4	0.060	0.022		
Winter	MR + DBH + CC + EL + NDVI + UD + Year				-0.002	0.999
	EL	76.9	0.455	<0.001		
	NDVI	5.0	0.052	0.028		
Density						
Summer	VT + MR + DBH + CC + EL + UD + Year				-0.030	0.985
	MR	7.2	0.073	0.009		
	CC	9.0	0.089	0.004		
	Year	12.0	0.206	<0.000		
Evenness						
Summer	MR + DBH + CC + EL + NDVI + VC + Year				0.047	1.024
	EL	8.9	0.088	0.004		
	NDVI	5.5	0.056	0.021		
Winter	VT + MR + DBH + CC + EL + UD + Year				0.002	0.999
	VT	6.1	0.062	0.016		

No significant spatial autocorrelations existed for summer or winter evenness (Table 3). Summer evenness was best predicted by a model with NDVI and vertical vegetation complexity, which fit slightly better than models with understory or vegetation type. Winter evenness was best predicted by a model with vegetation type and understory density, which fit slightly better than models with vertical vegetation complexity (Table 4).

Summer forest bird richness modestly increased as vegetation shifted from oak-dominated through increasingly mixed conifer–hardwood, pine–oak and coniferous forests (Fig. 2, Table 4) and weakly increased with decreasing canopy cover. Winter richness showed a strong increase with decreasing elevation latitude (Fig. 3a) as well as a weak increase with increasing NDVI (Table 4). Summer density increased weakly with decreasing canopy cover and increasing soil moisture (Table 4). Winter density increased modestly with decreasing elevation latitude⁻¹ (Fig. 3b) and more weakly with decreasing dbh and increasing deciduous forest cover (Table 3). Evenness showed

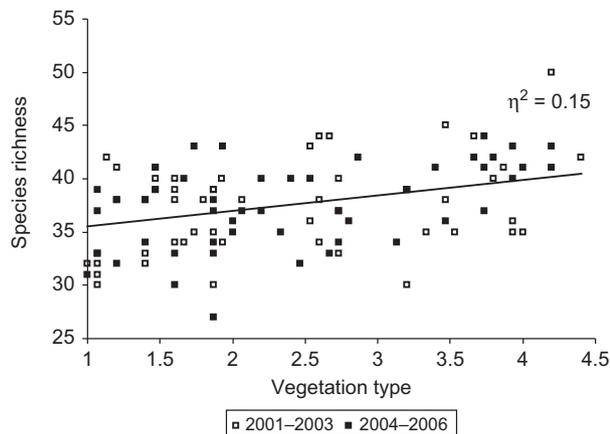


Figure 2. Summer species richness increases with vegetation types that exhibit greater conifer cover. 1 = oak-dominated, 2 = mixed deciduous, 3 = conifer-northern hardwood, 4 = pine–oak, 5 = coniferous.

a weak summer increase with increasing elevation latitude⁻¹ and decreasing NDVI. Moreover, evenness had a weak winter increase with increasingly coniferous vegetation (Table 4).

In evaluating predictions of the species–energy hypothesis, we found that log density and log richness (Fig. 4) positively co-varied with slopes from 0.28 (summer: n² = 0.18, F_{1,97} = 20.96, p < 0.001) to 0.57 (winter: n² = 0.52, F_{1,97} = 104.62, p < 0.001). Furthermore, with the exception of a weak positive relationship between mean summer individuals per species and elevation latitude⁻¹

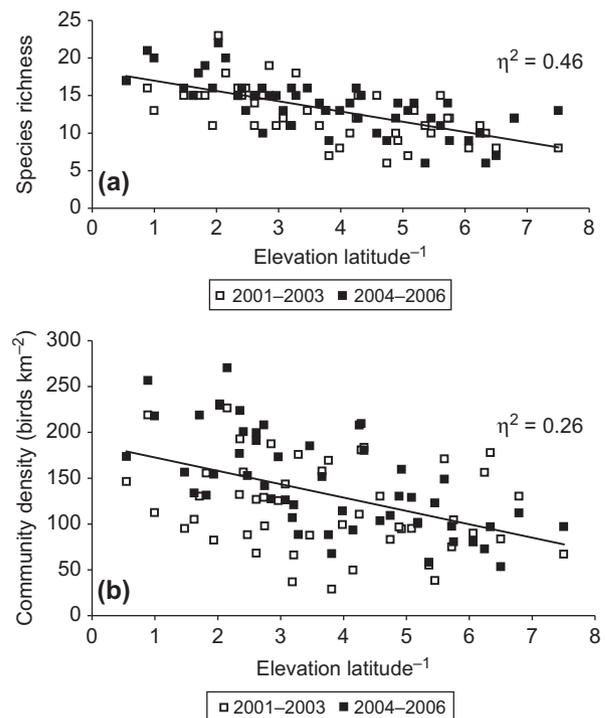


Figure 3. Species richness (a) and community density (b) increase with decreasing winter elevation latitude⁻¹.

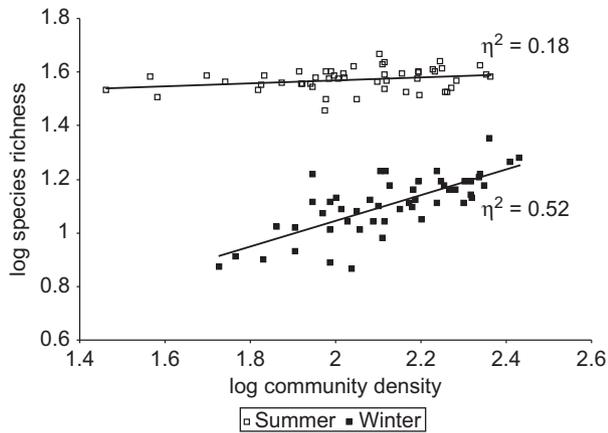


Figure 4. Species richness and community density are positively related.

($n^2 = 0.08$, $F_{1,96} = 7.84$, $p = 0.01$), we found little relationship between individuals/species and energy-related variables.

Discussion

This study demonstrates that forest bird communities showed geographic patterns in species richness, community density and evenness, with winter and summer patterns in these variables diverging. Richness and density tended to show the strongest pattern in winter, when a north-south increase in these appeared even in light of annual diversity fluctuations. Moreover, evenness increased from summer to winter. Relationships to habitat variables were: 1) summer richness and density were related, albeit rather weakly, to local forest conditions, particularly vegetation type and canopy cover, 2) winter richness and density were more strongly related to elevation latitude⁻¹ and again only weakly related to habitat, 3) evenness was weakly related particularly to elevation latitude⁻¹ in summer and vegetation type in winter.

That temperature plays the major role in winter variation in diversity was supported by winter richness and density decreasing with elevation latitude⁻¹, which in turn was strongly related to regional temperature. Indeed, no elevation-related habitat changes other than temperature were obvious over the range we considered (0–400 m). The low energy winter environment appears to make the availability of thermal kinetic energy a greater influence on diversity when it may reduce metabolic costs. Ongoing investigations in much more mountainous northwestern Connecticut, where we have made among the lowest counts yet for winter populations (Craig unpubl.), further support these findings. Bock and Lepthein (1974) and Root (1988) found similar winter diversity–temperature patterns at the continental scale.

Our data additionally indicated that low elevation forests, which reach their greatest extent toward the coast, assume particular importance as winter reservoirs for regional bird communities. Hence, conservationists must

take this fact into account when devising regional open space conservation plans. Doherty and Grubb (2000) also note that winter populations appear to play an important role in determining the distribution of permanent resident species.

In contrast to the role of energy in structuring winter communities, our data showed only a weak tendency for either potential or kinetic energy to influence summer diversity. The positive correlation between NDVI and proportionate cover of deciduous forest species suggests that, at the scale of this investigation, NDVI values may be determined more by forest appearance rather than by primary productivity. The modestly better fit of a model with vegetation rather than NDVI in accounting for variance in summer richness further indicates that vegetation was the variable that exerted direct influence on richness. The positive summer relationship of evenness with elevation latitude⁻¹ did, however, appear to be driven by reduced community dominance by ovenbirds and red-eyed vireos and with species of moderate abundance at sites with greater elevation latitude⁻¹ (Craig et al. 2003, unpubl.).

Evans et al. (2006) similarly found that, at the continental scale, temperature most closely related to winter diversity and energy in general more closely related to winter rather than summer diversity. In contrast, in continental North America, Hurlbert and Haskell (2003) found a positive relationship between avian richness and NDVI in winter and summer and, in eastern North America, Hawkins (2004) found a strong positive relationship between summer productivity and bird species richness.

The lack of a clear north-south trend in summer richness, a finding counter to the eastern North American north-south decrease in summer richness (Short 1979), may explain bird richness and density being generally high throughout the Northeast (Short 1979) due to a hypothesized concentrated pulse of production in this highly seasonal region (Rabenold 1979), which Schmidt and Ostfeld (2008) concur is of key importance in structuring communities. Hurlbert and Haskell (2003) further point out that summer productivity exhibits little latitudinal gradient in North America.

Among habitat variables, only vegetation type was related to diversity and then weakly, with effects most noticeable in summer. This provides only limited support for habitat explaining the bulk of remaining variation in diversity. The significant association of summer richness with increasing conifer cover is consistent, however, with O'Connor et al.'s (1996) finding that, at the continental scale, breeding bird species were particularly rich in conifer-northern hardwood forests. Greater forest openness, as is achieved through selective logging, also appeared to exert some positive influence on summer diversity. Weakly greater evenness in winter in increasingly more coniferous cover indicates that such habitats tend to exhibit conditions that reduce numerical dominance by few species and promote higher populations of other species.

Despite the weakness of habitat in predicting diversity parameters, they showed numerous significant relationships at the level of individual species' distributions (Craig et al. 2003, unpubl.), which suggests that the species level

is a more useful one for seeking bird-habitat relationships at regional scales. Our findings are consistent with Hurlbert and Haskell's (2003) continental scale finding that habitat exhibited comparatively weak effects on avian richness, but contrast with Pearson's (1993) regional level findings for Georgia, where habitat played a major role in influencing winter bird diversity.

That seasonal shifts in diversity provide additional clues about how environmental variables shape geographic patterns in communities was supported by our observation that seasonal patterns in diversity were related far more to temperature-related variables in winter than summer. Summer energy indeed appears not to be limiting to bird communities even over the much broader geographic region of the northeastern United States and southern maritime Canada (Short 1979, O'Connor et al. 1996).

The importance of scale for understanding community patterns has long been recognized (Wiens 1989), with Rahbek (2005) and Field et al. (2008) emphasizing that the type of pattern uncovered can be related to the scale of observation. Several of the geographic patterns we observed, notably the winter relationships of richness, density and thermal energy, are consistent with patterns also observed at the continental scale. Hence, this regional view provides a finer-grained view of the origin of the continental pattern. However, our finding of a general lack of strong habitat-diversity relationships suggests that habitat differences at this level are for the most part insufficiently variable to yield detectable community patterns.

Evidence supporting the species-energy hypothesis (Currie et al. 2004) was limited and comes primarily from winter: 1) density and energy-related variables positively co-vary most strongly in winter, although a weak summer relationship occurs as well, 2) density and richness co-vary with a slope similar to the predicted value of 0.26 in summer but with a slope double that in winter, 3) richness and energy-related variables positively co-vary only in winter, 4) contrary to prediction, the strength of the winter richness-energy relationship was greater than that for density-energy, the richness-density relationship was greatest of all, and no significant relationships occurred in summer, 5) winter changes in energy appeared to lead to changes in numbers and species in that more individuals and species occurred at lower elevation latitude^{-1} , but only a weak relationship was present in summer, 6) contrary to prediction, except for a weak positive relationship between mean summer individuals/species and elevation latitude^{-1} , we found no association between individuals per species and energy-related variables. Hurlbert (2004) similarly found that species-energy theory was insufficient to account for observed continental patterns of species richness.

Higher evenness observed in winter vs summer contradicts expectations that the lower energy, less predictable winter environment should have lower evenness (Tramer 1969). Greater richness, such as is found in summer appears, in fact, unrelated or negatively related to evenness in birds (Bock et al. 2007). Rotenberry et al. (1979) also found no support for this prediction, instead finding little seasonal periodicity in evenness. Despite this finding, our observation of greater daily and annual variation in winter vs. summer richness, density and evenness was consistent

with winter environments being less predictable than those of summer.

Even with the inclusion of temperature and habitat effects, nearly half the variation in winter richness as well as most summer variation was still unexplained. Root (1988) similarly found that 40% of wintering bird species had northern range limits not associated with temperature, although Hurlbert and Haskell (2003) found 61% of continental scale summer richness explained by temperature-related variables. Greater demonstrated variability in winter data certainly contributes to such diversity variance during a season when species are less confined to territories and may move nomadically in search of food (Grubb and Pravosudov 1994). However, the comparatively low variance in summer data suggests that still other unquantified variables may contribute to summer diversity patterns. Moreover, as predicted by neutral models of biodiversity (Hubbell 2001), a large stochastic component to diversity also may exist at the scale of this study. Variables like recent historical events, including weather-related population declines, site fidelity effects, disease outbreaks and continental shifts in populations and distributions that occur for reasons unrelated to local habitats (Wiens 1989, Rosenzweig 1995) may contribute to apparent stochasticity in regional communities.

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Appendix 1

Figures showing the strength of the relationship between elevation latitude⁻¹ and regional temperature for summer and winter.

