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Biodiversity Dynamics of Forest Birds in Fragmented Landscapes: A Multidimensional Approach for Ecology and Conservation

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Approach for Ecology and Conservation

Brian Thomas Klingbeil, PhD

University of Connecticut, 2015

Anthropogenic modification of landscapes continues to be one of the greatest threats to biodiversity. As human populations grow and demands for natural resources and land increase, landscapes will experience intensified alteration and fragmentation, with potentially dramatic consequences for biodiversity. Consequently, development of appropriate conservation policies requires effective monitoring programs as well as an understanding of how communities are affected by human-modified landscapes. To address this, I explored how multiple dimensions of temperate forest bird biodiversity (taxonomic, functional, and phylogenetic) respond to human-modified landscapes by investigating the relative importance of habitat area, habitat configuration, and matrix heterogeneity. I evaluated relationships between biodiversity and landscape pattern at multiple spatial scales and considered relationships at the community and metacommunity levels of organization. Additionally, I used patterns of phylogenetic relatedness and functional similarity among co-existing species to explore mechanisms underlying the assembly of ecological communities. This approach is used to investigate relative importance of deterministic factors (e.g., environmental conditions and interspecific interactions) versus stochastic processes (e.g., importance of chance colonization, random extinction, and ecological drift) for determining local species composition. Lastly, I evaluated the efficacy of Autonomous Recording Units as an alternative to traditional point counts conducted by human observers as they are a potential cost-effective data collection technique that could increase the spatial and temporal range of observations while expanding the number and diversity of studied organisms.

Biodiversity Dynamics of Forest Birds in Fragmented Landscapes: A Multidimensional

Approach for Ecology and Conservation

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A Dissertation

Submitted in Partial Fulfillment of the

Requirements for the Degree of Doctor of Philosophy

at the

University of Connecticut

2015

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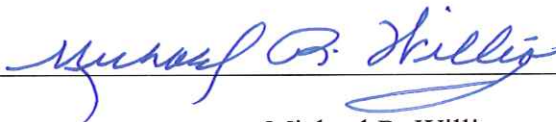
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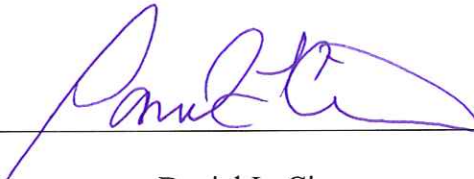
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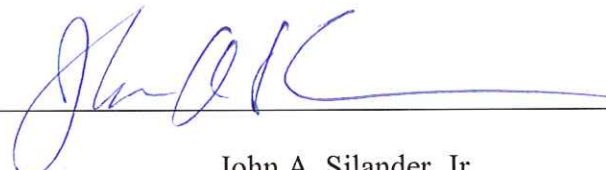
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CHAPTER ONE

BIRD BIODIVERSITY ASSESSMENTS IN TEMPERATE FOREST: THE VALUE OF POINT COUNT VERSUS ACOUSTIC MONITORING PROTOCOLS

Abstract

Effective monitoring programs for biodiversity are needed to assess population trends and evaluate the consequences of management. This is particularly true for interior forest and other areas of low human population density that are frequently under-sampled compared to other habitats. Autonomous Recording Units (ARUs) have been proposed as a supplement or alternative to point counts made by human observers to enhance monitoring efforts. We employed two strategies (i.e., simultaneous-collection and same-season) to compare point count and ARU methods for quantifying species richness and composition of birds in temperate interior forests. The simultaneous-collection strategy compares surveys by ARUs and point counts, with methods matched in time, location, and survey duration such that the person and machine simultaneously collect data. The same-season strategy compares surveys from ARUs and point counts conducted at the same locations throughout the breeding season, but methods differ in the number, duration, and frequency of surveys. Estimates of richness (but not species composition) differed between methods; however, the nature of the relationship was dependent on the assessment strategy. Estimates of richness from point counts were greater than estimates from ARUs in the simultaneous-collection strategy. Woodpeckers in particular, were less frequently identified from ARUs than point counts with this strategy. Conversely, estimates of richness were lower from point counts than ARUs in the same-season strategy. Moreover, in the same-season strategy, ARUs detected the occurrence of passerines at a higher frequency than did point counts. If single visits to sites or short-term monitoring are the goal, point counts will likely perform better than ARUs, especially if species are rare or vocalize infrequently. However, if seasonal or annual monitoring of sites is the goal, ARUs offer a viable alternative to standard point-count methods, especially in the context of large-scale or long-term monitoring of temperate forest birds.

Introduction

Standardized long-term programs for monitoring biodiversity that span large geographic areas are needed to determine species responses to global change and to inform conservation efforts. Effective monitoring programs identify changes in species distributions, assess population trends and evaluate the efficacy of management practices. In this context, birds represent one of the most well studied groups of wildlife, with a history of long-term studies, including a number of large-scale monitoring programs (e.g., Christmas Birds Count, North American Breeding Bird Survey; BBS). Nonetheless, considerable gaps exist in our knowledge of the current status and recent population trends of forest birds (Sauer, Fallon & Johnson 2003; Blancher et al. 2009; Francis, Blancher & Phoenix 2009).

Point-count surveys, where an observer records all birds seen or heard at a point location for a specified time (Ralph, Sauer & Droege 1995), are one of the most common survey methods for long-term avian studies of landbirds (Rosenstock et al. 2002). Interior forest and other areas of low human population density are frequently under-sampled in such large-scale monitoring programs because surveys are often conducted by volunteers (Francis, Blancher & Phoenix 2009). Surveys by volunteers are often employed because they are cost-effective, and the involvement of non-scientists in science (i.e., citizen science) enhances public appreciation of biodiversity and conservation (Dickinson et al. 2012; Price & Lee 2013). Nonetheless, volunteer-based surveys are not without drawbacks, including data quality concerns (e.g., variation in identification accuracy related to age, education, collection skills, and length of participation in the program; Dickinson, Zuckerberg & Bonter 2010). The use of Autonomous Recording Units (ARUs) to survey birds and other taxa has been suggested as a supplement to enhance monitoring efforts, especially in remote or inaccessible areas, like interior forest (Haselmayer and Quinn 2000; Hobson et al. 2002; Acevedo and

Villanueva-Rivera 2006; Hutto and Stutzman 2009; Campbell and Francis 2011; Venier et al. 2011; Tegeler, Morrison & Szewczak 2012; Furnas and Callas 2015).

ARUs reduce several types of bias associated with point-count surveys and facilitate consistent data collection among surveys and sites and have been found to improve detection of species and estimation of species richness. By using ARUs, biases and problems associated with monitoring can be reduced because: (1) data collection does not depend on observer skill level, reducing observer bias; (2) recorders can be left unattended to regularly record vocalizations for long periods of time, reducing temporal restrictions (Hobson et al. 2002; Tegeler, Morrison & Szewczak 2012); (3) multiple sites can be monitored simultaneously, eliminating temporal bias (Venier et al. 2011; Tegeler, Morrison & Szewczak 2012); (4) data collection provides permanent records of vocalizations that can be played repeatedly and, if necessary, independently verified by multiple experts, reducing identification errors (Rempel et al. 2005); and (5) human observers are absent during recordings, eliminating attractions or deterrents for some bird species, reducing biases in detectability (Bye, Robel & Kemp 2001). Furthermore, ARUs have the potential to significantly reduce the number of trained observers that need to be sent to the field, freeing time and personnel resources during field seasons that could be spent surveying for species undetectable by acoustic approaches or accomplishing other scientific or management goals.

Like any method, ARUs suffer from a number of shortcomings. They are subject to malfunction or breakage, and their performance may be affected by adverse environmental conditions for extended periods of time (e.g., microphones can become waterlogged reducing sound quality). Most importantly, ARUs lack the visual component of traditional point count surveys, making detection more difficult for vocally cryptic species and reducing reliability of estimates for species abundance. As a result, ARUs are often suggested as a supplement to point counts, but have

not been embraced as a viable alternative to be used in place of them (e.g., Venier et al. 2011; Tegeler, Morrison & Szewczak 2012; Furnas and Callas 2015).

Most previous comparisons between point counts and ARUs have generally relied on assessments when point counts conducted by a trained observer and audio recordings made by a single ARU are paired in time and space (e.g., Haselmayer and Quinn 2000; Hobson et al. 2002; Acevedo and Villanueva-Rivera 2006; Celis-Murillo, Deppe & Allen 2009; Hutto and Stutzman 2009; but see Tegeler, Morrison & Szewczak 2012). Additional studies have made comparisons between an observer and multiple ARU models to evaluate differences between equipment types (Venier et al. 2011; Rempel et al 2013). Such studies are important for evaluating new technologies and provide information to conservation managers in a rapidly developing field (with many new equipment options). However, these studies may not provide the best assessment of ARUs as a monitoring alternative because comparisons fail to capitalize on one of the primary assets of ARUs: repeated unattended surveys over an extended time period. Consequently, we use two assessment strategies (Table 1) to identify if differences exist in the efficacy of point count and ARU methods with respect to estimating species richness and composition of bird communities in interior forest.

The simultaneous-collection strategy compares surveys by ARUs and point counts, for which methods are exactly matched in time, location, and survey duration. The simultaneous-collection strategy is similar to previous studies that compare point counts and ARUs in that an observer stands next to an ARU, and both simultaneously collect data. Consequently, results from this strategy can be compared to previous studies to determine if the performance of ARUs in temperate interior forest is similar to other habitats (e.g., burned conifer forest-riparian gradient-Hutto and Stutzman 2009; boreal forest-Venier et al 2011; alpine meadows-Tegeler, Morrison & Szewczak 2012; BBS survey route-Rempel et al. 2013). The same-season strategy compares

surveys from ARUs and point counts conducted at the same locations throughout the breeding season, but methods differ in the number, duration, and frequency of surveys (but total sample effort is equal). This comparison evaluates if a substantially higher number of days sampled by ARUs corresponds to different estimates of species richness and composition than do point counts, without confounding estimates with the effects of increased effort. Holding total sample effort (i.e., number of survey minutes) constant between methods represents a conservative estimate of the utility of ARUs, because they can record for extended time (hours per day and number of days) without additional effort or cost.

Methods

Research was conducted in eastern deciduous and coniferous forests of Connecticut, USA, excluding coastal areas. Currently, 60% of land cover in the state is forest, dominated by oak-hickory and northern hardwood forest types, although pine forests are common along the northern border of the state (Butler et al., 2012). Like many areas, Connecticut has experienced profound anthropogenic alteration of landscapes (Drummond & Loveland 2010), so that forest currently exists as patches or fragmented parcels of various sizes and ages, interwoven with various types of human-altered land covers (i.e., urban and suburban developments, agricultural fields, road networks, and power line rights of way; Figure 1A).

Twenty sites were established on public land within interior forest patches of various sizes and shapes. Roughly one-third of the forests in the lower 48 states are on public lands, supporting 45% of the U.S. distribution of 149 obligate forest bird species, and representing the largest unfragmented forests in many regions (NABCI, 2011). Site locations were selected by processing a 2010 land cover map (CLEAR, 2010b) with the Landscape Fragmentation Tool (LFT v2.0; CLEAR 2010a) add-on to Arc Toolbox to identify suitable sites with sufficient area of interior forest (i.e.,

forest pixels located at least 100 m from non-forest pixels) to contain 5 plots, each containing an ARU. Within each site, plots were spaced at least 250 m apart to avoid overlap in the sampled acoustic environment (Figure 1B). Sites were at least 10 km from other sites and from Long Island Sound. Prospective sites were visited and ground-truthed to evaluate accuracy of land cover maps and to ensure accessibility.

Birds were surveyed via both point counts (Ralph, Sauer & Droege 1995) and recordings from ARUs. For point counts, each plot within each site (Figure 1B) was visited on two occasions during the breeding season (May 21- August 1, 2012) and sampled with a 10 minute survey. Surveys were conducted within the first 4 hours of local sunrise, and all species heard or seen were recorded as present. In addition to point counts, each of the 5 plots within a site contained an ARU (Wildlife Acoustics Song Meter Sm2+) and was surveyed for 4 hours on a daily basis, beginning at local sunrise during the same time period as point counts. ARUs were equipped with an omnidirectional microphone (flat frequency response between 20 Hz and 20 kHz) and signals were sampled at 24,000 Hz. ARUs were attached to trees at a height of 2 m with microphones pointing horizontally. Recordings were analyzed and spectrograms were viewed with Song Scope software (Wildlife Acoustics Inc.). To assist in identification of species, field recordings were compared with sonograms of previously identified species obtained from the Macaulay Library at the Cornell Lab of Ornithology. We focus our analyses on two orders, Passeriformes and Piciformes that are well represented and comprise the majority of species in temperate interior forest. We followed the nomenclature and taxonomic recommendations of the North American Classification Committee of the American Ornithologists' Union (Chesser et al., 2013).

Two assessment strategies were used to compare forest bird richness and composition between ARU and point count methods (Table 1). In the same-season strategy, point count data

were compared to a random subset of recordings collected throughout the breeding season. For each site, recordings from 5 ARUs were sampled randomly by selecting a plot and 2-minute time period on each of 50 days during the breeding season, exclusive of the 2 days when point counts were conducted at particular sites to eliminate biases associated with observer presence. This approach results in equal sample effort in recordings and point count surveys for each site (Table 1). This acoustic sampling strategy represents a compromise between maximizing the number of days sampled, while including a sufficient amount of time per day to capture multiple vocalizations of a species.

In the simultaneous-collection strategy, we evaluate if the same species are identified by point counts and ARUs when paired in time, location, duration, and observer (Table 1). Three plots from each site were selected randomly and a 10 minute recording that corresponded to a 10 minute point count conducted by the same observer was selected (i.e., 60 samples from each method paired in time, location, and observer). Plots within sites were randomly selected when possible but some sites did not have more than three paired recordings because not all ARUs were recording at the time of point counts due to weather, animal induced damage, or equipment malfunction.

To determine if the local environment influences the efficacy of methods, the habitat surrounding ARUs and point count locations was quantified. At each plot, five habitat characteristics were estimated. Elevation was determined with a handheld GPS receiver. Slope was estimated on a scale of 0-3, with 0 indicating no slope and 3 indicating a very steep slope (> 45 degrees). Canopy openness was estimated with a concave spherical densiometer at the center of a plot and at a distance of 5 m in each of the 4 cardinal directions. Understory density was estimated on a scale from 0 to 5, with 0 indicative of completely open understory commonly associated with old growth coniferous forest and with 5 indicative of very dense understory that is commonly

associated with dense patches of mountain laurel (*Kalmia latifolia*) or invasive Japanese barberry (*Berberis thunbergii*). Percent ground cover of leaves (including pine needles) and herbs was estimated within a 5 m radius circle at the center of each plot.

We evaluated if differences in species richness or in species composition exist between ARU and point count methods, and determined if differences arise as a consequence of assessment strategy. We held total survey effort (i.e., number of minutes) constant in comparisons of data between methods for each strategy. We used a paired t-tests to assess if differences in estimates of richness exist between approaches in the same-season strategy. For comparisons based on the simultaneous-collection strategy, we partitioned site richness (gamma) into within (alpha) and among (beta) plot richness. Alpha (α) is the average richness of plots within a site. Beta (β) is the average number of compartments (i.e. groups of plots with similar species composition that are distinct from other such groups of plots) and reflects the heterogeneity of a site (from the perspective of the sampled birds). Gamma (γ) is the cumulative richness of a site (pooling all three plots). We used a multiplicative approach ($\alpha\beta = \gamma$) to determine partitions (Whitaker 1972). Paired t-tests quantified differences in richness between methods at each of these 3 levels.

The frequency of occurrence of each species was used to characterize species composition of the region (interior forest of Connecticut) separately for each combination of method and strategy. Frequency of occurrence in the simultaneous-collection strategy was determined by counting the number plots a species was observed in ($n = 60$) via ARUs or point counts. Frequency of occurrence in the same-season strategy was determined by counting the number of times a species was observed at sites ($n = 20$) via ARUs or point counts. Estimates of regional species composition derived from point counts and ARUs were compared with chi-square randomization tests separately for each strategy. In addition, we evaluated if a taxonomic bias existed between

methods by comparing the frequency of occurrence of birds in the orders Piciformes and Passeriformes separately with paired t-tests for each strategy.

Lastly, we determined if differences in species composition between point counts and ARUs were related to habitat characteristics of forest interior plots. We used the additive inverse of Jaccard's similarity coefficient (J) to estimate dissimilarity in species composition between methods in the simultaneous collection strategy. Spearman rank correlations evaluated associations between habitat characteristics and species dissimilarity.

Results

Forty-one species were identified with point counts and thirty-nine species were identified with ARUs (Table 2). Five species (Yellow-bellied Sapsucker, Great Crested Flycatcher, Yellow-throated Vireo, Hooded warbler, and Canada warbler) were identified only with point counts, whereas three species (Common Raven, Winter Wren, and Gray Catbird) were identified only with ARUs.

Simultaneous-collection strategy. Alpha or beta components of richness (Table 3) were not significantly different between methods. In contrast, gamma was higher for point counts than ARUs (Table 4). Regional species composition did not differ between survey types ($X^2 = 13.11$, $p = 1.0$). However, a significant difference existed between methods in the frequency of occurrence of birds in Piciformes (Table 5). Dissimilarity (1-J) of species identified by surveys and recordings varied from 0.0 to 0.5 (Table 3), and was associated negatively with elevation ($P = -0.511$, $p = 0.021$; Table 6).

Same-season strategy. Compared to point counts, ARUs result in greater estimates of richness at sites (Paired t-test: $t = -2.7979$, $p = 0.012$). Nevertheless, point count and ARU methods resulted in similar estimates of species richness in the region (i.e., 38 species by ARUs and 40

species by point counts). Species composition was similar between methods ($X^2 = 46.26$, $p = 0.999$). Although both methods produced similar estimates of regional species composition, at the site level, passerines were more frequently detected by ARUs than by point counts (Table 5).

Discussion

In general, ARU and point count methods provided similar estimates of species composition for the region and similar estimates of richness for individual plots within sites. Conversely, methods differed in estimates of richness at the site level and relationships were dependent on assessment strategy. Comparison of results between assessment strategies provides insight into why other studies have found that ARUs can produce lower, similar, or higher estimates of species richness compared to point counts (e.g., Haselmayer and Quinn 2000; Hobson et al. 2002; Acevedo and Villanueva-Rivera 2006; Celis-Murillo, Deppe & Allen 2009; Hutto and Stutzman 2009).

Same-season strategy. ARUs offer a viable alternative to standard point-count methods, especially in the context of large-scale or long-term avian species richness surveys of temperate forest birds. We found no difference in species composition of the regional community detected by point counts or ARUs. Furthermore, even when sample effort was held constant between protocols (representing a conservative estimate of a potential ARU sampling protocol) ARUs identified a greater number of species at sites than point count surveys. This is likely because each site was sampled on 50 different days with ARUs rather than only 2 different days with point counts. This is a clear advantage of ARU methods. Repeated visits to sites over the course of the breeding season should sample the same community of birds because the majority of forest bird species are territorial and breeding is relatively synchronous. Consequently, it is likely that higher richness estimates based on additional surveys with ARUs represent improved estimates, rather than changes in space use by species.

Passerines were more frequently identified by ARUs than by point counts in the same-season strategy. This may reflect temporal constraints associated with traditional point count surveys. The optimal period for detecting species is when they are most vocal, usually when they are establishing and defending breeding territories (Anderson, Ohmart & Rice J 1981; Best 1981; Ralph 1981; Skirven 1981). Hence, typical point count surveys of breeding birds in this region begin in mid-May and end in July. However, three problems may arise with this standard protocol. First, some non-migratory or short-distance migratory species may be missed or underestimated by surveys that target migratory species during such a narrow temporal window. This is possible because some residents or short-distant migrants establish territories and breed before long distance migrants arrive, hence vocalizations may have significantly decreased by the time traditional surveys begin (Hejl and Thompson 2000). Second, if a small number of observers are tasked with conducting point counts for a region, sites will rarely be sampled more than a few times in the period when migrants are most vocal, and weeks may pass between visits to sites, potentially missing the most vocal periods for some species at some sites. This problem is only exacerbated if monitoring programs increase in geographic area or numbers of trained observers are reduced because of budget constraints. Third, as effects of climate change become more pronounced, regional variation in arrival times of migrants may increase, with some species arriving earlier and others delaying migration (Walther et al. 2002; Jenni and Kery 2003; Van Buskirk, Mulvihill & Leberman 2009), further complicating the planning of point count surveys. ARUs do not suffer from the same constraints as point counts, since they can be placed at multiple sites to record simultaneously for extended periods. Furthermore, if ARUs are in place well before migrants historically arrive, they will be able to capture vocalizations from residents that may breed earlier in

the season, and they can be used to identify if particular species are returning from their wintering grounds earlier in the season in response to changes in climate and altered phenology.

Simultaneous-collection strategy. Fewer species were identified from ARUs than from point counts when data were collected simultaneously. A potential explanation for this difference reflects a common criticism of ARUs: they do not allow visual cues (except for spectrograms) to aide in species identification, representing a shortcoming of audio recording devices. Woodpeckers (Piciformes) in particular, were less frequently identified from ARUs than from point counts.

Compared to other groups of birds, little research has been conducted on acoustic communication in woodpeckers (Stark, Dodenhoff & Johnson 1981). The functions of the majority of acoustic signals used by woodpeckers are not fully understood, and variation in their acoustic behavior has received little attention (Tremain, Swiston & Mennill 2008). Woodpeckers typically have larger territories and vocalize less frequently compared to most song birds (Blackburn, Lawton & Gaston 1998; Farnsworth et al. 2002). Moreover, it is unknown if the presence of an observer affects the frequency of acoustic signals by these birds (i.e., warning calls or drumming). Only songs and calls were used to identify bird species from ARU recordings, so even if drumming was recorded (which it frequently was) it was not used for identification. Conversely, when in the field, drumming could be used to direct an observer's attention to facilitate visual identification of the birds, even if the individual was not otherwise vocalizing. This increases the likelihood of detection and could represent a bias in species detection frequencies between methods for woodpeckers. Indeed, when comparing single-visit recordings with field observations, the latter are likely more effective at identifying rarely heard species, whereas recordings would be more beneficial in areas of high species richness when many birds are calling, and repeated listening and viewing of spectrograms can be employed to identify species with overlapping vocalizations (Hasselmayr and Quinn 2000;

Hutto and Stutzman 2009). Importantly, when data collected from ARUs and point counts were compared for the full season (i.e., same-season strategy), no significant difference existed in the frequency of occurrence of woodpeckers. Ultimately, the advantage of being able to sample more frequently or over a longer time frame with ARUs may offset the lack of visual detection associated with ARUs, making ARUs a viable solution to detecting species that vocalize less frequently.

Differences in the number of species detected between paired point counts and ARUs may also reflect variation among sites within which surveys were conducted. We found no differences in estimates of alpha or beta diversity between surveys and recordings, but we did identify significant difference between estimates of gamma diversity. This intimates that recordings and surveys were equally efficient in capturing variation in richness that manifests at the plot level and to account for microhabitat variation within sites. Conversely, variation among sites had the greatest influence on the ability of recordings to estimate richness when compared with field observations, at least over the short-term. This is critically important to consider from a monitoring perspective, because it suggests that differences between field observations and recordings may be habitat-specific, and that ARUs may not perform equally in all environments. Accordingly, if study designs incorporate multiple habitat types, preliminary analyses should be conducted to determine if biases exist between habitats included in the program.

Dissimilarity in the identity of species between field surveys and recordings was negatively related to elevation, indicating that lower elevation sites generally shared the lowest proportion of species between surveys and recordings. However, mean elevation of plots only ranged from 96.5 – 389.33 m above sea level, thus it is unlikely that changes in environmental characteristics (i.e. temperature, solar irradiation, precipitation, productivity, or habitat type) often associated with changes in elevation affected these patterns. Other general site characteristics (e.g., canopy

openness or understory density) that might be expected to play a role in interfering with the audio or visual components of surveys were unrelated to differences between recordings and field observations, suggesting that unmeasured aspects of forest structure or forest community composition that co-vary with elevation in this system may influence bird identification (e.g., diversity or richness of trees, vertical heterogeneity of forests). Alternatively, as evidenced by fewer detections of woodpeckers with ARU methods in the simultaneous-collection strategy, not all species have equal detection probabilities. Consequently, it is possible that sites at lower elevations contain a greater number of species with lower acoustic detection probabilities as a result of species-specific elevational associations.

Conclusions

ARUs provide data on the presence of birds that are comparable to that obtained by field observers. Our results support previous studies in other habitats (Haselmayer and Quinn 2000; Hobson et al. 2000; Campbell and Francis 2011; Tegeler, Morrison & Szewczak 2012) in suggesting that ARUs can be used as a viable alternative to skilled field observers to collect data. However, the full benefit of ARUs will only be realized when they are deployed for an extended duration, rather than a single visit to sites. If single visits to sites or short-term monitoring are the goal, point counts will likely perform better than ARUs, especially if species are rare, or vocalize infrequently. Conversely, if long-term or large-scale monitoring programs are to provide useful estimates to facilitate adaptive management in the face of changing climate and habitats, efforts need to be made to reduce biases and constraints associated with traditional sampling approaches. ARUs do not suffer from the same constraints or biases as do point counts (although they do suffer from different biases). When surveys are executed across remote or large geographic areas, use of ARUs can be logistically and financially more efficient than point counts, creating a permanent record that can

easily be archived and shared, and represent important tools for use by biodiversity scientists, conservation biologists or land managers.

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Table 1. Methodological details of two assessment strategies used to compare point count and ARU methods for estimating richness and composition of temperate interior forest bird communities.

Method details	Simultaneous-collection		Same-season	
	ARU	Point count	ARU	Point count
Surveys per site	3	3	50	10
Survey duration	10 minutes	10 minutes	2 minutes	10 minutes
Total number of surveys	60	60	1000	200
Survey effort	600 minutes	600 minutes	2000 minutes	2000 minutes

Table 2. Frequency of occurrence of birds in temperate interior forest identified with two assessment strategies (i.e., simultaneous-collection and same-season). Methodological details of each assessment strategy are listed in Table 1 and described in the text. A dash indicates the species was not identified with a particular strategy.

Order	Family	Scientific name	Common name	Simultaneous-collection		Same-season	
				Point count	ARU	Point count	ARU
Piciformes	Picidae	<i>Melanerpes erythrocephalus</i>	Red-headed Woodpecker	0.02	0.00	0.10	0.05
Piciformes	Picidae	<i>Melanerpes carolinus</i>	Red-bellied Woodpecker	0.07	0.07	0.45	0.40
Piciformes	Picidae	<i>Sphyrapicus varius</i>	Yellow-bellied Sapsucker	0.02	0.00	0.05	0.00
Piciformes	Picidae	<i>Picoides pubescens</i>	Downy Woodpecker	0.02	0.00	0.25	0.50
Piciformes	Picidae	<i>Picoides villosus</i>	Hairy Woodpecker	0.05	0.03	0.55	0.40
Piciformes	Picidae	<i>Colaptes auratus</i>	Northern Flicker	0.02	0.00	0.40	0.15
Piciformes	Picidae	<i>Dryocopus pileatus</i>	Pileated Woodpecker	0.02	0.00	0.15	0.30
Passeriformes	Tyrannidae	<i>Contopus virens</i>	Eastern Wood-pewee	0.38	0.28	0.90	0.95
Passeriformes	Tyrannidae	<i>Sayornis phoebe</i>	Eastern Phoebe	0.02	0.02	0.15	0.05
Passeriformes	Tyrannidae	<i>Myiarchus crinitus</i>	Great Crested Flycatcher	-	-	0.05	0.00
Passeriformes	Vireonidae	<i>Vireo flavifrons</i>	Yellow-throated Vireo	-	-	0.25	0.00
Passeriformes	Vireonidae	<i>Vireo olivaceus</i>	Red-eyed Vireo	0.55	0.68	1.00	1.00
Passeriformes	Corvidae	<i>Cyanocitta cristata</i>	Blue Jay	0.25	0.23	0.85	0.85
Passeriformes	Corvidae	<i>Corvus brachyrhynchos</i>	American Crow	0.03	0.07	0.40	0.50
Passeriformes	Corvidae	<i>Corvus corax</i>	Common Raven	-	-	0.00	0.05
Passeriformes	Paridae	<i>Baeolophus bicolor</i>	Tufted Titmouse	0.27	0.30	0.75	0.95
Passeriformes	Paridae	<i>Poecile atricapillus</i>	Black-capped Chickadee	0.13	0.17	0.90	0.90
Passeriformes	Sittidae	<i>Sitta canadensis</i>	Red-breasted Nuthatch	0.03	0.02	0.15	0.05
Passeriformes	Sittidae	<i>Sitta carolinensis</i>	White-breasted Nuthatch	0.13	0.17	0.90	0.95
Passeriformes	Troglodytidae	<i>Troglodytes heimalis</i>	Winter Wren	-	-	0.00	0.25
Passeriformes	Turdidae	<i>Catharus fuscescens</i>	Veery	0.30	0.27	0.80	0.85
Passeriformes	Turdidae	<i>Catharus guttatus</i>	Hermit Thrush	0.13	0.13	0.65	0.55
Passeriformes	Turdidae	<i>Hylocichla mustelina</i>	Wood Thrush	0.25	0.27	0.80	0.90
Passeriformes	Turdidae	<i>Turdus migratorius</i>	American Robin	0.02	0.02	0.05	0.10
Passeriformes	Mimidae	<i>Dumetella carolinensis</i>	Gray Catbird	-	-	0.00	0.05
Passeriformes	Parulidae	<i>Seiurus aurocapilla</i>	Ovenbird	0.85	0.83	1.00	1.00
Passeriformes	Parulidae	<i>Parkesia motacilla</i>	Louisiana Waterthrush	0.02	0.02	0.05	0.00
Passeriformes	Parulidae	<i>Parkesia noveboracensis</i>	Northern Waterthrush	-	-	0.05	0.05
Passeriformes	Parulidae	<i>Mniotilta varia</i>	Black-and-white Warbler	0.05	0.07	0.20	0.60
Passeriformes	Parulidae	<i>Geothlypis trichas</i>	Common Yellowthroat	0.00	0.02	0.05	0.10
Passeriformes	Parulidae	<i>Setophaga citrina</i>	Hooded Warbler	-	-	0.05	0.00
Passeriformes	Parulidae	<i>Setophaga ruticilla</i>	American Redstart	0.05	0.03	0.05	0.60
Passeriformes	Parulidae	<i>Setophaga cerulea</i>	Cerulean Warbler	0.02	0.02	0.05	0.20
Passeriformes	Parulidae	<i>Setophaga magnolia</i>	Magnolia Warbler	-	-	0.05	0.15
Passeriformes	Parulidae	<i>Setophaga caerulescens</i>	Black-throated Blue Warbler	0.03	0.02	0.15	0.10
Passeriformes	Parulidae	<i>Setophaga pinus</i>	Pine Warbler	0.03	0.02	0.25	0.25
Passeriformes	Parulidae	<i>Setophaga virens</i>	Black-throated Green Warbler	0.12	0.10	0.20	0.55
Passeriformes	Parulidae	<i>Cardellina canadensis</i>	Canada Warbler	0.02	0.00	0.05	0.00
Passeriformes	Emberizidae	<i>Pipilo erythrophthalmus</i>	Eastern Towhee	0.03	0.05	0.15	0.30
Passeriformes	Emberizidae	<i>Spizella passerina</i>	Chipping Sparrow	0.05	0.02	0.25	0.45
Passeriformes	Cardinalidae	<i>Piranga olivacea</i>	Scarlet Tanager	0.30	0.33	0.85	1.00
Passeriformes	Cardinalidae	<i>Cardinalis cardinalis</i>	Northern Cardinal	-	-	0.10	0.20
Passeriformes	Cardinalidae	<i>Pheucticus ludovicianus</i>	Rose-breasted Grosbeak	-	-	0.15	0.20

Table 3. Estimates of richness and compositional dissimilarity from point count and ARU methods based on data from the simultaneous-collection strategy. Richness is partitioned into alpha, beta, and gamma components based on the multiplicative model (Whitaker 1972). Alpha refers to the mean richness of 3 plots within each site. Gamma refers to the cumulative richness of 3 plots within each site. Beta is the average number of compartments in a site and reflects the heterogeneity of a site. Dissimilarity ($1 - \text{Jaccard's coefficient}$) estimates the difference in species composition for each site determined by point count versus ARU methods.

Site number	Site	Alpha		Beta		Gamma		Dissimilarity
		Point count	ARU	Point count	ARU	Point count	ARU	
1	Algonquin	3.67	3.67	1.91	1.91	7	7	0.25
2	Babcock	3.00	3.00	1.67	1.33	5	4	0.20
3	Canaan	3.67	4.00	2.18	2.00	8	8	0.40
4	Cockaponsett	4.33	3.67	1.85	1.91	8	7	0.33
5	Collis	5.67	5.33	2.29	2.25	13	12	0.33
6	Housatonic	4.67	4.67	1.93	1.71	9	8	0.11
7	Macedonia	3.33	3.33	1.80	1.80	6	6	0.29
8	Mattatuck	7.67	7.33	1.70	1.50	13	11	0.15
9	Mohegan	4.67	4.33	1.50	1.85	7	8	0.33
10	Natchaug	4.67	4.67	1.71	1.50	8	7	0.13
11	Naugatuck	3.67	2.67	1.91	2.25	7	6	0.14
12	Nipmuck	4.67	4.67	2.14	1.93	10	9	0.10
13	PachaugN	3.33	3.67	2.40	2.18	8	8	0.00
14	PachaugS	4.33	2.33	1.85	2.57	8	6	0.44
15	Paugusset	2.67	3.33	2.25	1.80	6	6	0.50
16	Roraback	4.00	4.00	2.25	2.25	9	9	0.20
17	Salmon	4.67	6.00	2.36	1.83	11	11	0.43
18	Shenipsit	4.33	4.00	2.08	1.75	9	7	0.22
19	Sleeping	5.00	5.33	1.60	1.50	8	8	0.22
20	UConn	3.33	4.67	2.10	1.93	7	9	0.40

Table 4. Results from two-tailed significance tests (paired t-test) to evaluate mean differences in richness components estimated from the simultaneous-collection strategy. Significant relationships are indicated in bold.

Component	Point count	ARU	t-statistic	df	p-value
Alpha	4.27	4.23	0.204	19	0.841
Beta	1.97	1.89	1.315	19	0.204
Gamma	8.35	7.85	2.236	19	0.038

Table 5. Results from two-tailed significance tests (paired t-test) to evaluate mean differences in frequency of occurrence of birds from two orders identified with point count and ARU methods. Comparisons were made separately for each assessment strategy. Significant relationships are indicated in bold.

Strategy	Order	n	Point count	ARU	t-statistic	df	p-value
Simultaneous-collection							
	Piciformes	7	0.029	0.014	6.000	6	<0.001
	Passeriformes	26	0.156	0.159	-0.498	25	0.623
Same-season							
	Piciformes	7	0.279	0.257	0.333	6	0.751
	Passeriformes	36	0.342	0.408	-2.646	35	0.012

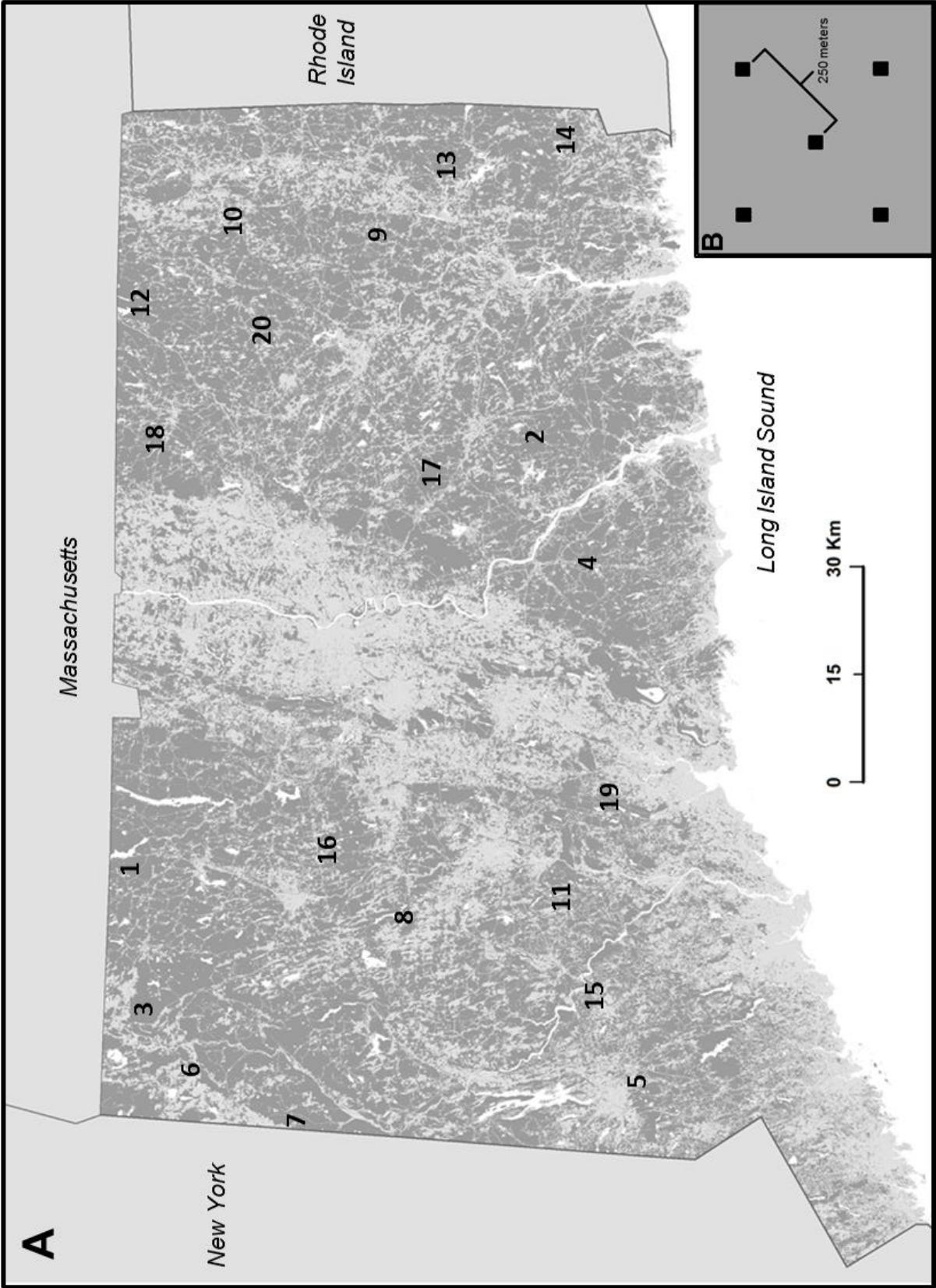
Table 6. Spearman Rank correlations (Rho) and associated p-values between habitat characteristics and Jaccard's dissimilarity coefficient. For each site Jaccard's Index evaluates differences in species composition identified with Point count and ARU methods determined with the simultaneous collection strategy. Significant relationships are indicated in bold.

Habitat characteristic	Rho	p-value
Elevation	-0.511	0.021
Slope	-0.175	0.462
Understory density	0.308	0.187
Canopy openness	0.147	0.537
Ground cover	-0.327	0.159
Herb cover	0.057	0.811

Figure Legend

Figure 1. (A) Map of study area in Connecticut, USA represented by forest (dark gray) non forest (light gray) and water (white). Location of 20 interior forest sites are indicated by number (see supplementary material for geographic coordinates). (B) Diagram illustrating the arrangement of five plots (black squares) within a site. Each square represents a paired ARU and point count location.

Figure 1



Supporting Information

Table S1. Geographic location of interior forest sites and mean habitat characteristics of each site based on three randomly selected plots used in the simultaneous-collection strategy. Latitude and longitude (decimal degrees) represent the center of each site. Numbers correspond to site locations indicated on Figure 1. See text for description of habitat characteristics.

Site number	Site name	Latitude	Longitude	Elevation	Slope	Understory density	Canopy openness	Ground cover	Herb cover
1	Algonquin	41.988	-73.058	337.00	3.00	0.67	0.90	66.67	6.67
2	Babcock Pond	41.522	-72.405	170.67	0.00	1.00	0.30	40.00	50.00
3	Canaan Mountain	42.005	-73.296	285.67	0.67	1.67	0.10	50.00	30.00
4	Cockaponsett	41.473	-72.536	137.00	0.67	4.33	0.30	60.00	3.33
5	Collis P. Huntington	41.346	-73.349	216.33	0.67	1.67	0.57	46.67	6.67
6	Housatonic	41.905	-73.406	310.33	1.33	2.00	0.17	53.33	16.67
7	Macedonia Brook	41.775	-73.488	389.33	2.00	0.00	0.23	20.00	6.67
8	Mattatuck	41.646	-73.089	214.00	2.00	0.67	0.47	56.67	13.33
9	Mohegan	41.670	-72.069	125.00	0.67	1.00	0.10	65.00	16.67
10	Natchaug	41.856	-72.057	244.67	0.67	1.33	0.13	70.00	13.33
11	Naugatuck	41.461	-73.046	160.33	1.33	1.33	0.40	76.67	3.33
12	Nipmuck	42.025	-72.176	307.33	1.67	0.67	0.10	76.67	3.33
13	Pachaug North	41.595	-71.887	145.00	0.00	1.67	0.17	60.00	16.67
14	Pachaug South	41.484	-71.859	96.50	1.33	2.67	0.37	38.33	15.00
15	Paugusset	41.405	-73.197	119.00	0.67	1.33	0.40	80.00	0.00
16	Roraback	41.732	-73.059	206.00	0.67	3.00	0.97	56.67	26.67
17	Salmon River	41.618	-72.378	134.33	0.33	2.67	0.43	36.67	50.00
18	Shenipsit	42.000	-72.399	241.00	0.67	1.00	0.63	23.33	73.33
19	Sleeping Giant	41.436	-72.889	142.33	0.67	1.67	0.10	56.67	16.67
20	Uconn	41.820	-72.236	131.67	0.00	2.33	0.17	26.67	43.33

CHAPTER TWO

MATRIX COMPOSITION AND LANDSCAPE HETEROGENEITY STRUCTURE MULTIPLE DIMENSIONS OF TEMPERATE FOREST BIRD BIODIVERSITY

Abstract

We identify characteristics of landscape composition and configuration that influence taxonomic (TD), functional (FD), and phylogenetic (PD) dimensions of bird biodiversity, and evaluate three hypotheses that predict responses of biodiversity to landscape structure. We quantified relationships of interior forest bird biodiversity with measures of landscape structure at multiple spatial scales and assessed the congruence of responses for the three dimensions for all birds, residents only, and migrants only. Residents had greater FD and PD than did migrants, and biodiversity of migrants was only weakly related to landscape structure. Relationships between dimensions of biodiversity and landscape structure were more frequently identified for FD and PD than for TD. TD was only associated with matrix composition, whereas other dimensions were associated more frequently with habitat composition and landscape heterogeneity.

Differences in the effects of landscape structure on dimensions of biodiversity among all birds, migrants, and residents indicate that management decisions should be sensitive to the different scale-dependent responses of these groups to landscape structure. Habitat amount and configuration only had moderate effects on patterns of biodiversity. In contrast, matrix composition and landscape heterogeneity were frequently associated with dimensions of biodiversity. Consequently, incorporating the identity, relative proportions, or configuration of non-focal habitat cover types in analyses is necessary to gain a comprehensive view of how landscape structure influences spatial variation in biodiversity.

Introduction

Widespread declines in terrestrial biodiversity have largely been driven by the loss and fragmentation of natural habitats, particularly in forested regions (Fahrig 2003). As human populations grow and demands for natural resources and land increase, landscapes will experience intensified alteration and fragmentation, with potentially dramatic consequences for biodiversity

(Sala *et al.* 2000; McLaughlin 2011; Allen *et al.* 2013). Consequently, understanding how the spatial structure of human-modified landscapes shape the distribution of biodiversity has become a key issue in studying the effects of global change, the identification of vulnerable species or ecosystems, and the determination of meaningful conservation measures to mitigate the current diversity crisis (Díaz *et al.* 2007; Reiss *et al.* 2009).

Spatial dynamics of biodiversity historically have been evaluated from taxonomic perspectives that are insensitive to interspecific variation in ecological or evolutionary characteristics. However, ecological studies have increasingly pointed to the multidimensional nature of biodiversity, by incorporating phylogenetic or functional dimensions along with the taxonomic dimension (Díaz *et al.* 2007; Cavender-Bares *et al.* 2009; Reiss *et al.* 2009; Devictor *et al.* 2010; Meynard *et al.* 2011; Cisneros *et al.* 2014; Stevens & Tello 2014; Dreiss *et al.* 2015). Phylogenetic diversity reflects the accumulated evolutionary history of an assemblage, and may indicate a region's capacity to generate new evolutionary solutions in the face of change or to persist despite those changes (Faith 1992; Webb *et al.* 2002; Faith 2008). Functional diversity characterizes eco-morphological, physiological, or ecological traits within assemblages (Tilman 2001; Petchey & Gaston 2006), and may reflect the ability of a particular assemblage to respond effectively to global change, allowing the maintenance of functional processes, including the ecosystem services that are of interest to human societies (Hooper *et al.* 2005; Díaz *et al.* 2007; Cadotte *et al.* 2009; Reiss *et al.* 2009). Under some circumstances, functional and phylogenetic diversity may be closely related due to evolutionary conservatism (Webb *et al.* 2002; Cavender-Bares *et al.* 2009). In those situations, conserving phylogenetic diversity could potentially ensure the maintenance of ecosystem function as well (Forest *et al.* 2007; Cadotte *et al.* 2009; Devictor *et al.* 2010; Flynn *et al.* 2011).

Birds are diurnal, conspicuous, and their behavior can be documented relatively easily. As a result, they are among the most well-known classes of animals. They have been of particular interest to ecologists and have contributed greatly to the conceptual and theoretical framework of community ecology (Weins 1983). Despite their historical significance, considerable gaps remain in our knowledge of the current status and recent population trends of forest species (Sauer, Fallon & Johnson 2003; Blancher *et al.* 2009; Francis, Blancher & Phoenix 2009). Birds are species rich in temperate forests, comprise considerable variation in functional traits with multiple links to ecosystem functioning (Sekercioglu 2006; Lislevand, Figuerola & Székely 2007; Vandewalle *et al.* 2010), and have well resolved phylogenetic relationships (Jetz *et al.* 2012). Importantly, birds perform critical ecological roles in forest systems, partly through top-down processes, such as predation on insect herbivores (Van Bael, Brawn & Robinson 2003), but also through plant–animal mutualisms that sustain pollination or seed dispersal (Anderson *et al.* 2011). Moreover, ample evidence suggests a strong influence of landscape modification on avian biodiversity (e.g. Villard, Trzcinski & Merriam 1999; Flynn *et al.* 2009; Meynard *et al.* 2011; Smith, Fahrig & Francis 2011). Although differences in likelihood of extinction and in responses to habitat fragmentation exist between migratory and resident bird species, responses of these groups to landscape structure have rarely been evaluated simultaneously (Faaborg *et al.* 1993; Shimieglow & Monkkonen, 2002, Sekercioglu 2007).

In general, the effects of landscape heterogeneity or matrix composition on biodiversity have been understudied compared to assessments based on habitat amount or configuration in landscapes (Fahrig *et al.* 2011). This arises from the historical predominance of the habitat-matrix paradigm in landscape ecology (Fischer & Lindenmayer 2006) and reflects the pervasive influence of island biogeographic theory (MacArthur & Wilson 1967) on ecology in general. In this approach, the landscape is divided into two categories: the focal habitat, in which all necessary resources are

found, and an inhospitable matrix. Traditionally, the habitat-matrix paradigm relies on patch-based measures of fragmentation, such as patch area, density, or isolation because they are perceived to capture the effects of a diminished resource base or population subdivision and are easy to quantify with modern geospatial tools. However, species in human-modified environments perceive landscapes in complex scale-dependent ways, and responses are shaped by resources or interactions with species from different cover types (Ewers & Didham 2006). Indeed, habitat remnants are rarely surrounded by ecologically neutral or completely inhospitable environments. Edge effects are dependent on the identity of land cover bordering habitat patches (Ries *et al.* 2004). Moreover, processes outside a patch have the potential to influence populations and communities as much or more than processes within remnant patches of focal habitat (Wiens 1995). What remains unclear is the relative importance of matrix composition and landscape heterogeneity when compared to focal habitat composition and configuration. Consequently, we evaluate the support for three competing hypotheses derived from the literature that predict associations between biodiversity and landscape structure:

- (1) Habitat area hypothesis: The total area of focal habitat in a landscape is the underlying characteristic that molds patterns of biodiversity, independent of the size of the local patch in which biodiversity is measured, and the identity of the matrix within which it is embedded (Fahrig 2013).
- (2) Habitat configuration hypothesis: Habitat configuration should have the strongest influence on biodiversity when habitat amount in the landscape is intermediate (Villard & Metzger 2014).
- (3) Matrix heterogeneity hypothesis: Matrix composition or heterogeneity of the landscape influences patterns of biodiversity in modified landscapes as much as or more than the composition and configuration of the focal habitat (Kupfer, Malanson & Franklin 2006).

Recent studies have questioned the ability of taxonomic diversity to adequately capture aspects of biodiversity related to ecosystem functioning and evolutionary history (Webb *et al.* 2002; Petchey & Gaston 2006; Pavoine & Bonsall 2011). To ensure effective management and policy decisions, the effects of landscape modifications on multiple dimensions should be considered. To address this, we quantified relationships of taxonomic, functional, and phylogenetic diversity of temperate forest birds with landscape structure at multiple spatial scales. If responses of dimensions of biodiversity to landscape structure are incongruent, greater attention should be placed on dimensions that are most sensitive to changes in the landscape when determining conservation priorities. Lastly, we assessed the congruence of responses between dimensions of biodiversity for all birds, residents only, and migrants only to determine if assessments based on full assemblages reflect responses of groups with well-known ecological and evolutionary differences.

Methods

Study area and landscape structure

Research was conducted in eastern deciduous and coniferous forests of Connecticut, USA, excluding coastal areas. Currently, 60% of land cover in the state is forest, dominated by oak-hickory and northern hardwood forest types, although pine forests are common along the northern border of the state (Wharton *et al.* 2004). Like many areas, Connecticut has experienced profound anthropogenic alteration of landscapes (Drummond & Loveland 2010), so that forest currently exists as patches or fragmented parcels of various sizes and ages, interwoven with various types of human-altered land covers (i.e. urban and suburban developments, agricultural fields, road networks, and power line rights of way; Fig. 1).

Twenty sites were established in interior forest patches of various sizes and shapes within a matrix comprising a variety of land cover types. Site selection was guided by a number of criteria. Site locations were constrained so that inter-site distances, as well as distances between sites and the

coast of Long Island Sound, were at least 10 km (Fig. 1). Sites needed to be sufficiently large to contain 5 plots (inter-plot distances of at least 250 m) within which Autonomous Recording Units (ARUs) could be attached to trees to detect bird vocalizations. Site locations were selected by processing a 2010 land cover map developed by the Center for Land Use Education and Research (CLEAR 2010b) that was classified into nine cover classes (agriculture, barren land, developed land, forest, forested wetland, nonforest wetland, shrubland, turf and grass, and water). The Landscape Fragmentation Tool (LFT v2.0; CLEAR 2010a) add-on to Arc Toolbox was used to identify suitable sites with sufficient core forest (i.e. forest pixels located at least 100 m from non-forest pixels) to contain 5 plots. The subset of suitable sites was further reduced by overlaying files containing boundaries of state owned land to determine areas of interior forest that were public land. Sites were located on public land based on the rationale that if this research were to be conducted over the long term, there would need to be a consistent level of protection and access to sites in the future. Additionally, roughly one-third of the forests in the lower 48 states are on public lands, supporting 45% of the U.S. distribution of 149 obligate forest bird species. These often represent the largest unfragmented forests in many regions (NABCI 2011). Prospective sites were visited and ground-truthed to evaluate accuracy of land cover maps and to ensure accessibility. Ultimately, sites were selected to represent the range in composition and configuration of forest and nonforest land cover types that are common in the study area.

Landscapes corresponding to 6 spatial scales (i.e. circles of 1, 1.5, 2, 2.5, 3 and 5 km radius) centered on each site, were described by eight characteristics of landscape structure (Table 1). To discriminate among proposed hypotheses, characteristics were selected to quantify focal habitat composition, focal habitat configuration, matrix composition, and landscape heterogeneity, which were required to evaluate proposed hypotheses. Landscape characteristics were quantified at multiple spatial scales because species perceive their environment at multiple spatio-temporal scales

and differ from each other in this regard as a consequence of species-specific life-history, dispersal, resource acquisition, and predator avoidance characteristics. Furthermore, we hope to avoid the pitfalls of previous multi-scale research that may have relied on either too few or too narrow a range of scales to determine effects of landscape structure on species (Jackson and Fahrig 2014).

Landscape characteristics were estimated with Fragstats 4.1 (McGarigal, Cushman & Ene 2012) from the same land cover map that was used in site selection.

Avian surveys

Birds were surveyed with a combination of point counts (Ralph, Sauer & Droege 1995) and recordings from ARUs. For point counts, each plot within a site (Fig. 2B) was visited on two occasions during the breeding season (May - August 2012) and sampled with a 10 minute survey. Surveys were conducted within the first 4 hours of local sunrise, and all species heard or seen were considered present. In addition to point counts, each of the 5 plots within a site contained an ARU (Wildlife Acoustics Song Meter Sm2+) and was surveyed for 4 hours on a daily basis, beginning at local sunrise during the same time period as point counts. To complement point-count data, recordings from ARUs were sampled randomly by selecting a plot and 2-minute time period on each of 50 days (exclusive of those days when point counts were conducted). This sampling strategy represents a compromise between maximizing the number of sampling days, while including a sufficient amount of time per day to capture multiple vocalizations of a species. Furthermore, this approach results in equal sample effort for acoustic surveys and point count surveys for each site (i.e. 100 minutes of point counts and 100 minutes of ARU recordings). To compare efficacy of point counts and ARUs for sampling interior forest birds, three plots from each site were selected randomly (i.e. 60 samples from each method paired in time and location). Recordings were analyzed and sonograms were viewed with Song Scope software (Wildlife Acoustics Inc.). To assist in identification of species, field recordings were compared with

sonograms of previously identified species obtained from the Macaulay Library at the Cornell Lab of Ornithology. Statistical analyses were based on the incidence of bird species identified from all sampling approaches, as this represents the best estimate of species composition of each assemblage at a site. Analyses were restricted to birds from the Passeriformes and Piciformes because these orders contain both migratory and resident species in the study area, and multiple genera within them are known to occur in interior forest.

Dimensions of biodiversity

Data

To evaluate the taxonomic dimension, we estimated species richness from each of the 20 interior forest sites. We followed the nomenclature and taxonomic recommendations of the North American Classification Committee of the American Ornithologists' Union (Chesser *et al.* 2013). The functional dimension was estimated from 3 categorical (i.e. food guild, foraging guild, residency) and 6 continuous characteristics (i.e. body mass, wing length, bill length, tail length, clutch size and egg mass). Information for all functional attributes was derived from the literature, but was restricted to records from adults captured in North America, with preference for studies in Eastern North America (Pyle 1997; Poole 2005; Lislevand, Figuerola & Székely 2007). Categorical characteristics were associated with aspects of resource use including the type of food eaten (insectivore or omnivore), where and how food is obtained (bark forager, ground forager, foliage gleaner, or flycatcher), and time period during which resources are obtained from the habitat (resident or migrant). Although considerable seasonal or environmental variation in resource use exists in some bird species, as well as intraspecific variation in migratory behavior of a few species, categorizations were based on the dominant resources used during the breeding season, and the majority of individuals in each species. Continuous characteristics represent an average for each species based on measurements of multiple adult individuals. Continuous characteristics associated

with body size (mass, bill length, wing length and tail length), reflect resource use and physiological constraints related to diet and foraging capabilities, whereas clutch size and egg mass are estimates of reproductive effort and energetic demands, respectively.

The phylogenetic dimension was estimated from branch lengths based on a comprehensive phylogeny of the world's bird species (Jetz *et al.* 2012). This phylogeny was inferred using a two-step protocol in which time-calibrated phylogenetic trees were estimated for well-supported bird clades and subsequently joined onto a backbone tree representing deep phylogenetic relationships (see Jetz *et al.* 2012 for methodological details). This tree represents an up-to-date synthesis of phylogenetic information for birds, allowing species-level inference that reflects uncertainty. To incorporate this uncertainty into the quantification of the phylogenetic dimension of biodiversity, we randomly selected 1000 trees from the set of 10,000 trees based on the “Hackett All Species” backbone (available at <http://birdtree.org>) and conducted all analyses based on this suite of phylogenetic information.

Metrics

At each site, three dimensions of biodiversity were estimated separately for all birds, for residents only, and for migrants only, as these groups respond differently to landscape structure (Flather and Sauer 1996). The taxonomic dimension of biodiversity (TD) was quantified as the cumulative number of species detected at the five plots by either method. Functional and phylogenetic dimensions of biodiversity (FD and PD, respectively) were estimated as Rao's Quadratic Entropy (Rao's Q; Botta-Dukat 2005). When incidence data are used, Rao's Q is the sum of the distances (phylogenetic or functional) between all possible pairs of species, divided by the square of the number of species in the assemblage (Weiher 2011). In general, Rao's Q measures the average difference among species and reflects multivariate dispersion. Gower's distances, which can quantify dissimilarities based on categorical and continuous attributes at the same time (Botta-

Dukát 2005), estimated pairwise functional differences between species at each site, and were calculated using the cluster and ade4 packages for R (Chessel *et al.* 2004, Maechler *et al.* 2005). Numerous metrics are available to estimate functional diversity and most differ in data requirements, assumptions, and ease of interpretation (Petchey & Gaston 2006, Mouchet *et al.* 2010). Rao's Q requires fewer assumptions than do many measures, is easy to interpret, and can be applied to any distance matrix regardless of source (e.g. functional, phylogenetic, or geographic distances). Nonetheless, all measures of functional diversity have limitations. Most notably, the number and type of functional traits, together with their correlations, affect the level of redundancy that assemblages appear to exhibit. Consequently, selection of traits represents an effort to balance between having a comprehensive set of functional traits and concerns about multicollinearity. Pairwise phylogenetic distance matrices were calculated for species at sites based on all 1000 phylogenetic trees via the "cophenetic" function of the ape package in R (Paradis, Claude & Strimmer 2004). Consequently, phylogenetic Rao's Q, represents the mean of values calculated separately for each of 1000 phylogenetic trees.

To promote meaningful comparisons among dimensions, Rao's Q was transformed into its Hill number or numbers equivalent. In its original formulation, Hill numbers (Hill 1973) represent the effective number of species in a community (i.e. the number of equally abundant species needed to produce an empirical metric). Species richness is its own numbers equivalent as richness ignores species abundances (i.e. all species are considered to be equally abundant). The numbers equivalent for PD or FD based on Rao's Q, a dispersion metric, represents the number of species with equal phylogenetic or functional distinctiveness that are needed to produce an empirical value of the corresponding metric. The numbers equivalent for Rao's Q was quantified using R functions developed by de Bello *et al.* (2010).

Statistical analyses

Hierarchical partitioning (Chevan & Sutherland 1991) assessed the relationship between eight landscape characteristics and each dimension of biodiversity. We assessed these relationships separately for each of six spatial scales (i.e. circles of 1, 1.5, 2, 2.5, 3 and 5 km radius). Hierarchical partitioning is a regression technique in which all possible linear models are jointly considered to identify the most likely explanatory factors, while minimizing the influence of multi-collinearity. Such an analysis provides a measure of the strength of effect of each factor that is largely independent from effects of other factors (Chevan & Sutherland 1991; Mac Nally 2000). As hierarchical partitioning only quantifies the magnitude of effect, the direction (sign) of the relationships was determined with correlation analysis. Patterns of diversity were modeled using Gaussian errors and goodness of fit based on r^2 . Significance ($\alpha = 0.05$) of independent contributions of variables was estimated using a randomization test with 1000 iterations (Mac Nally 2002). Although multi-scale studies are critical for identifying effects of landscape structure on biodiversity (Jackson and Fahrig 2014), the probability of concluding significance by chance alone increases with the number of scales assessed. Consequently, for each combination of bird group (all birds, residents, or migrants) and dimension of biodiversity, we interpret an effect of landscape structure to be strong if at least 3 of 6 spatial scales indicate a significant relationship. If analyses at multiple scales are independent, then the experiment-wise error rate associated with this criterion is ≤ 0.002 . Hierarchical partitioning and associated randomization tests of significance were executed using the hier.part package in the R computing environment (<http://www.R-project.org/>).

Results

Study Area

Sites were characterized by low canopy openness, low understory density, and a greater percentage of leaf and needle coverage than of herbaceous cover (unpublished data). Mean elevation ranged from 105 to 375 meters above sea level. Landscapes encompassing sites were dominated by forest,

regardless of spatial scale. Minimum percent forest cover ranged from 92% (mean = $98.6\% \pm 2.2$) at 1 km landscape scale to 65% (mean = $80.2\% \pm 7.7$) at 5 km landscape scale (see Appendix S1 in Supporting Information). However, minimum percent cover of core forest was less extensive ranging from 77% (mean = $95.78\% \pm 6.0$) at 1 km scale to 51% (mean = $67.1\% \pm 9.2$) at 5 km scale. In general, landscapes were more diverse and heterogeneous at larger scales than at smaller scales. For example, mean contagion was lowest and mean Shannon diversity of land cover types was greatest in the 5 km scale.

All birds

Most of the 43 bird species in the study area are insectivores and most obtain food by foraging on the ground or by gleaning insects from foliage (Table 2). Seven species (i.e. Black-capped Chickadee, Eastern Wood-Pewee, Ovenbird, Red-eyed Vireo, Scarlet Tanager, White-breasted Nuthatch, and Wood Thrush) occurred at all 20 sites, and seven species (i.e. Canada Warbler, Gray Catbird, Great Crested Flycatcher, Hooded Warbler, Louisiana Waterthrush, Northern Waterthrush) occurred exclusively at a single site. Dimensions of biodiversity were not correlated with each other ($P_{TD-FD} = 0.358$, $p = 0.121$; $P_{TD-PD} = -0.201$, $p = 0.395$; $P_{FD-PD} = -0.084$, $p = 0.724$). Taxonomic diversity was the most variable dimension of biodiversity, ranging from 14 species to 28 species. Functional and phylogenetic dimensions ranged from 1.25 to 1.39 and 2.08 to 3.36, respectively (Table 3).

Relationships between biodiversity and landscape structure differed among dimensions (Table 4). Neither taxonomic nor functional diversity were associated with habitat composition or configuration. Taxonomic diversity was associated with matrix composition (percent cover of developed land) at multiple spatial scales. Functional diversity was associated with matrix composition as well as landscape heterogeneity at multiple scales. In contrast, phylogenetic

diversity was associated with habitat composition and configuration at small scales and with landscape heterogeneity at large scales.

In general, residents differed from migrants in functional attributes (Table S3) and responses to landscape structure (Table 4). Furthermore, residents and migrants differed from each other in all three dimensions of biodiversity (Paired t-tests: $t_{TD} = -4.25$, $p < 0.001$; $t_{FD} = 5.773$, $p < 0.001$; $t_{PD} = 10.457$, $p < 0.001$).

Residents

Residents comprised a little more than a third (15/43) of the bird species in the study area, but sites generally contained a similar number of resident and migrants (Table 3). Phylogenetic diversity was correlated positively with taxonomic diversity ($P_{TD-PD} = 0.773$, $p < 0.001$), but other associations were not significant ($P_{TD-FD} = -0.172$, $p = 0.469$; $P_{FD-PD} = 0.05$, $p = 0.824$).

Relationships between dimensions of biodiversity and landscape structure were scale-dependent (Table 4). Taxonomic diversity was weakly associated with landscape structure, however functional and phylogenetic diversity showed strong relationships. Functional diversity was associated with habitat composition (edge forest) and landscape heterogeneity (contagion and diversity) at multiple scales. Similarly, phylogenetic diversity was associated with habitat composition and matrix composition at multiple scales. However, associations with habitat composition were confined to the smallest scales.

Migrants

Associations between dimensions of biodiversity and landscape structure were weak (Table 4). Phylogenetic diversity was negatively correlated with taxonomic ($P_{TD-PD} = -0.517$, $p = 0.019$) and with functional ($P_{FD-PD} = -0.495$, $p = 0.026$) diversity, whereas taxonomic and functional dimensions were positively correlated with each other ($P_{TD-FD} = 0.501$, $p = 0.025$).

Discussion

Support for hypotheses

Evidence convincingly supported only one (i.e., matrix heterogeneity hypothesis) of the three hypotheses that predict associations between biodiversity and landscape structure. Matrix composition and landscape heterogeneity most strongly influenced bird biodiversity. Hypotheses that received little support are both derived from a binary habitat-matrix perspective that has historically been most prominent in landscape ecology. Consequently, we consider how the effects of habitat amount and configuration on biodiversity may be moderated by matrix characteristics and the overall composition of the landscape.

An appealing simplification of the habitat-matrix paradigm is that only habitat area matters for species richness (and possibly other dimensions of biodiversity), regardless of the size and isolation of patches, or the identity of the land cover types within the matrix (habitat area hypothesis; Fahrig, 2013). If true, this would greatly simplify management decisions because maximization of habitat area would maximize biodiversity. We found minimal support for the habitat area hypothesis for FD and PD, and no support for TD. At small scales, PD was associated with habitat amount for all birds and for residents. This may indicate that maximizing forest habitat for birds is necessary to maintain the evolutionary potential of bird assemblages, but not sufficient to do so.

The general lack of support for the habitat area hypothesis and the absence of a relationship between TD and habitat area suggest that the underlying idea may be better suited for species-specific assessments, even if it was originally conceived to assess TD. Testing the hypothesis requires that focal habitat be correctly defined for the species group under consideration. Except in highly restrictive assemblages, classification of the focal habitat for a group of species will likely be an over-simplification for at least some of the species. This arises because a species may use

multiple cover types in the landscape, albeit with reduced frequency or reduced breeding success in them. Furthermore the decision to use other habitats is context dependent (i.e. landscape-specific), reflecting the distribution of resources, territories of conspecifics, and competitors, which jointly determine the quality of the patch (i.e. ideal free distribution or ideal despotic distribution, Fretwell and Lucas 1970; Fretwell 1972). Consequently, use of non-focal habitats may differ across the study region, among species, or through time for individuals of the same species. In a single-species context, these issues can be dealt with using habitat suitability mapping. In contrast, this is not easily implemented when evaluating assemblage-level responses. Particularly because species may use alternate habitats with different frequencies, and species richness, as well as other incidence-based approaches, only require a single individual of a species to be detected for a presence to be registered. Biodiversity was positively related to core forest and to edge forest (as well as to developed and agricultural land), indicating that birds are using more than the focal habitat. Although, birds were only sampled in core forest, the high vagility and dietary flexibility of many of the species likely allows them to exploit other cover types, even if they primarily reside in the focal habitat.

Habitat configuration is predicted to have the greatest influence on biodiversity when the percent of focal habitat is intermediate in a landscape, and will be less important when the focal habitat is pervasive or rare (habitat configuration hypothesis; Villard & Metzger 2014). As a consequence of the landscapes surrounding our sites, we cannot effectively test the main premise of this hypothesis and can only confirm that configuration is less important than are other aspects of landscape structure when the focal habitat is pervasive. A more effective test of this hypothesis requires evaluation of a suite of sites dispersed in a regional landscape that offers a gradient in focal habitat area ranging from low to high amounts, with considerable variation in the number of habitat patches. In this study, variation among sites in the number and sizes of core forest patches was low

at small scales (most sites had only one or two patches). Although variation in the percent cover of core forest at the largest scale was greater, landscapes generally comprised a large patch of focal habitat, with the cumulative area of forest covering more than 50% of the landscape. Consequently, we did not detect a strong influence of habitat configuration on any dimension of bird biodiversity.

We found strong evidence supporting the matrix heterogeneity hypothesis. Regardless of dimension, matrix composition and landscape heterogeneity are important, and they are critical for understanding spatial variation in taxonomic and functional diversity of birds (Table 4). The simplification of landscapes into a dichotomous habitat and matrix has been challenged by many who argue that the matrix is not uniformly inhospitable and that the degree to which fragmentation effects (i.e. those attributed to area and isolation) arise in particular cases is as much a function of characteristics of the matrix as it is of attributes regarding habitat remnants (e.g. Ricketts 2001; Fischer & Lindenmayer 2006; Kupfer, Malanson & Franklin 2006; Fahrig *et al.* 2011). In this study, the identity of the matrix (i.e. percent cover of developed or agricultural land), and heterogeneity of the landscape (i.e. diversity, contagion) were most frequently associated with dimensions of biodiversity. All dimensions for each species group were significantly related to one of these general characteristics, and often to multiple aspects of matrix composition and landscape heterogeneity. Although habitat amount and configuration may be important, studies that do not incorporate the identity, relative proportions, or configuration of cover types other than the focal habitat likely will fail to gain a comprehensive view of how landscape structure influences patterns of bird biodiversity or how to manage it effectively.

Differences among dimensions and species groups

Although matrix composition and landscape heterogeneity were frequently associated with dimensions of biodiversity, relationships differed among dimensions and groups of birds. For migrants, the association of landscape structure with all dimensions of biodiversity was weak (Table

4). However, when relationships between landscape structure were significant, they differed from those observed for residents. Migrants are adapted to cope with a broad suite of habitats and food sources during migration, and many are generalists in their resource use. Consequently, migrants may be responding to landscape structure at scales > 5 km or to attributes of the landscape that are not captured with the current suite of characteristics.

In the current study, TD was exclusively related to matrix composition. FD was also associated with matrix composition, but additionally was associated positively with heterogeneity of the landscape and with the proportion of edge forest. Bird FD often increases with landscape diversity (Tews *et al.* 2004; Tschardtke *et al.* 2008; Barbaro *et al.* 2014). As more cover types are represented in a landscape, biodiversity should increase through an accumulation of species associated with each cover type. Furthermore, landscapes with a greater diversity of land cover types in the matrix likely have more available niche space and as a result, can often support more functions than landscapes with a less heterogeneous matrix. A greater diversity of cover types also leads to a higher density of edge habitats. Edge effects alter species composition and trophic interactions with important functional consequences. Edges may increase vulnerability of some species to nest predation or brood parasitism, and represent lower quality habitats that are only used when higher quality habitats are occupied (Ries *et al.* 2004). Conversely, an increase in the amount and type of edges as a result of high configurational heterogeneity and interspersed cover types may increase landscape complementation for species that rely on or can exploit more than one cover type to obtain resources (Brotons, Herrando & Martin 2004, Fahrig *et al.* 2011). Indeed, FD of resident birds was associated negatively with contagion, indicating a greater interspersed cover types enhances FD. Moreover FD was associated with percent cover of edge forest at multiple scales.

Relationships between PD and landscape structure differed from that of other dimensions principally due to associations with habitat composition at multiple scales and configuration at smaller spatial scales (i.e. ≤ 2 km). Influences of human land-use practices on the phylogenetic structure of bird assemblages are far less studied than are their influences on other dimensions (Frishkoff *et al.* 2014). However, when forest is converted to other land uses, species loss alone does not account for declining phylogenetic diversity, because forests contain a greater proportion of evolutionarily distinctive species than do other habitats (Gaston & Blackburn 1997, Frishkoff *et al.* 2014). PD of all birds and of residents was associated positively with percent cover of core forest, indicating that greater amounts of unfragmented forest may increase or maintain levels of phylogenetic diversity. In contrast to small scale associations, PD of each of the three assemblages was associated with either landscape heterogeneity or matrix composition at the largest scale. Diversity of cover types in the surrounding landscape likely influences the species pool available to colonize forest patches and may consequently increase phylogenetic diversity.

Relationships between dimensions of biodiversity

Dimensions of biodiversity were not correlated when migrants and residents were considered as a single fauna. Furthermore, the characteristics of landscape structure that had the greatest independent effect on patterns of biodiversity were distinct for each dimension (Table 4). Clearly, if dimensions of biodiversity do not respond equivalently to aspects of human-modified landscapes, adopting an integrated view of biodiversity poses challenges for conservation planning. Non-congruence among dimensions suggests that local assemblages originate from a regional species pool with multiple biogeographical and evolutionary histories (Webb *et al.* 2002; Losos 2008; Prinzing *et al.* 2008; Cumming & Child 2009; Devictor *et al.* 2010). Temperate forest birds, when analyzed as a single group, exemplify such a complex mix of biogeographical and evolutionary histories (i.e. migratory and resident assemblages comprise species with very different

levels of evolutionary relatedness; Lovette & Bermingham 1999; Winger, Lovette & Winkler 2012; Rolland *et al.* 2014). Indeed, when migrants and residents are analyzed separately, dimensions of biodiversity exhibited strong associations. For residents, PD was positively correlated with TD, whereas PD was negatively correlated with TD and FD for migrants. A closer evaluation of the evolutionary histories and phylogenies of the two groups provides insight into why differences may exist between residents and migrants, and if it is possible to determine the relative importance of particular dimensions.

The migratory assemblage is dominated by a single family (Parulidae; Table 2), some of which experienced a well-documented explosive radiation (Lovette & Bermingham 1999) and exhibit high levels of sympatry in forests of northeastern North America. Thus, many of the migrants from the regional species pool (i.e. species that could inhabit forest sites in the study area) are closely related, and can exploit similar niches, but do not compete strongly with each other for resources because of microhabitat specialization (e.g., feeding zones; MacArthur 1958). Consequently, if TD or FD only moderately differs among sites, PD is likely to be relatively invariant. In contrast, the resident assemblage comprises species representing many families. This results in a higher likelihood of species from more distantly related clades occurring at sites for residents than for migrants. As a result, the likelihood of adding or losing evolutionarily distinctiveness is much greater for residents than for migrants when TD differs among sites. Consequently, it could be argued that PD should be weighted less than other dimensions in decisions regarding migrants, but weighted more heavily in decisions regarding residents. Ideally, preserving several components of biodiversity simultaneously could be achieved by maximizing the protection of TD. However, as indicated above, and in other situations (e.g. Flynn *et al.* 2009; Devictor *et al.* 2010), this is not always the case. When maximizing protection of TD does not

maximize protection of other dimensions, a formal way to combine information from the different dimensions and to weight them appropriately is needed to effectively inform conservation action.

Conclusions

Area and configuration of focal habitat only had moderate effects on patterns of biodiversity. In contrast, all dimensions were significantly related to matrix composition or landscape heterogeneity at multiple spatial scales. Consequently, incorporating aspects that describe the identity, relative proportions, and configuration of all cover types are necessary to gain a comprehensive view of how landscape structure influences spatial variation in biodiversity. In addition, these results indicate that multi-scale analyses are necessary to disentangle complex spatial relationships between landscapes and biodiversity. Relationships between dimensions of biodiversity and landscape structure were more frequently identified for FD and PD than for TD. This supports the growing awareness that multi-dimensional assessments are critical for understanding spatial patterns of biodiversity, and indicates that TD may be less useful than other dimensions for understanding effects of landscape structure. However, in the absence of a framework to determine when and how to weight each dimension of biodiversity, effective management strategies may remain elusive.

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Table 1. Description of landscape characteristics quantified at each of 6 focal scales, and the hypothesis associated with a particular characteristic. See text for description of hypotheses and McGarigal, Cushman & Ene 2012 for details on calculation of characteristics.

Landscape Characteristic	What it quantifies	Description	Relevance to hypothesis
Percent core forest	Habitat composition	Percent of the focal scale that is core forest (i.e., forest > 100 m from any non forest cover type).	Habitat area hypothesis
Percent edge forest	Habitat composition	Percent of the focal scale that is edge forest (i.e., forest < 100 m from any non forest cover type).	Habitat area hypothesis
Mean core forest patch density	Habitat configuration	Number of forest patches per unit area within a focal scale.	Habitat configuration hypothesis
Mean core forest proximity	Habitat configuration	An average measurement of core forest patch isolation, weighted by the size each patch. A scale with many large patches in close proximity will have a large index value (i.e., high proximity, low isolation).	Habitat configuration hypothesis
Percent Agriculture	Matrix composition	Percent of the focal scale that is agriculture land cover (includes fields for grazing, hay, corn, and tobacco).	Matrix heterogeneity hypothesis
Percent Developed	Matrix composition	Percent of the focal scale that is developed land cover (includes roads, urban and suburban developments, and buildings).	Matrix heterogeneity hypothesis
Contagion	Landscape heterogeneity	Measures the dispersion and interspersion of land cover types. Contagion approaches 0 when the patch types are maximally disaggregated (i.e., every cell is a different patch type) and interspersed. Contagion = 100 when all patch types are maximally aggregated or there is only one patch type in the focal scale.	Matrix heterogeneity hypothesis
Shannon diversity	Landscape heterogeneity	Diversity index that quantifies the relative proportion of nine land cover types in each focal scale.	Matrix heterogeneity hypothesis

Table 2. Functional attributes of bird species that were used to estimate functional diversity. Each numerical value represents the mean for the trait. Data were extracted from Pyle (1997), Lislevand, Figuerola & Székely (2004), and Poole (2005).

Order	Family	Scientific name	Common name	Diet	Foraging	Residency	Mass	Wing length	Bill length	Tail length	Clutch size	Egg mass
Piciformes	Picidae	<i>Melanerpes erythrocephalus</i>	Red-headed Woodpecker	Omnivore	Flycatching	Migratory	71.60	138.00	26.95	74.70	4.74	5.10
Piciformes	Picidae	<i>Melanerpes carolinus</i>	Red-bellied Woodpecker	Insectivore	Bark forager	Resident	70.45	140.50	29.10	77.25	4.24	4.60
Piciformes	Picidae	<i>Sphyrapicus varius</i>	Yellow-bellied Sapsucker	Insectivore	Bark forager	Migratory	50.30	124.20	23.05	72.10	4.79	3.40
Piciformes	Picidae	<i>Picoides pubescens</i>	Downy Woodpecker	Insectivore	Bark forager	Resident	28.20	97.03	15.86	56.10	4.79	2.50
Piciformes	Picidae	<i>Picoides villosus</i>	Hairy Woodpecker	Insectivore	Bark forager	Resident	65.50	121.73	32.40	77.15	3.93	4.30
Piciformes	Picidae	<i>Colaptes auratus</i>	Northern Flicker	Insectivore	Ground forager	Resident	135.70	151.11	26.23	105.80	6.66	7.30
Piciformes	Picidae	<i>Dryocopus pileatus</i>	Pileated Woodpecker	Insectivore	Bark forager	Resident	287.00	236.35	47.10	170.50	3.83	11.00
Passeriformes	Tyrannidae	<i>Contopus virens</i>	Eastern Wood-pewee	Insectivore	Flycatching	Migratory	14.10	81.45	11.55	64.60	3.00	1.77
Passeriformes	Tyrannidae	<i>Sayornis phoebe</i>	Eastern Phoebe	Insectivore	Flycatching	Migratory	18.30	84.45	14.45	70.85	4.58	2.32
Passeriformes	Tyrannidae	<i>Myiarchus cinerascens</i>	Great Crested Flycatcher	Insectivore	Flycatching	Migratory	33.50	101.35	14.98	88.35	5.00	3.65
Passeriformes	Vireonidae	<i>Vireo flavifrons</i>	Yellow-throated Vireo	Insectivore	Foliage gleaner	Migratory	18.00	76.05	11.20	48.80	3.60	2.40
Passeriformes	Vireonidae	<i>Vireo olivaceus</i>	Red-eyed Vireo	Insectivore	Foliage gleaner	Migratory	16.40	78.40	12.60	50.60	3.18	2.33
Passeriformes	Corvidae	<i>Cyanocitta cristata</i>	Blue Jay	Omnivore	Ground forager	Resident	71.65	122.74	24.98	117.60	4.18	5.90
Passeriformes	Corvidae	<i>Corvus brachyrhynchos</i>	American Crow	Omnivore	Ground forager	Resident	516.00	310.45	32.50	176.10	4.68	17.50
Passeriformes	Corvidae	<i>Corvus corax</i>	Common Raven	Omnivore	Ground forager	Resident	782.50	421.40	76.30	211.50	4.10	28.80
Passeriformes	Paridae	<i>Baeolophus bicolor</i>	Tufted Titmouse	Insectivore	Foliage gleaner	Resident	21.15	78.25	12.05	67.65	6.00	1.90
Passeriformes	Paridae	<i>Poecile atricapillus</i>	Black-capped Chickadee	Insectivore	Foliage gleaner	Resident	12.95	64.65	9.05	60.50	7.00	1.16
Passeriformes	Sittidae	<i>Sitta canadensis</i>	Red-breasted Nuthatch	Insectivore	Bark forager	Resident	10.50	67.00	13.80	36.00	5.78	1.15
Passeriformes	Sittidae	<i>Sitta carolinensis</i>	White-breasted Nuthatch	Insectivore	Bark forager	Resident	21.10	90.05	19.10	47.30	7.30	1.95
Passeriformes	Troglodytidae	<i>Troglodytes heimalis</i>	Winter Wren	Insectivore	Ground forager	Resident	8.90	48.35	13.65	29.05	5.61	1.32
Passeriformes	Turdidae	<i>Catharus fuscescens</i>	Veery	Insectivore	Ground forager	Migratory	41.50	96.40	13.50	65.05	3.90	3.40
Passeriformes	Turdidae	<i>Catharus guttatus</i>	Hermit Thrush	Insectivore	Ground forager	Migratory	27.31	91.00	14.10	64.10	3.38	3.10
Passeriformes	Turdidae	<i>Hylocichla mustelina</i>	Wood Thrush	Insectivore	Ground forager	Migratory	50.15	106.75	11.20	69.60	3.30	4.85
Passeriformes	Turdidae	<i>Turdus migratorius</i>	American Robin	Insectivore	Ground forager	Resident	79.95	127.60	23.50	99.05	3.15	6.25
Passeriformes	Mimidae	<i>Dumetella carolinensis</i>	Gray Catbird	Omnivore	Ground forager	Migratory	37.65	89.10	11.40	88.85	3.68	3.80
Passeriformes	Parulidae	<i>Seiurus aurocapilla</i>	Ovenbird	Insectivore	Ground forager	Migratory	22.10	74.90	11.80	54.05	4.31	2.59
Passeriformes	Parulidae	<i>Parkesia motacilla</i>	Louisiana Waterthrush	Insectivore	Ground forager	Migratory	20.65	79.75	13.35	51.30	4.96	2.51
Passeriformes	Parulidae	<i>Parkesia noveboracensis</i>	Northern Waterthrush	Insectivore	Ground forager	Migratory	16.50	74.80	10.25	51.30	4.21	2.19
Passeriformes	Parulidae	<i>Mniotilta varia</i>	Black-and-white Warbler	Insectivore	Bark forager	Migratory	12.00	66.50	11.33	42.85	5.00	1.60
Passeriformes	Parulidae	<i>Geothlypis trichas</i>	Common Yellowthroat	Insectivore	Foliage gleaner	Migratory	10.10	53.00	10.60	47.50	3.99	1.62
Passeriformes	Parulidae	<i>Setophaga citrina</i>	Hooded Warbler	Insectivore	Foliage gleaner	Migratory	10.55	66.25	10.00	55.55	3.61	1.68
Passeriformes	Parulidae	<i>Setophaga ruticilla</i>	American Redstart	Insectivore	Foliage gleaner	Migratory	8.65	62.30	8.65	54.60	3.89	1.33
Passeriformes	Parulidae	<i>Setophaga cerulea</i>	Cerulean Warbler	Insectivore	Foliage gleaner	Migratory	8.65	63.40	9.59	41.65	3.53	1.49
Passeriformes	Parulidae	<i>Setophaga magnolia</i>	Magnolia Warbler	Insectivore	Foliage gleaner	Migratory	8.60	59.31	8.98	48.75	3.96	1.31
Passeriformes	Parulidae	<i>Setophaga caerulea</i>	Black-throated Blue Warbler	Insectivore	Foliage gleaner	Migratory	9.40	63.15	9.30	49.80	3.80	1.49
Passeriformes	Parulidae	<i>Setophaga pinus</i>	Pine Warbler	Insectivore	Foliage gleaner	Migratory	11.90	71.25	10.75	51.00	3.74	1.73
Passeriformes	Parulidae	<i>Setophaga virens</i>	Black-throated Green Warbler	Insectivore	Foliage gleaner	Migratory	9.30	61.90	12.76	46.90	4.00	1.44
Passeriformes	Parulidae	<i>Cardellina canadensis</i>	Canada Warbler	Insectivore	Foliage gleaner	Migratory	10.40	62.30	10.70	52.85	4.37	1.56
Passeriformes	Emberizidae	<i>Pipilo erythrophthalmus</i>	Eastern Towhee	Omnivore	Ground forager	Migratory	40.50	83.75	14.15	88.55	3.40	3.65
Passeriformes	Emberizidae	<i>Spizella passerina</i>	Chipping Sparrow	Omnivore	Ground forager	Migratory	12.75	69.90	9.40	60.55	3.70	1.60
Passeriformes	Cardinalidae	<i>Piranga olivacea</i>	Scarlet Tanager	Insectivore	Foliage gleaner	Migratory	28.30	92.90	11.30	66.75	3.45	3.31
Passeriformes	Cardinalidae	<i>Cardinalis cardinalis</i>	Northern Cardinal	Insectivore	Ground forager	Resident	41.35	93.85	12.65	97.60	2.50	4.58
Passeriformes	Cardinalidae	<i>Phoenicurus ludovicianus</i>	Rose-breasted Grosbeak	Insectivore	Foliage gleaner	Migratory	44.60	103.45	16.90	72.25	3.27	4.08

Table 3. Taxonomic (TD), functional (FD), and phylogenetic (PD) dimensions of biodiversity for each of three bird groups (all species, migratory species only, and resident species only) at 20 sites in Connecticut. Taxonomic dimension is estimated by species richness, whereas functional and phylogenetic dimensions are estimated by the numbers equivalent of Rao's quadratic entropy.

Site number	Site name	All species			Migratory species			Resident species		
		TD	FD	PD	TD	FD	PD	TD	FD	PD
1	Algonquin	20	1.31	2.35	13	1.48	1.74	7	1.58	2.70
2	Babcock Pond	17	1.37	3.15	7	1.29	2.09	10	1.49	2.98
3	Canaan Mountain	20	1.30	2.76	12	1.41	1.76	8	1.50	2.73
4	Cockaponsett	24	1.37	2.86	12	1.34	1.80	12	1.52	3.01
5	Collis P. Huntington	23	1.34	2.60	14	1.27	2.13	9	1.48	2.67
6	Housatonic	14	1.34	2.35	9	1.40	1.82	5	1.27	2.40
7	Macedonia Brook	19	1.38	2.70	11	1.37	1.81	8	1.51	2.86
8	Mattatuck	28	1.40	2.55	18	1.51	1.73	10	1.47	2.86
9	Mohegan	21	1.33	2.88	11	1.31	1.93	10	1.56	2.99
10	Natchaug	16	1.36	2.65	10	1.29	2.31	6	1.53	2.33
11	Naugatuck	16	1.26	2.90	8	1.38	1.94	8	1.49	2.86
12	Nipmuck	21	1.29	2.81	14	1.42	2.34	7	1.54	2.73
13	Pachaug North	15	1.25	2.73	9	1.41	2.10	6	1.67	2.59
14	Pachaug South	18	1.27	2.50	11	1.28	1.65	7	1.49	2.60
15	Paugusset	17	1.34	2.28	11	1.37	1.81	6	1.53	2.33
16	Roraback	23	1.31	2.08	15	1.54	1.63	8	1.50	2.29
17	Salmon River	23	1.34	2.90	12	1.31	1.99	11	1.55	3.01
18	Shenipsit	17	1.29	2.86	10	1.35	1.98	7	1.52	2.78
19	Sleeping Giant	16	1.37	3.36	6	1.28	2.79	10	1.49	2.97
20	UConn	25	1.39	2.23	15	1.42	1.66	10	1.49	2.66

Table 4. Landscape characteristics with significant independent effects (determined via hierarchical partitioning analyses) on variation in each of 3 dimensions of biodiversity (taxonomic, functional and phylogenetic) at each of 6 spatial scales for three assemblages of birds (all birds, residents, and migrants) in temperate forest. Direction of relationship is indicated by a plus or minus, and was determined via Spearman rank correlation. A dash indicates no significant effect of landscape characteristics on variation in biodiversity.

Dimension	Scale	All	Residents	Migrants
Taxonomic	1 km	—	—	—
	1.5 km	—	—	—
	2 km	+ Developed	+ Agriculture	—
	2.5 km	—	—	—
	3 km	– Developed	—	– Developed
	5 km	+ Developed	+ Developed	—
Functional	1 km	—	—	—
	1.5 km	+ Developed	—	—
	2 km	+ Developed	+ Diversity, + Edge forest	+ Developed
	2.5 km	– Contagion	+ Diversity, + Proximity	—
	3 km	+ Diversity	– Diversity, – Edge forest	—
	5 km	—	—	—
Phylogenetic	1 km	+ Edge forest	+ Core forest, – Edge forest, – Diversity	—
	1.5 km	+ Core forest	+ Core forest	—
	2 km	– Proximity	– Developed	– Contagion, – Proximity
	2.5 km	—	—	—
	3 km	—	—	—
	5 km	+ Diversity	+ Developed	– Core forest, – Contagion

Figure Legends

Figure 1. Map of study area represented by major land cover types derived from 2010 land cover data. Grided area indicates land outside the study area that was not classified into land cover types. Location of study area in northeastern North America delimited with rectangle in lower left corner map. Location of 20 sites (indicated by number; see appendix 1 for geographic coordinates) in study area in lower right corner.

Figure 2. (A) Illustrative example of multiple landscapes delimited by black circles centered on a site (black point). (B) Enhanced view of smallest focal scale. Black squares indicate location of ARUs within a site.

Figure 1

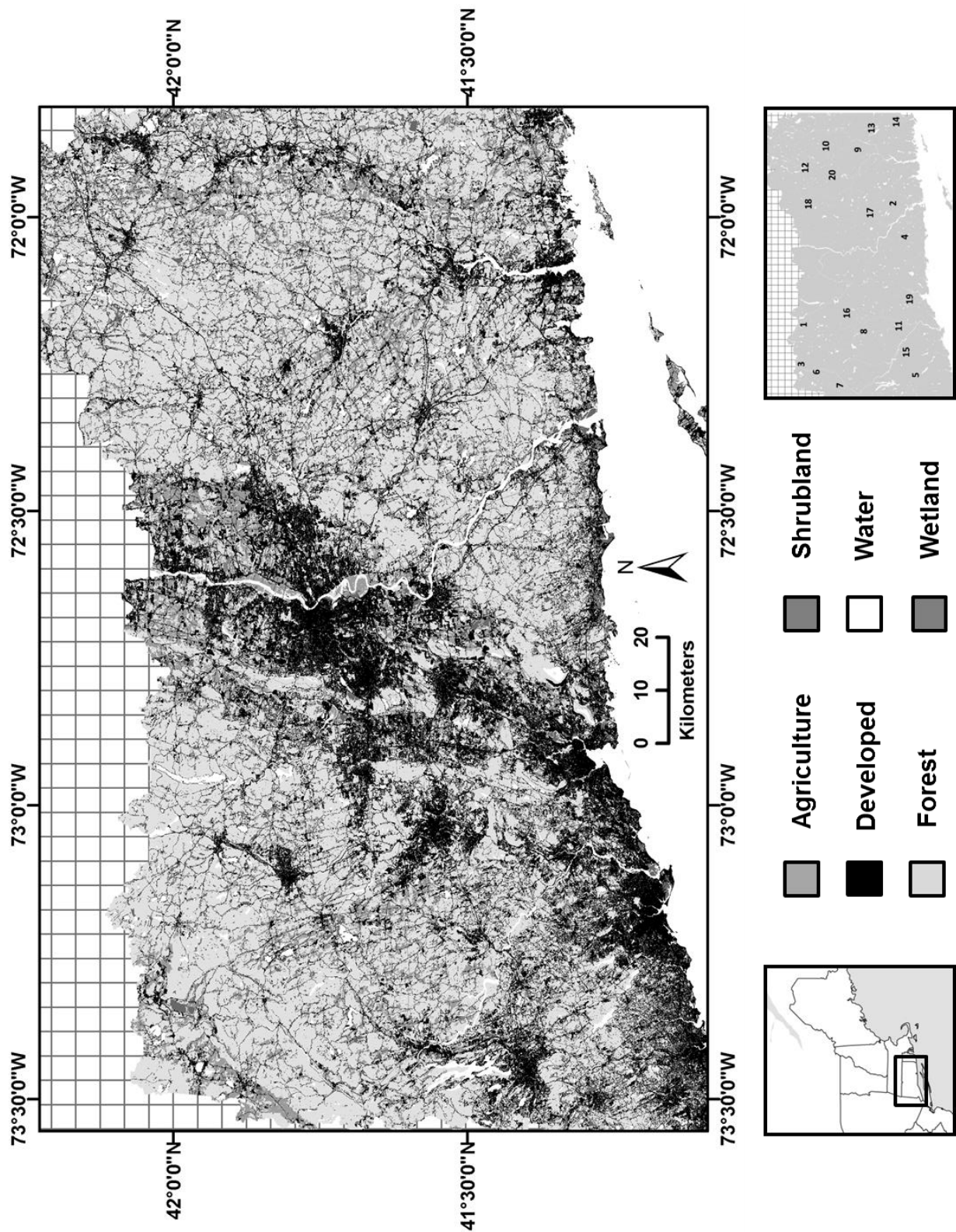
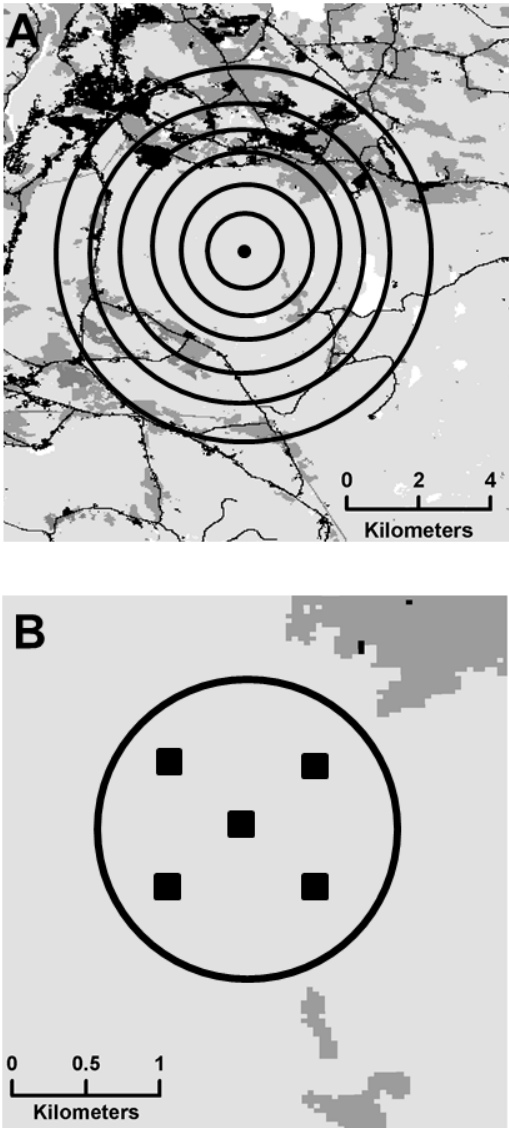


Figure 2



Supporting Information

Table S1. Geographic location of interior forest sites. Latitude and longitude (decimal degrees) represent the center of each site. Numbers correspond to site locations indicated on inset map of Figure 1.

Site number	Site name	Latitude	Longitude
1	Algonquin	41.988	-73.058
2	Babcock Pond	41.522	-72.405
3	Canaan Mountain	42.005	-73.296
4	Cockaponsett	41.473	-72.536
5	Collis P. Huntington	41.346	-73.349
6	Housatonic	41.905	-73.406
7	Macedonia Brook	41.775	-73.488
8	Mattatuck	41.646	-73.089
9	Mohegan	41.670	-72.069
10	Natchaug	41.856	-72.057
11	Naugatuck	41.461	-73.046
12	Nipmuck	42.025	-72.176
13	Pachaug North	41.595	-71.887
14	Pachaug South	41.484	-71.859
15	Paugusset	41.405	-73.197
16	Roraback	41.732	-73.059
17	Salmon River	41.618	-72.378
18	Shenipsit	42.000	-72.399
19	Sleeping Giant	41.436	-72.889
20	Uconn	41.820	-72.236

Table S2. Descriptive statistics of landscape characteristics for 20 sites at each of 6 spatial scales. Landscape characteristics estimated from 2010 land cover data (CLEAR 2010b) with Fragstats 4.1 (McGarigal, Cushman & Ene 2012).

Spatial scale	Descriptive statistic	Percent core forest	Percent edge forest	Percent agriculture	Percent developed	Core patch density	Core proximity	Diversity	Contagion
1 km	Mean \pm SD	95.78 \pm 5.96	1.42 \pm 2.42	0.00 \pm 0.00	0.01 \pm 0.04	0.32 \pm 0.00	0.00 \pm 0.00	0.06 \pm 0.08	94.77 \pm 7.6
	Range	77.19 - 100.00	0.00 - 9.43	0.00 - 0.00	0.00 - 0.17	0.32 - 0.32	0.00 - 0.00	0.00 - 0.29	72.93 - 100.00
1.5 km	Mean \pm SD	91.44 \pm 6.20	3.15 \pm 2.57	0.33 \pm 1.13	0.57 \pm 1.13	0.16 \pm 0.06	4.19 \pm 18.75	0.17 \pm 0.13	90.32 \pm 6.56
	Range	81.14 - 100.00	0.00 - 8.67	0.00 - 4.85	0.00 - 4.14	0.14 - 0.40	0.00 - 83.85	0.00 - 0.47	76.00 - 100.00
2 km	Mean \pm SD	86.33 \pm 8.41	5.21 \pm 3.22	1.01 \pm 2.96	1.83 \pm 2.70	0.13 \pm 0.08	27.47 \pm 37.28	0.30 \pm 0.18	88.92 \pm 6.26
	Range	70.97 - 98.18	0.53 - 11.32	0.00 - 11.07	0.00 - 11.63	0.08 - 0.41	0.00 - 120.82	0.02 - 0.67	78.29 - 98.97
2.5 km	Mean \pm SD	81.58 \pm 9.11	6.80 \pm 3.50	1.54 \pm 3.57	2.94 \pm 3.74	0.15 \pm 0.09	276.83 \pm 239.73	0.38 \pm 0.17	87.2 \pm 5.36
	Range	60.78 - 93.72	1.54 - 15.09	0.00 - 12.07	0.00 - 15.84	0.05 - 0.41	15.65 - 899.21	0.13 - 0.73	75.95 - 94.12
3 km	Mean \pm SD	77.43 \pm 10.32	8.10 \pm 3.44	2.00 \pm 4.02	4.19 \pm 4.20	0.19 \pm 0.08	190.77 \pm 125.42	0.51 \pm 0.22	84.26 \pm 6.43
	Range	56.31 - 91.84	2.61 - 16.16	0.00 - 14.02	0.59 - 18.26	0.07 - 0.32	40.34 - 591.85	0.18 - 0.98	69.04 - 93.83
5 km	Mean \pm SD	67.13 \pm 9.17	10.93 \pm 2.40	3.75 \pm 4.57	6.77 \pm 4.97	0.22 \pm 0.09	493.17 \pm 432.92	0.77 \pm 0.22	78.42 \pm 5.74
	Range	50.98 - 81.28	5.95 - 14.29	0.00 - 15.43	2.54 - 20.27	0.09 - 0.40	110.00 - 1999.75	0.44 - 1.25	66.78 - 87.75

Table S3. Means of functional attributes of resident (n = 18) or migratory (n = 25) species, and results from significance tests (t-test with unequal variances) to evaluate mean differences between groups.

Attribute	Resident	Migrant	t-statistic	Adjusted df	p-value
Mass	143.53	23.71	2.08	14.08	0.056
Wing	144.74	81.28	2.37	14.58	0.322
Bill	25.88	12.67	2.92	14.83	0.011
Tail	95.28	60.49	2.46	14.97	0.027
Clutch size	4.92	3.94	2.55	16.57	0.021
Egg mass	6.68	2.55	2.12	14.32	0.052

CHAPTER THREE

INDEPENDENT ASSEMBLY PROCEESS STRUCTURE RESIDENT AND MIGRATORY SUBSETS OF TEMPERATE BREEDING BIRD COMMUNITIES

Abstract

A primary goal of ecology is to understand the processes governing species coexistence and the mechanisms underlying the assembly of ecological communities. Recent attempts to understand these mechanisms have increasingly focused on patterns of phylogenetic relatedness and functional similarity among co-existing species. Moreover, decisions made regarding the domain of the species pool or the number and identity of functional traits to consider have increasingly come to the forefront of the field because these decisions can affect the ability to detect non-random patterns of community structure.

We evaluated the phylogenetic relatedness and functional structure of 20 temperate forest bird assemblages in northeastern North America. Functional traits were evaluated for the presence of phylogenetic signal, and three approaches for characterizing functional characteristics of species were compared. Assemblages were rarely more or less similar in functional characteristics than expected by chance, regardless of functional approach employed. In contrast, phylogenetic structures of bird assemblages were overdispersed, clumped or consistent with random assembly. We found little evidence for differences in phylogenetic community structure arising as a consequence of the definition of the species pool. Our results suggest that independent assembly mechanisms structure resident and migratory subsets of temperate breeding bird communities. These findings suggest that priority effects may play a critical role in determining the phylogenetic structure of temperate breeding bird communities, and have the potential to lead to multiple alternative community structures in similar environments. Consequently, the study of phylogenetic community structure may benefit from considerations of the effects of colonization history or other stochastic effects in addition to

deterministic assembly processes when communities are phylogenetically clumped or overdispersed.

Introduction

A primary goal of ecology is to understand the processes governing species coexistence and the mechanisms underlying the assembly of ecological communities. To this end, community ecologists have long debated the relative importance of deterministic factors (e.g., environmental conditions and interspecific interactions) versus stochastic processes (e.g., importance of chance colonization, random extinction, and ecological drift) for determining local species composition (e.g., Gleason 1926 vs. Clements 1936; Diamond 1975 vs. Connor & Simberloff 1979; Hubbell 2001 vs. Chase & Leibold 2003). In general, these opposing processes lead to alternative predictions of community structure for habitats with similar environmental conditions that share a regional species pool. Deterministic processes should result in convergent communities with similar species composition. In contrast, stochastic forces should result in divergent communities dominated by different species. Ending the debate about community assembly may not be as simple as explicitly considering the spatial scale of inference, as some have suggested (Chase 2014). However, there is a growing consensus that processes operating at a diverse range of spatiotemporal scales can structure communities (HilleRisLambers et al. 2012). For example, large-scale biogeographic patterns in diversity are generated by environmental factors (Wiens & Donoghue 2004), whereas local coexistence can be the result of competitive interactions (Chesson 2000). Furthermore, the composition of local communities is constrained by the evolutionary history of the regional species pool (Ricklefs 2004), but may also be influenced by demographic stochasticity (Tilman 2004).

Recent attempts to understand mechanisms underlying the assembly of ecological communities have increasingly focused on patterns of phylogenetic relatedness among co-existing species (e.g., Cavender-Bares et al. 2009; Vamosi et al. 2009). The underlying reasoning is that some assembly mechanisms lead to the co-existence of closely related species, whereas others lead to the co-existence of distantly related species, and patterns of relatedness among species in existing communities can be used to infer the processes governing assembly (Webb et al. 2002; Cavender-Bares et al. 2006; Swenson et al. 2006; Cavender-Bares et al. 2009; Vamosi et al. 2009). Generally, to identify patterns of coexistence, empirical communities are sampled, and the distribution of phylogenetic distances between coexisting species is compared with that of null communities that are randomly assembled from the regional species pool. Two mechanisms are commonly used to explain why empirical communities differ from randomly assembled ones. In the first, environmental characteristics play the dominant role in structuring community assembly. Habitats act as filters selecting for a subset of species from a regional pool on the basis of functional traits associated with beneficial adaptations to the environment (Webb et al. 2002). As a result, if closely related species are similar in function and have similar ecological requirements because of niche conservatism (Wiens & Graham 2005; Losos 2008), environmental filtering will lead to closely related species co-occurring more frequently than expected by chance (i.e., species in communities are more clustered across a phylogenetic tree than expected; Webb et al. 2002; Cavender-Bares et al. 2009). Alternatively, species interactions could play a key role in driving community assembly. If closely related species share more similar morphological and physiological traits and share niche requirements, they tend to compete more strongly for the same resources than do distantly related species, and this limiting similarity (MacArthur & Levins 1967) could result in patterns of phylogenetic overdispersion

within communities (i.e., species in communities are more evenly represented across the phylogenetic tree than expected; Webb et al. 2002; Cavender-Bares et al. 2009).

In addition to environmental filtering and biotic interactions, processes related to differences in relative fitness or to stabilizing niche differences could contribute to patterns of phylogenetic clustering or overdispersion, complicating interpretations of associations between processes and patterns of local communities (Mayfield & Levine 2010; HilleRisLambers et al. 2012). Moreover, phylogenetic overdispersion (rather than clustering) may result from environmental filtering of species with similar traits (if traits are convergent rather than conserved; Cavender-Bares et al. 2004, 2009; Kraft et al. 2007). However, a comprehensive approach that incorporates information on phylogenetic community structure and species functional traits, as well as considerations of the environmental conditions or the spatial relationships among communities can resolve some difficulties isolating effects of particular processes (Cavender-Bares et al. 2006; Helmus et al. 2007; Cavender-Bares et al. 2009).

Understanding the role of stochastic effects has played an important part in the modern study of community assembly (Hubbell 2001). However, community phylogenetic approaches do not generally consider the role of stochastic processes beyond a possible explanation for patterns that do not differ from randomly assembled communities. Patterns of phylogenetic clumping or overdispersion are rarely attributed to stochastic processes despite the recognition that stochasticity in the order and timing of species colonization can result in substantial differences in species composition among sites (e.g., Drake 1991; Law and Morton 1993; Chase 2003; Fukami, 2004; Urban & De Meester 2009; Fukami et al. 2010). Multiple community states associated with different colonization histories frequently arise from priority effects, in which early colonizing species affect the establishment and abundance of later colonizers (Lewontin

1969). Priority effects can lead to high variability in community structure, among environmentally similar sites (Chase 2003; Fukami 2004; Chase 2010). Nonetheless, the link between phylogenetic relatedness, community assembly, and priority effects has rarely and only recently been explored (Peay et al. 2012; Tan et al. 2012).

The issue of scale-dependence is a challenge in any study of phylogenetic community structure (Swenson et al. 2006; Kraft and Ackerly 2010; Eiserhardt et al 2013; Trisos, et al. 2014). Interspecific competition is generally assumed to be strongest at the local scale (capturing direct interactions among individuals) and its effects on community structure becomes progressively weaker as the spatial scale increases (Weiher and Keddy 1995; Vamosi et al. 2009; but see Gotelli *et al.* 2010). In contrast, habitat filtering is expected to be stronger than competition at larger spatial scales because habitat heterogeneity allows species to coexist that may have been excluded from certain habitats due to niche requirements (Swenson et al. 2007; Kraft and Ackerly 2010). As a consequence, if closely related species share similar trait values, community phylogenetic structure should shift from the co-occurrence of more distantly related (phylogenetic overdispersion) to more closely related (phylogenetic clustering) species with an increase in spatial scale or a less restricted species pool (Swenson et al. 2007; Cavender-Bares et al. 2009). However, the generality of these scale-dependent patterns is unknown because previous studies have focused on only a few taxonomic groups and produced mixed results and thus require further study (Vamosi et al. 2009; McGill 2010, Munkemuller et al 2014).

Most research exploring community assembly processes from a phylogenetic perspective have focused on plants, as these organisms are easily observed and amenable to experimental manipulation (Vamosi et al. 2009). As a consequence, most of the ecological and evolutionary patterns describing communities are based on systems where interactions between individuals

and the influence of the environment are likely to be highly constrained. In contrast, birds are highly mobile with few natural barriers that impede their movement or the distribution of their populations. Furthermore, species composition of temperate bird communities varies substantially in time and space, and the potential for interspecific interactions is high. Temperate forest birds, have well described phylogenetic relationships (Jetz et al. 2012), and morphological characteristics show well-established links to niche dimensions (e.g., Schoener 1965; Miles and Ricklefs 1984; Grant and Grant 2006). Despite being well studied and providing important contributions to the conceptual and theoretical framework of community ecology (e.g., MacArthur 1958; Cody 1974; Wiens 1982), research using phylogenetic approaches to study bird assemblages are few (Vamosi et al. 2009) and most have focused on South America (Graham et al. 2009; Gomez et al. 2010; Gianuca et al. 2013; Dehling et al 2014; Trisos et al. 2014; but see Lovette & Hochachka 2006; Price et al. 2014). Consequently, the relative importance of particular assembly mechanisms that structure temperate forest bird assemblages are unclear.

We used three approaches to evaluate assembly of local temperate bird communities: (1) we evaluated patterns of phylogenetic relatedness in 20 temperate interior forest bird assemblages to determine the relative influence of assembly mechanisms; (2) we determined the strength of phylogenetic signal in functional traits that reflect important niche characteristics of birds to facilitate the identification of mechanisms, and compared patterns of functional assemblage structure based on three functional classification schemes that differ in the number and identity of described niche axes; and (3) we investigated if identification of assembly mechanisms based on the phylogenetic structure of communities was dependent on the species pool definition.

Methods

Study Area

Research was conducted in eastern deciduous and coniferous forests of Connecticut, USA, excluding coastal areas. Currently, 60% of land cover in the state is forest, dominated by oak-hickory and northern hardwood forest types, although pine forests are common along the northern border of the state (Butler et al. 2012). Like many areas, Connecticut has experienced profound anthropogenic alteration of landscapes (Drummond & Loveland 2010), such that forest currently exists as patches or fragmented parcels of various sizes and ages, interwoven with various types of human-altered land covers (i.e., urban and suburban developments, agricultural fields, road networks, and power line rights of way; Figure 1A).

Approximately one-third of the forests in the lower 48 states are on public lands, support 45% of the U.S. distribution of 149 obligate forest bird species, and represent the largest unfragmented forests in many regions (NABCI 2011). Consequently, twenty sites were established on public land within interior forest patches of various sizes and shapes. Sites were selected by processing a 2010 land cover map (CLEAR 2010a) with the Landscape Fragmentation Tool (LFT v2.0; CLEAR 2010b) add-on to Arc Toolbox to identify suitable locations with sufficient area of interior forest (i.e., forest pixels located at least 100 m from non-forest pixels) to contain 5 plots spaced at least 250 m apart. Plots were separated by at least 250 m to reduce the potential of counting the same birds in multiple samples. Sites were separated from other sites and from the coast by least 10 km. Prospective sites were visited and ground-truthed to evaluate accuracy of land cover maps and to ensure accessibility.

Avian Surveys

Birds were surveyed with a combination of point counts (Ralph, Sauer & Droege 1995) and recordings from Autonomous Recording Units (ARUs). For point counts, each plot within a site (Fig. 2B) was visited on two occasions during the breeding season (May - August 2012) and sampled via a 10 minute survey. Surveys were conducted within the first 4 hours of local sunrise, and all species heard or seen were considered to be present. In addition to point counts, each of the 5 plots within a site contained an ARU (Wildlife Acoustics Song Meter Sm2 +) and was surveyed for 4 hours on a daily basis, beginning at local sunrise during the same time period as point counts. To supplement point-count data, recordings from ARUs were sampled randomly by selecting a plot and 2-minute time period on each of 50 days (exclusive of those days when point counts were conducted). This approach results in equal sample effort for acoustic surveys and point count surveys for each site (i.e. 100 minutes of point counts and 100 minutes of ARU recordings). Using both ARU and point count approaches enhances the likelihood of identifying species present at sites when compared to using either method alone (Venier et al. 2011; Tegeler et al. 2012; Chapter 1). Recordings were analyzed and sonograms were viewed with Song Scope software (Wildlife Acoustics Inc.). To assist in identification of species, field recordings were compared to sonograms of previously identified species obtained from the Macaulay Library at the Cornell Lab of Ornithology. Statistical analyses were based on the incidence of bird species identified from all sampling approaches, as this represents the best estimate of species composition of each assemblage at a site. We followed the nomenclature and taxonomic recommendations of the North American Classification Committee of the American Ornithologists' Union (Chesser et al. 2013). Analyses were restricted to birds from the Passeriformes and Piciformes. These two orders are the most species-rich in temperate interior forests of the region and have well-described phylogenetic relationships.

Phylogenetic Structure

We estimated phylogenetic relatedness of species in assemblages at each site relative to the relatedness of randomly constructed assemblages. Two related metrics were calculated from a pairwise phylogenetic distance matrix based on the branch lengths connecting each pair of species on a phylogenetic tree. Mean pairwise phylogenetic distance (MPD) is the average phylogenetic distance between all possible pairs of species in an assemblage; it quantifies the overall relatedness of the species in the assemblage (Webb et al. 2002). Mean nearest taxon distance (MNTD) is the average phylogenetic distance between each focal species and its most closely related species in the assemblage; it quantifies the relatedness of closest relatives in an assemblage (Webb et al. 2002).

To determine if assemblages are more phylogenetically clustered or even than expected by chance, we compared each assemblage to 999 randomly generated assemblages derived from a species pool. We used two species pools for these randomizations. The first included only species observed in at least one of the 20 forest sites in the region. This sample-based species pool reflects the definition of a species pool frequently applied in analyses of phylogenetic structure in the literature (Vamosi et al. 2009). We refer to this species pool as the “filtered species pool” as it potentially reflects the consequences of habitat filtering since all species were observed in a single habitat. We compare results of randomizations based on the filtered species pool to randomizations based on a larger species pool that includes potential species that are known to occur in the region, but that were not observed at any of the study sites. This “unfiltered species pool” was defined by including all species identified at study sites as well as all species (from the orders Passeriformes and Piciformes) identified during 2012 from Breeding Bird Survey routes in Connecticut. Importantly, the two species pools shared the same

geographic and temporal extent from which species were drawn. However, the species pools differed in the proportion of species likely to reside in the sampled habitat (i.e., interior forest). We generated random assemblages from the filtered species pool using the independent swap algorithm. This approach constrains species occurrence frequency and richness in randomized assemblages to be the same as in the empirical assemblages (Gotelli 2000). This null model has been shown to have high power to detect niche-based community assembly and does not suffer from high Type I error rates associated with many other community phylogenetic null models (Kembel 2009). Because the independent swap algorithm only uses species that occurred in empirical assemblages, we generated random assemblages from the unfiltered species pool with the “phylogeny pool” null model. This approach constrains species richness in randomized assemblages to be the same as in the empirical assemblages but draws species from the unfiltered pool with equal probability. Each empirical value of the metric (MPD or MNTD) is compared to the distribution generated via randomization to determine significance (two-tailed test, $\alpha = 0.05$). Significant phylogenetic overdispersion or clustering characterize an assemblage if an empirical metric occurred in the lowest or highest 2.5% of the corresponding simulated distribution, respectively.

We calculated a standard effect size for values of MPD and MNTD; these are analogous to the net relatedness index (NRI) and nearest taxon index (NTI) of Webb et al. (2002), respectively, where

$$\text{NRI} = -1(\text{MPD}_{\text{observed}} - \text{meanMPD}_{\text{random}})/\text{sdMPD}_{\text{random}}$$

$$\text{NTI} = -1(\text{MNTD}_{\text{observed}} - \text{meanMNTD}_{\text{random}})/\text{sdMNTD}_{\text{random}}$$

In particular, $\text{sdMPD}_{\text{random}}$ and $\text{sdMNTD}_{\text{random}}$ represent the standard deviation of the MPD and MNTD values, respectively, for the randomly generated assemblages at a site. Positive values of

NRI or NTI indicate that species in empirical assemblages are more phylogenetically related (i.e., phylogenetic clustering) than are those in random assemblages. Conversely, negative values indicate that species in empirical assemblages are less related (i.e., phylogenetic overdispersion) than are those in random assemblages. Assemblages that are randomly assembled with respect to phylogeny may reflect the outcomes of neutral processes such as dispersal (Kembel 2009) or multiple processes that act simultaneously but in opposite directions, obscuring any overall phylogenetic structure (Helmus et al. 2007).

To determine if changing the identity of the species pool had a significant effect on the outcome of tests of phylogenetic structure, we calculated the difference in values of NRI or NTI between unfiltered and filtered species pools. We used a paired t-test to quantify if the mean difference in indices based on the different species pools was equal to zero. A significant positive difference indicates weaker clustering or stronger overdispersion with the filtered pool than with the unfiltered pool, whereas a significant negative difference indicates stronger clustering or weaker overdispersion with the filtered pool than with the unfiltered pool.

Phylogenetic comparisons were based on branch lengths extracted from a comprehensive phylogeny of the world's bird species (Jetz et al. 2012). This phylogeny was inferred using a two-step protocol in which time-calibrated phylogenetic trees were estimated for well-supported bird clades and subsequently joined onto a backbone tree representing deep phylogenetic relationships (see Jetz et al. 2012 for methodological details). This tree represents an up-to-date synthesis of phylogenetic information for birds, allowing species-level inference that reflects uncertainty. To incorporate this uncertainty into the quantification of phylogenetic-based assessments, we randomly selected 1000 trees from the set of 10,000 trees based on the “Hackett

All Species” backbone (available at <http://birdtree.org>) and conducted all analyses based on this suite of phylogenetic information.

Functional Structure

We estimated functional similarity of species in assemblages at each site relative to the functional similarity of randomly constructed assemblages, by substituting a trait distance matrix for the phylogenetic distance matrix, and calculating functional equivalents of NRI (Net Functional Relatedness Index; NFRI) and NTI (Nearest Taxon Functional Index; NTFI) as above. We characterized functional traits of species with 3 categorical (i.e. food guild, foraging guild, residency) and 6 continuous characteristics (i.e. body mass, wing length, bill length, tail length, clutch size and egg mass). Categorical characteristics were associated with aspects of resource use, including type of food (insectivore or omnivore), where and how food is obtained (bark forager, ground forager, foliage gleaner, or flycatcher), and time over which resources are used locally (resident or migrant). Categorizations were based on the dominant resources used during the breeding season by the majority of individuals in each species. Continuous characteristics associated with body size and shape (mass, bill length, wing length and tail length), reflect resource use and physiological constraints related to diet and foraging, whereas clutch size and egg mass are estimates of reproductive effort and energetic demand, respectively. Continuous characteristics represent a mean for each species based on measurements of multiple adult individuals. Information for all functional attributes was derived from the literature, but was restricted to records from adults captured in North America, with preference for studies in Eastern North America (Pyle 1997; Poole 2005; Lislevand, Figuerola & Székely 2007).

Characterizations of species based on functional traits are more subjective than characterizations based on phylogenetic relationships. Most notably, the number and type of

functional traits, together with their correlations, can affect the level of redundancy that assemblages appear to exhibit (Petchey and Gaston 2006). Consequently, selection of traits represents an effort to balance between having a comprehensive set of functional traits and concerns about multicollinearity. To address this issue, we characterized functional attributes of species with two approaches. We evaluated the degree of similarity in assemblages based on all traits using Gower's distances, and refer to these as NFRI-all and NTFI-all. In addition, we characterize functional attributes of species on a subset of traits derived from morphological measurements (i.e., NFRI-morph and NTFI-morph). The link between morphological traits and ecology is relatively well established in birds. Avian bill measurements are a classic index of trophic niche (Hutchinson 1959; Schoener 1965; Grant and Grant 2006) and other measurements such as tail and wing length can be related to foraging ability, microhabitat, and substrate use (Miles and Ricklefs 1984). However, sets of traits often provide information about the same or overlapping niche axes. In addition, traits usually covary and measurements may differ by an order of magnitude within assemblages. To address differences in the scale of measurements, traits were log transformed and scaled to a mean of zero and variance of one. To identify independent trait axes from related morphological measurements, we used principal components analysis. The degree of morphological similarity in assemblages was ultimately estimated with metrics calculated from a distance matrix containing multiple orthogonal trait axes. Lastly, to evaluate individual niche axes, we used principal components axes separately to construct distance matrices.

In each functional approach, positive values of NFRI or NTFI indicate that species in an empirical assemblage are more similar in functional characteristics than are species in random assemblages, whereas negative values indicate that species in an empirical assemblage are less

similar in functional characteristics than are species in random assemblages. Significance of functional trait similarity was assessed using the independent swap algorithm, and the same randomization approach that was used in assessments of phylogenetic relatedness. All analyses were executed using the Picante package in R (Kembel et al. 2010).

Phylogenetic Signal

Determining the strength of phylogenetic signal is a critical step when using functional or phylogenetic information to infer mechanisms about community assembly (Losos 2008). Several methods have been developed for measuring the strength of phylogenetic signal in functional traits (i.e., a measure of the statistical dependence among species' trait values due to their phylogenetic relationships; Revell et al. 2008), and detailed assessments of the strengths and weaknesses of different measures exist (Munkemuller et al. 2012; Hardy and Pavione 2012). Consequently, we use two methods to assess the strength of phylogenetic signal in traits of birds. Pagel's λ (Freckleton et al. 2002, Pagel 1999) was used to evaluate functional traits estimated by continuous data (e.g. mass, wing length), whereas the D-statistic (Fritz and Purvis 2010) evaluated functional traits estimated by categorical data (e.g., foraging mode, migratory status). Each approach compares an empirical trait distribution on a phylogenetic tree to a simulated distribution based on a Brownian motion model; a null model of evolution widely used for testing hypotheses concerning trait evolution (Felsenstein, 1985, 1988). In a Brownian motion model, the state of a character can increase or decrease at each instant in time. The magnitude and direction of these shifts are random and independent of the current state of the character, and have a net change of zero (Felsenstein, 1988; O'Meara et al., 2006). When evolution occurs as a result of Brownian motion, variance among species accumulates in direct proportion to the phylogenetic branch lengths that separate them (Felsenstein, 1985, 2004).

A maximum-likelihood approach was used to estimate Pagel's λ for each continuous trait distribution and corresponding phylogeny. A maximum likelihood ratio test was used to determine whether estimated values of λ differed significantly from 0 (Freckleton et al. 2002). In general, if $\lambda = 0$, evolution of traits is independent of phylogeny; if $\lambda = 1$, the distribution of trait values in a phylogeny is consistent with a model of Brownian motion. Intermediate values of λ indicate that traits have evolved according to a process in which the effect of phylogeny is weaker than in the Brownian model, whereas values greater than 1 indicate a strong phylogenetic signal.

The D statistic provides an estimate of the strength of phylogenetic signal (Figure 2) in binary traits. To determine significance, this metric can be compared to a random rearrangement of trait values at the tips of a phylogeny as well as a Brownian threshold model (Fritz & Purvis 2010). If $D = 1$, traits are randomly distributed at the tips of the phylogeny. If $D = 0$, trait distributions correspond to a Brownian motion model of evolution. If $D < 0$, traits are highly conserved, whereas $D > 1$ indicates phylogenetic overdispersion. Significance was estimated by comparing estimates of D for each binary trait with simulated distributions based on 1000 permutations of D under (1) randomly reshuffled trait values across the tips of the tree, and (2) trait allocation based on Brownian motion. The strength of phylogenetic signal in functional traits was estimated as the mean of a test statistic (D or λ) and of a p-value derived from 1000 phylogenetic trees. Tests of phylogenetic signal were executed with the R packages Caper (Orme et al. 2012) and phytools (Revell et al. 2012).

Results

Forty-three species were identified with the combination of ARU and point count methods (filtered species pool). Most species were insectivores that obtain food by foraging on

the ground or by gleaning insects from foliage (Table 1). Species richness of empirical assemblages ranged from 15 to 28 species. In contrast, 88 species were identified as members of the unfiltered species pool. A phylogenetic signal was present in continuous (Table 2) and categorical traits (Table 3). A strong signal characterized most continuous traits, whereas a signal consistent with Brownian evolution characterized most categorical traits.

From a phylogenetic perspective, minimal variation was observed among estimates of phylogenetic structure derived from 1000 trees, regardless of metric (Figure 2). Variation in NRI was not related to variation in NTI. In contrast, phylogenetic structure based on metrics derived from different species pools (filtered vs. unfiltered) were highly correlated for both NRI and NTI (Table 4). Although estimates of phylogenetic structure were correlated, estimates of NRI derived from the unfiltered species pool were more strongly indicative of phylogenetic overdispersion than were estimates derived from the filtered species pool (paired t-tests: $t = -8.37$, $p < 0.001$). Conversely, estimates of NTI derived from the unfiltered species pool were more indicative of phylogenetic clustering than were estimates derived from the filtered species pool (paired t-tests: $t = 3.25$, $p = 0.004$). Regardless of species pool, variation in NRI was associated with variation in the proportion of residents in assemblages (NRI-unfiltered: $R^2 = 0.490$, $p\text{-value} < 0.001$; NRI-filtered: $R^2 = 0.449$, $p\text{-value} < 0.001$) but not with variation in the species richness of assemblages (NRI-unfiltered: $R^2 = 0.001$, $p\text{-value} = 0.326$; NRI-filtered: $R^2 = 0.107$, $p\text{-value} = 0.086$).

Two orthogonal functional trait axes were identified from principal components analysis of four morphological traits. The first axis explained 92% of the variation and most strongly reflected the influence of mass and wing length, and can be considered to be an index of body size. The second axis explained 6% of variation and was an index of shape (i.e., bill length to

tail length ratio) and potentially reflects prey selection and foraging location (Table S5). Variation in functional structure based on combined axes of functional characteristics (i.e., all traits vs. morphological axes) were highly correlated for NFRI, but were not significantly correlated for NTFI (Table S5). In contrast, variation in functional structure based on independent functional axes (i.e., principal component axis 1 vs. principal component axis 2) was not significantly correlated for either metric (Table S6). In general, variation in NFRI was not related to variation in NTFI if both metrics were derived from the same characteristics. Regardless of metric, functional similarity of species in empirical assemblages generally did not differ significantly from randomly constructed assemblages (Tables S4, S5).

Discussion

Functional structure of assemblages

Different traits of species are often associated with particular niche axes (Violle et al. 2007). Furthermore, the number and identity of traits included in an analysis can influence the strength or type of community structure identified (Petchey and Gaston 2006). Metrics that combine traits from multiple niche axes may have the advantage of providing an integrated overview of community structure. Nonetheless, a potential drawback of metrics that incorporate multiple traits is that they may combine the signals of contrasting assembly processes (Swenson and Enquist 2009). This could obscure identification of niche-based assembly processes if multiple processes nullify each other's signal, generating patterns indistinguishable from neutral dynamics (Kraft et al. 2007; Weiher et al. 2011; Spasojevic and Suding 2012; Trisos et al. 2014). We employed three functional classifications of species that differed in the number and identity of niche axes described to determine if these uncertainties with trait-based approaches would influence conclusions.

We rarely identified assemblages that were more or less similar in functional characteristics than expected by chance (Table S5, S6) regardless of classification used to characterize the functional characteristics of species or the metric of functional structure (i.e., NFRI or NTFI). As a result, it is likely that absence of functionally clumped or overdispersed assemblage structure in temperate interior forest birds reflects true similarity among sites in species composition rather than an artifact of using single or multi-trait assessments (Trisos et al. 2014). The species pool for these analyses included only the individuals identified from the 20 study sites. By restricting the species pool to only include species found in a single habitat type, it is highly likely that species are functionally similar in many regards, and that the likelihood of detecting significant departures from random assembly may be lower than in studies that incorporate a range of habitat types. We are aware of only one other study that has evaluated variation in patterns of functional assemblage structure in birds using similar approaches (Dehling et al. 2013), although others have evaluated phylogenetic structure (e.g., Graham et al. 2009; Gianuca et al. 2013). Dehling and colleagues evaluated functional structure along an extensive elevational gradient in the tropics and found evidence of clustering and overdispersion, as well as no structure. Variation in functional structure generally corresponded to variation in habitat types. Furthermore the species pool used in analyses included species from all habitat types which may influence their ability to detect significant functional structure. Consequently, we are unable to determine the nature of differences between studies in the identification of functional structure of bird communities. Differences in results could be a consequence of differences in biogeographic or evolutionary history between temperate and tropical assemblages, or a consequence of habitat heterogeneity and the makeup of the species pool.

Role of the species pool

The nature of the species pool, and the domain from which it is constructed, plays a critical role in determining the strength of environmental signals (Cavender-Bares et al. 2006; Swenson et al. 2006; Kraft & Ackerly 2010). Indeed, the strength and nature of phylogenetic structure in interior forest bird assemblages was predicated on the identity of the species pool. Species in the filtered pool were all observed in a single habitat type whereas species in the unfiltered pool were observed in multiple different habitat types. Consequently, if habitat filtering is driving assemblage structure, this mechanism should result in more clustering when phylogenetic structure is compared to assemblages derived from an unfiltered, rather than a filtered species pool (Cavender-Bares et al. 2006; Swenson et al. 2006; Kraft et al. 2007; Swenson et al. 2007; Eiserhardt et al. 2013). Our results contradict these expectations. Phylogenetic structure of assemblages (based on NRI) was more frequently indicative of overdispersion when compared to randomized assemblages drawn from an unfiltered species pool than when randomized assemblages were drawn from a filtered species pool. Based on traditional interpretations of phylogenetic clustering and overdispersion in assemblages, our results suggest there are at least two mechanisms that could lead to differences between our results and what was expected based on prior research. Our explanations take into account results of statistical tests indicating that functional traits show a phylogenetic signal that suggests closely related species are more similar than expected due to chance (Tables 2, 3; Cavender-Bares et al. 2009). One explanation is that habitat filtering is occurring, but results in many small (2 or 3 species) clusters of closely related species occurring at sites, and these clusters are evenly distributed across the phylogeny. An alternative explanation is that competition between closely-related species structures assemblages, and the effect of this process is magnified when additional species from the region are included. This would suggest that additional species in the

unfiltered species pool that were not observed in the study are closely related to species that were observed, and that those species more frequently occur in other habitat types (e.g., edge habitats, grasslands, shrublands). This could indicate that either these species were historically outcompeted in forests habitat or that the habitat component of species niches are not conserved. A suggestion that species niches in general are not conserved seems unlikely, considering results from tests of phylogenetic signal (Table 2, 3). However we did not explicitly test for a phylogenetic signal in habitat specificity, and previous studies in vertebrates suggest that habitat selection or specificity may be more labile than other niche-associated traits (Losos et al. 2003; Trisos et al. 2014).

We gain insight into which of these explanations is more likely by comparing relationships between NRI and NTI, and visually inspecting phylogenetic positions of species in assemblages with different structures (Figure 3). NRI provides a measure of phylogenetic clumping of taxa over the complete phylogeny, whereas NTI is a measure of the degree of clumping among only the most closely related species (i.e., terminal taxa, or tips of the phylogeny) in the assemblage. Consequently, NRI is more sensitive to patterns that result from habitat filtering whereas NTI is more sensitive to patterns that result from interactions between closely-related species (Webb et al. 2002; Kraft et al. 2007). Based on these assumptions, we should see a stronger pattern of overdispersion with NTI if competition is strongly influencing assemblage structure, and variation in NRI should be related to variation in NTI. In contrast, if habitat filtering is leading to assemblages that comprise several small clusters of closely related species that are evenly distributed across the phylogeny, we would expect estimates of NRI and NTI to be uncorrelated, and estimates of NTI should generally be indicative of clustering, even when NRI is not. Our results favor the idea that phylogenetic structure in interior forest bird

assemblages is more strongly influenced by habitat filtering rather than competition. However, support for this explanation is not overwhelming, particularly considering the variation in strength of phylogenetic patterns among sites, metrics, and species pools (Figure 2). Moreover, when comparing the distribution of species on the phylogeny from an overdispersed and a clumped assemblage (Figure 3), we see mixed support for habitat filtering and exclusion of closely-related species in a single assemblage. In the overdispersed assemblage, a clump of closely-related species are present at the top of the phylogeny, but few closely-related species co-occur throughout the remainder of the tree. Furthermore, when comparing the filtered species pool tree to the unfiltered species pool tree we can identify instances where closely-related species are added to existing clades as well as instances where new clades are added. Uncertainty regarding the dominant mechanism structuring assemblages is not unusual in studies of community phylogenetic structure (Vamosi et al. 2009). This uncertainty is often attributed to environmental differences among sites or to the consequences of competition and filtering acting at different scales (e.g., Lovette and Hochachka 2006). Although these explanations are reasonable, it is possible another mechanism is structuring patterns of phylogenetic relatedness of interior forest bird assemblages.

Determinants of phylogenetic structure

Most forest interior bird assemblages exhibited phylogenetic structure consistent with random assembly (Figure 2). However, twenty-five percent of sites were either significantly clumped or significantly over-dispersed in at least one test. Such results could be viewed as evidence that multiple assembly processes (e.g., habitat filtering, competition of closely related species) are acting simultaneously. Such an explanation seems most reasonable if the geographic domain of the study spans biogeographic regions, or if the locations being compared differ

significantly in habitat quality, or if species differ greatly in competitive ability (Lovette and Hochachka 2006; Gomez et al. 2010; Mayfield and Levine 2010). In contrast, the geographic extent of this study represented a single biogeographic region. Moreover, all assemblages were located in a single habitat type (forest), with species from a single species pool colonizing sites. These characteristics make the idea of multiple assembly processes exerting highly divergent degrees of influence, leading to multiple different phylogenetic structures less compelling. Alternatively, we propose that variation in the phylogenetic structure of temperate forest interior bird assemblages in our study domain is the consequence of priority effects exerted by residents and the first arriving migrants that influences subsequent colonization of sites by later-arriving migrants. Priority effects can cause unexpectedly high variability in community structure, among environmentally similar sites (Chase 2003; Fukami 2004; Chase 2010), rather than a single pervasive phylogenetic structure determined by environmental conditions and interspecific interactions (e.g. Drake 1991; Chase 2003; Fukami 2004; Fukami et al. 2010; Tan et al. 2012). Essentially, assemblages of temperate forest bird communities may represent alternative stable states (Lewontin 1969), from a phylogenetic perspective.

In general, temperate bird communities annually assemble and disassemble, with only a portion of the inhabitants (i.e., migrants) participating in yearly colonization. Consequently, the phylogenetic structure of temperate breeding bird assemblages likely reflects the influence of assembly processes occurring on two distinct groups of birds. Assembly processes determine the presence of resident species, with the structure of resident assemblages likely being relatively similar from year to year. In contrast, separate assembly processes annually influence colonization by migrant species, potentially leading to greater variation among sites and years.

Consequently, local assemblages from sites with similar environmental conditions can be quite variable in their species composition.

Residents have territories established prior to arrival of migrants and can invest more time and energy in directly assessing the relative quality of available habitat patches. Furthermore, offspring of residents exhibit high natal philopatry (Weatherhead and Forbes 1994), and populations of resident species are influenced by the environmental conditions of the non-breeding season (Lack, 1966; Fretwell, 1972; Forsman & Mönkkönen, 2003), suggesting that environmental characteristics play a dominant role in determining where residents reside. In contrast, migrants are more time-constrained in their decisions, because habitat selection, pairing, nest building, and reproduction must be accomplished within a few weeks after arrival. Moreover, migrants generally exhibit low natal philopatry and adults may change breeding sites from year to year (Weatherhead & Forbes 1994; Schlossberg 2009), suggesting that environmental characteristics may play less of a role in site selection and colonization may be more strongly influenced by interactions with residents and early-arriving migrants that are already established at sites.

We identified a strong relationship between the proportion of residents and phylogenetic relatedness (NRI; Figure 3), and these relationships were unrelated to the species richness of assemblages. Assemblages comprising a greater proportion of residents than migrants were phylogenetically overdispersed (Figure 2). In contrast, assemblages with relatively equal numbers of residents and migrants were generally either phylogenetically clustered or indistinguishable from random. Assemblages with many more migrants than residents were not observed in the study, so we could not ascertain if these assemblages would always be phylogenetically clustered. It has been hypothesized that an inverse relationship between the

relative proportions of migrants and residents occurs because of asymmetric interspecific competition in which residents are superior (MacArthur 1972; Herrera 1978; Morse 1989). This hypothesis is consistent with the pattern that assemblages with a greater proportion of residents results in greater phylogenetic overdispersion as a consequence of interspecific interactions where residents prevent migrants with similar niches from colonizing. Alternatively, it has been suggested that resident bird densities in northern environments (i.e., boreal and temperate forests) will rarely reach high enough densities to initiate competitive effects (Thomson et al. 2003). In fact, migrants may actually use the presence of residents as an indicator of habitat quality (especially if there is high niche overlap between species) and their presence in a habitat patch may be used as a settlement cue for migrants (i.e., heterospecific attraction, Monkkonen et al. 1990; Monkkonen et al. 1997; Monkkonen and Forsman 2002). If this was occurring, we would expect to see few assemblages with disproportionately high numbers of residents and evidence of assemblages that were more functionally similar than expected due to chance (Table S4); this was not the case. Regardless of mechanism, it is clear that residents play a dominant role in affecting the structure of breeding bird assemblages in temperate forests (e.g., Gustafsson 1987; Monkkonen et al. 1990; Monkkonen et al. 1997; Martin and Martin 2001; Monkkonen and Forsman 2002; Thomson et al. 2003). Furthermore, our results are consistent with previous work suggesting that in temperate breeding bird communities, resident populations are limited by the period of lowest productivity whereas migrants respond primarily to the presence and abundances of other species in the community and their abundances depend on the production of the environment not used by residents. (MacArthur 1972; Herrera 1978; Hurlbert and Haskell 2003; Monkkonen et al. 2006). Akin to priority effects leading to alternative stable states, variation in resident species composition may lead to alternative phylogenetic structures of

assemblages even if environmental conditions of sites are similar and support similar numbers of species.

Conclusions

We found little evidence for differences in phylogenetic community structure as a result of changing the species pool of inference. Our results suggest that independent assembly mechanisms structure resident and migratory subsets of temperate breeding bird communities. These findings indicate that priority effects may play a critical role in determining the phylogenetic structure of temperate breeding bird communities, and have the potential to lead to multiple alternative community structures in similar environments. Priority effects present a fundamental challenge in explaining the composition of communities because species arrival history is often impossible to know in detail. Nonetheless, temperate breeding bird communities offer a unique opportunity to study this mechanism because a proportion of the species (residents) are known to occur in the community prior to colonization by other species, and represent an analog of the first colonists in other study systems. We hypothesize that priority effects may influence bird assemblages and lead to multiple stable states based on data from spatial replicates with similar environmental conditions. However, this system also allows for replicates in time that could more closely simulate “exact environmental conditions” required for stronger tests of theory if the same sites are surveyed across multiple years. Moreover, in a multi-year design, spatial replicates could represent a gradient in environmental conditions and additional predictions of derived from theory on alternative stable states could be tested (Chase 2003). Most studies that have examined factors that influence the phylogenetic structure of communities focus comparisons on the relative role of environmental filtering versus competition in determining observed patterns (Vamosi et al. 2009). An important avenue for

future research is to incorporate colonization history or similar effects when considering the relative roles of filtering and competition in structuring assemblages.

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Table 1. Functional attributes of bird species that were used to estimate functional diversity. Each numerical value represents the mean for the trait. Data were extracted from Pyle (1997), Lislevand, Figueroa & Székely (2004), and Poole (2005).

Order	Family	Scientific name	Common name	Diet	Foraging	Residency	Mass	Wing length	Bill length	Tail length	Clutch size	Egg mass
Piciformes	Picidae	<i>Melanerpes erythrocephalus</i>	Red-headed Woodpecker	Omnivore	Flycatching	Migratory	71.60	138.00	26.95	74.70	4.74	5.10
Piciformes	Picidae	<i>Melanerpes carolinus</i>	Red-bellied Woodpecker	Insectivore	Bark forager	Resident	70.45	140.50	29.10	77.25	4.24	4.60
Piciformes	Picidae	<i>Sphyrapicus varius</i>	Yellow-bellied Sapsucker	Insectivore	Bark forager	Migratory	50.30	124.20	23.05	72.10	4.79	3.40
Piciformes	Picidae	<i>Picoides pubescens</i>	Downy Woodpecker	Insectivore	Bark forager	Resident	28.20	97.03	15.86	56.10	4.79	2.50
Piciformes	Picidae	<i>Picoides villosus</i>	Hairy Woodpecker	Insectivore	Bark forager	Resident	65.50	121.73	32.40	77.15	3.93	4.30
Piciformes	Picidae	<i>Colaptes auratus</i>	Northern Flicker	Insectivore	Ground forager	Resident	135.70	151.11	26.23	105.80	6.66	7.30
Piciformes	Picidae	<i>Dryocopus pileatus</i>	Pileated Woodpecker	Insectivore	Bark forager	Resident	287.00	236.35	47.10	170.50	3.83	11.00
Passeriformes	Tyrannidae	<i>Contopus virens</i>	Eastern Wood-pewee	Insectivore	Flycatching	Migratory	14.10	81.45	11.55	64.60	3.00	1.77
Passeriformes	Tyrannidae	<i>Sayornis phoebe</i>	Eastern Phoebe	Insectivore	Flycatching	Migratory	18.30	84.45	14.45	70.85	4.58	2.32
Passeriformes	Tyrannidae	<i>Myiarchus cinerascens</i>	Great Crested Flycatcher	Insectivore	Flycatching	Migratory	33.50	101.35	14.98	88.35	5.00	3.65
Passeriformes	Vireonidae	<i>Vireo flavifrons</i>	Yellow-throated Vireo	Insectivore	Foliage gleaner	Migratory	18.00	76.05	11.20	48.80	3.60	2.40
Passeriformes	Vireonidae	<i>Vireo olivaceus</i>	Red-eyed Vireo	Insectivore	Foliage gleaner	Migratory	16.40	78.40	12.60	50.60	3.18	2.33
Passeriformes	Corvidae	<i>Cyanocitta cristata</i>	Blue Jay	Omnivore	Ground forager	Resident	71.65	122.74	24.98	117.60	4.18	5.90
Passeriformes	Corvidae	<i>Corvus brachyrhynchos</i>	American Crow	Omnivore	Ground forager	Resident	516.00	310.45	32.50	176.10	4.68	17.50
Passeriformes	Corvidae	<i>Corvus corax</i>	Common Raven	Omnivore	Ground forager	Resident	782.50	421.40	76.30	211.50	4.10	28.80
Passeriformes	Paridae	<i>Baeolophus bicolor</i>	Tufted Titmouse	Insectivore	Foliage gleaner	Resident	21.15	78.25	12.05	67.65	6.00	1.90
Passeriformes	Paridae	<i>Poecile atricapillus</i>	Black-capped Chickadee	Insectivore	Foliage gleaner	Resident	12.95	64.65	9.05	60.50	7.00	1.16
Passeriformes	Sittidae	<i>Sitta canadensis</i>	Red-breasted Nuthatch	Insectivore	Bark forager	Resident	10.50	67.00	13.80	36.00	5.78	1.15
Passeriformes	Sittidae	<i>Sitta carolinensis</i>	White-breasted Nuthatch	Insectivore	Bark forager	Resident	21.10	90.05	19.10	47.30	7.30	1.95
Passeriformes	Troglodytidae	<i>Troglodytes aedon</i>	Winter Wren	Insectivore	Ground forager	Resident	8.90	48.35	13.65	29.05	5.61	1.32
Passeriformes	Turdidae	<i>Catharus fuscescens</i>	Veery	Insectivore	Ground forager	Migratory	41.50	96.40	13.50	65.05	3.90	3.40
Passeriformes	Turdidae	<i>Catharus guttatus</i>	Hermit Thrush	Insectivore	Ground forager	Migratory	27.31	91.00	14.10	64.10	3.38	3.10
Passeriformes	Turdidae	<i>Hylocichla ustulata</i>	Wood Thrush	Insectivore	Ground forager	Migratory	50.15	106.75	11.20	69.60	3.30	4.85
Passeriformes	Turdidae	<i>Turdus migratorius</i>	American Robin	Insectivore	Ground forager	Resident	79.95	127.60	23.50	99.05	3.15	6.25
Passeriformes	Minidae	<i>Dumetella carolinensis</i>	Gray Catbird	Omnivore	Ground forager	Migratory	37.65	89.10	11.40	88.85	3.68	3.80
Passeriformes	Parulidae	<i>Seiurus aurocapilla</i>	Ovenbird	Insectivore	Ground forager	Migratory	22.10	74.90	11.80	54.05	4.31	2.59
Passeriformes	Parulidae	<i>Parkesia motacilla</i>	Louisiana Waterthrush	Insectivore	Ground forager	Migratory	20.65	79.75	13.35	51.30	4.96	2.51
Passeriformes	Parulidae	<i>Parkesia noveboracensis</i>	Northern Waterthrush	Insectivore	Ground forager	Migratory	16.50	74.80	10.25	51.30	4.21	2.19
Passeriformes	Parulidae	<i>Mniotilta varia</i>	Black-and-white Warbler	Insectivore	Bark forager	Migratory	12.00	66.50	11.33	42.85	5.00	1.60
Passeriformes	Parulidae	<i>Geothlypis trichas</i>	Common Yellowthroat	Insectivore	Foliage gleaner	Migratory	10.10	53.00	10.60	47.50	3.99	1.62
Passeriformes	Parulidae	<i>Setophaga citrina</i>	Hooded Warbler	Insectivore	Foliage gleaner	Migratory	10.55	66.25	10.00	55.55	3.61	1.68
Passeriformes	Parulidae	<i>Setophaga ruticilla</i>	American Redstart	Insectivore	Foliage gleaner	Migratory	8.65	62.30	8.65	54.60	3.89	1.33
Passeriformes	Parulidae	<i>Setophaga cerulea</i>	Cerulean Warbler	Insectivore	Foliage gleaner	Migratory	8.65	63.40	9.59	41.65	3.53	1.49
Passeriformes	Parulidae	<i>Setophaga magnolia</i>	Magnolia Warbler	Insectivore	Foliage gleaner	Migratory	8.60	59.31	8.98	48.75	3.96	1.31
Passeriformes	Parulidae	<i>Setophaga caerulescens</i>	Black-throated Blue Warbler	Insectivore	Foliage gleaner	Migratory	9.40	63.15	9.30	49.80	3.80	1.49
Passeriformes	Parulidae	<i>Setophaga pinus</i>	Pine Warbler	Insectivore	Foliage gleaner	Migratory	11.90	71.25	10.75	51.00	3.74	1.73
Passeriformes	Parulidae	<i>Setophaga virens</i>	Black-throated Green Warbler	Insectivore	Foliage gleaner	Migratory	9.30	61.90	12.76	46.90	4.00	1.44
Passeriformes	Parulidae	<i>Cardellina canadensis</i>	Canada Warbler	Insectivore	Foliage gleaner	Migratory	10.40	62.30	10.70	52.85	4.37	1.56
Passeriformes	Emberizidae	<i>Pipilo erythrophthalmus</i>	Eastern Towhee	Omnivore	Ground forager	Migratory	40.50	83.75	14.15	88.55	3.40	3.65
Passeriformes	Emberizidae	<i>Spizella passerina</i>	Chipping Sparrow	Omnivore	Ground forager	Migratory	12.75	69.90	9.40	60.55	3.70	1.60
Passeriformes	Cardinalidae	<i>Piranga olivacea</i>	Scarlet Tanager	Insectivore	Foliage gleaner	Migratory	28.30	92.90	11.30	66.75	3.45	3.31
Passeriformes	Cardinalidae	<i>Cardinalis cardinalis</i>	Northern Cardinal	Insectivore	Ground forager	Resident	41.35	93.85	12.65	97.60	2.50	4.58
Passeriformes	Cardinalidae	<i>Pheucticus ludovicianus</i>	Rose-breasted Grosbeak	Insectivore	Foliage gleaner	Migratory	44.60	103.45	16.90	72.25	3.27	4.08

Table 2. Evaluation of phylogenetic signal (λ) for continuous functional traits of birds. Significance tests determine whether empirical values differed significantly from 0 (i.e., those produced by random processes). Bold values indicate significance ($p \leq 0.05$).

Trait	λ	$\text{Pr}(\lambda) = 0$
Mass	1.036	<0.001
Bill	0.767	<0.001
Tail	1.044	<0.001
Wing	1.038	<0.001
Clutch size	0.983	<0.001
Egg mass	1.021	<0.001

Table 3. Evaluation of phylogenetic signal (D) for categorical functional traits of birds. Significance was determined by comparing empirical values of D for each binary trait with simulated distributions based on 1000 permutations of D obtained by randomly reshuffling trait values across the tips of the tree [$\text{Pr}(\text{D}) = 1$] and trait allocation based on Brownian motion [$\text{Pr}(\text{D}) = 0$]. Bold values indicate significance ($p \leq 0.05$).

Functional Component	Trait	D	$\text{Pr}(\text{D}) = 1$	$\text{Pr}(\text{D}) = 0$
Diet	Insectivore	-0.135	0.014	0.826
	Omnivore	-0.134	0.014	0.826
Foraging	Ground	-0.051	<0.001	0.894
	Flycatching	-1.083	<0.001	0.225
	Foliage	-0.510	<0.001	0.290
	Bark	0.025	0.006	0.952
Migratory	Resident	-0.134	<0.001	0.745
	Migrant	-0.135	<0.001	0.744

Table 4. Spearman rank correlations (Rho) and associated p-values between estimates of functional and phylogenetic structure of 20 interior forest assemblages. See text for descriptions of species pool (i.e., filtered and unfiltered) and functional characteristics (i.e., all, morph, size and shape) particular metrics are associated with. Bold values indicate significance ($p \leq 0.05$).

Comparison	Rho	p-value
Phylogenetic		
NRI-filtered - NTI-filtered	-0.340	0.143
NRI-unfiltered - NTI-unfiltered	-0.139	0.555
NRI-filtered - NRI-unfiltered	0.970	< 0.001
NTI-filtered - NTI-unfiltered	0.806	< 0.001
Functional		
NFRI-all - NTFI-all	0.388	0.092
NFRI-morph - NTFI-morph	0.156	0.509
NFRI-size - NTFI-size	-0.017	0.947
NFRI-shape - NTFI-shape	0.007	0.977
NFRI-all - NFRI-morph	0.899	< 0.001
NTFI-all - NTFI-morph	0.408	0.076
NFRI-size - NFRI-shape	-0.427	0.062
NTFI-size - NTFI-shape	0.332	0.152

Figure Legends

Figure 1. Map of study area in Connecticut, USA represented by forest (dark gray) non forest (light gray), and water (white). The locations of 20 interior forest sites are indicated by number (see supplementary material for geographic coordinates). The location of Connecticut in northeastern North America is indicated by shaded area in lower right corner map.

Figure 2. Net relatedness index (top) and nearest taxon index (bottom) of bird assemblages from each of 20 temperate interior forest sites. Light gray bars indicate results based on the filtered species pool. Dark gray bars indicate results based on the unfiltered species pool. Error bars indicate standard deviation of index values calculated from 1000 phylogenetic trees (see text for details). Positive index values indicate phylogenetic clustering; negative index values indicate phylogenetic evenness. Index values that significantly differed ($\alpha = 0.05$) from null expectations are indicated by an asterisk. The number of migratory and resident species in each assemblage, and the proportion of residents in each assemblage are included between graphs. Sites are ordered by the proportion of residents in assemblages.

Figure 3. Variation in phylogenetic relatedness (NRI) in relation to the proportion of resident bird species for twenty temperate forest bird assemblages. Black circles represent assemblages with phylogenetic structure (i.e., clustering or evenness) that significantly differed ($\alpha = 0.05$) from null expectations. Gray circles represent structure consistent with random assembly. Solid line represents significant linear relationship ($p \leq 0.05$) and R^2 indicates the fit of the model.

Figure 4. Example phylogenies (1 of 1000 analyzed for each species pool) of the filtered species pool (inset) and unfiltered species pool. Black dots indicate the phylogenetic positions of species present at 3 sites (from left to right, Sleeping, Macedonia and Roraback). Sites were selected as representations of overdispersed, random and clustered phylogenetic assemblage structure determined by NRI.

Figure 1

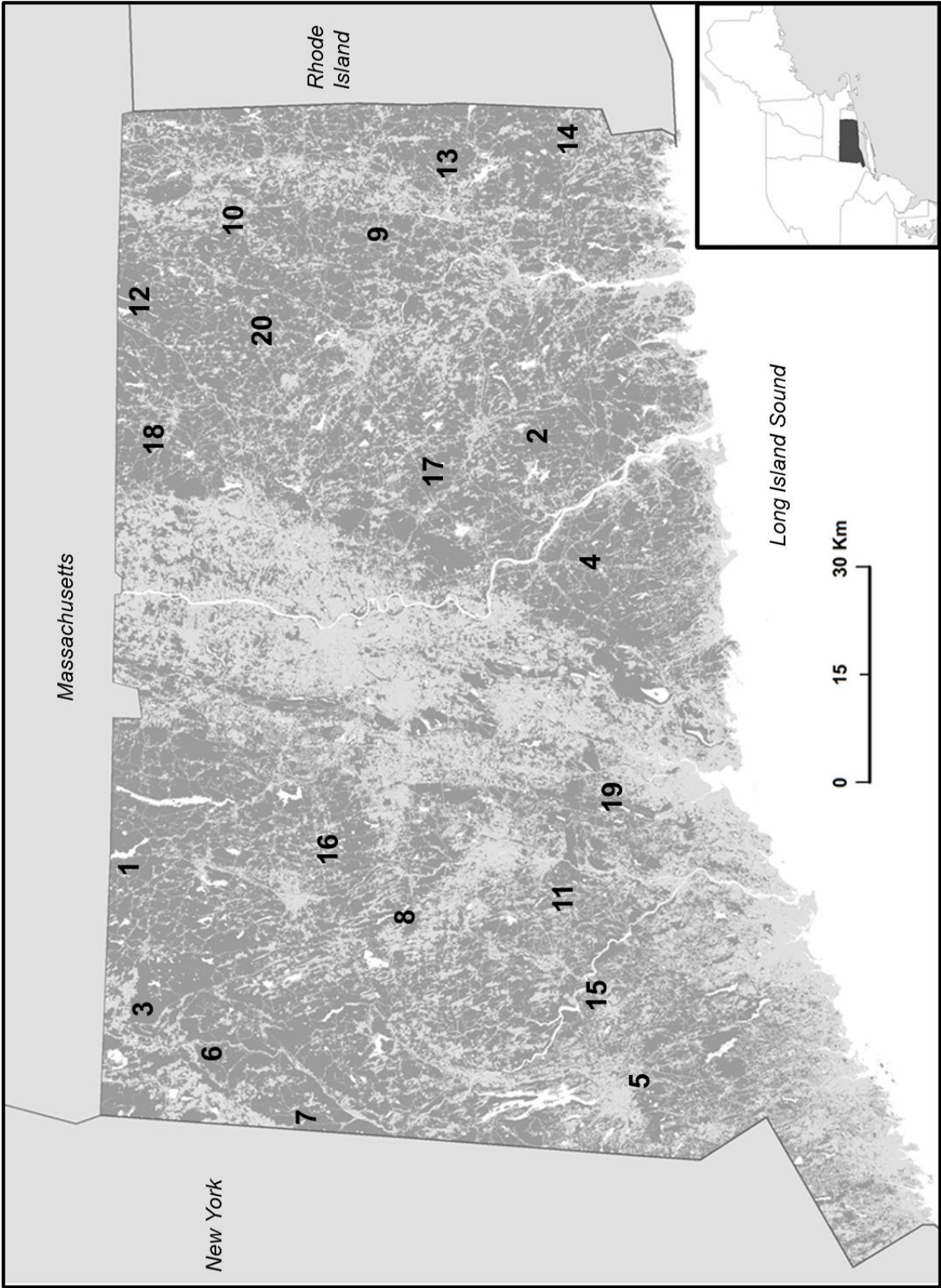


Figure 2

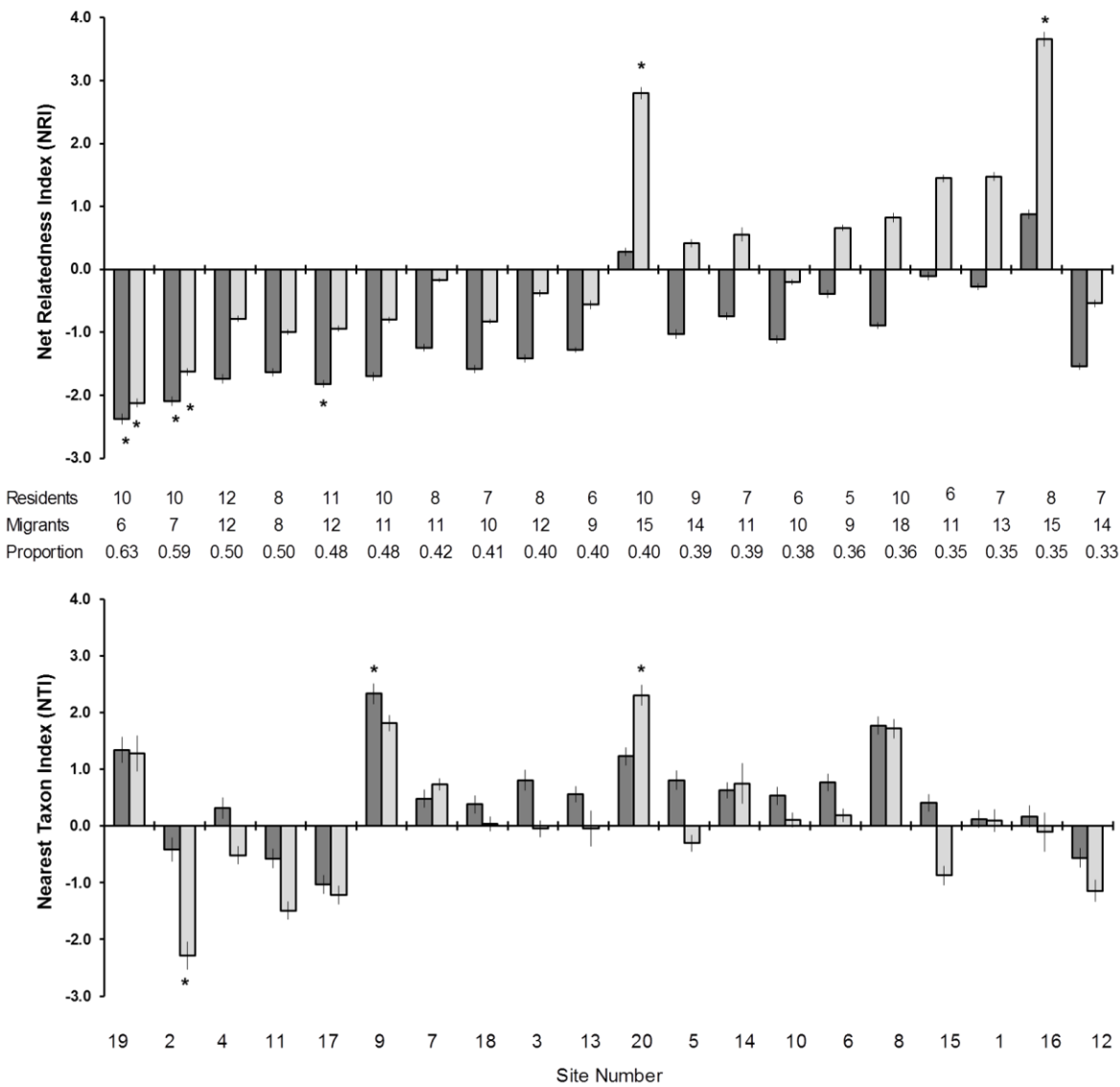


Figure 3

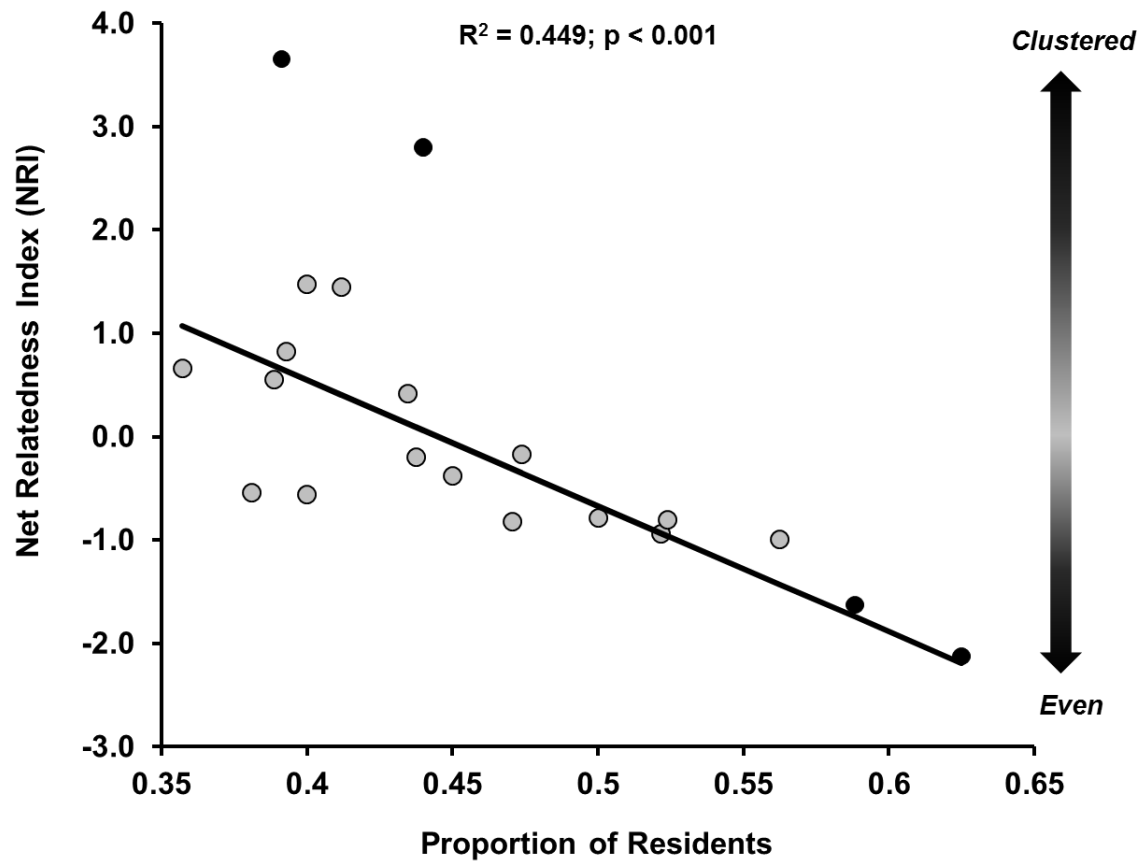
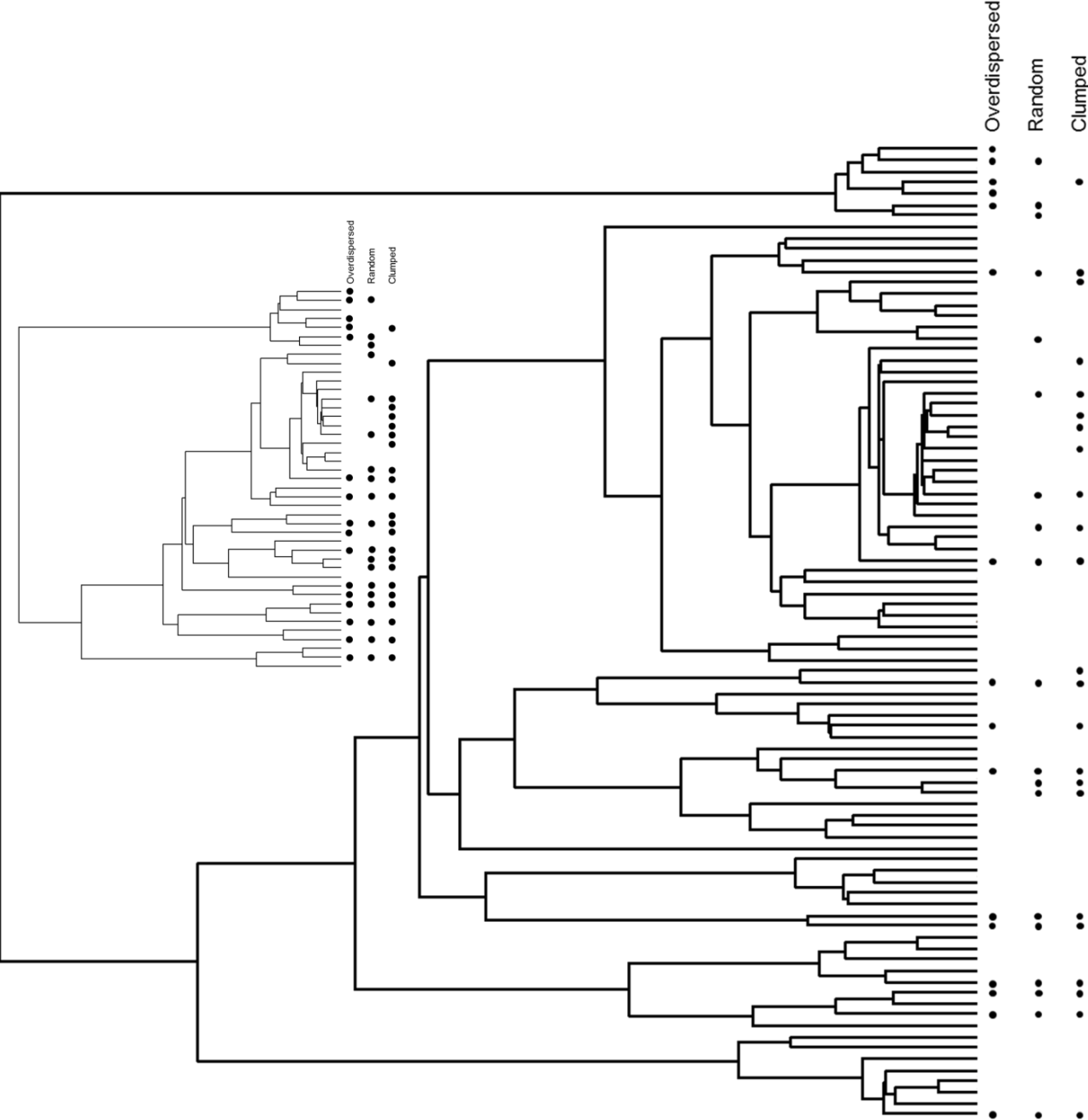


Figure 4



Supporting Information

Table S1. Geographic locations of 20 interior forest sites. Latitude and longitude (decimal degrees) represent the center of each site. Numbers correspond to site locations indicated on inset map of Figure 1.

Site number	Site name	Latitude	Longitude
1	Algonquin	41.988	-73.058
2	Babcock	41.522	-72.405
3	Canaan	42.005	-73.296
4	Cockaponsett	41.473	-72.536
5	Collis	41.346	-73.349
6	Housatonic	41.905	-73.406
7	Macedonia	41.775	-73.488
8	Mattatuck	41.646	-73.089
9	Mohegan	41.670	-72.069
10	Natchaug	41.856	-72.057
11	Naugatuck	41.461	-73.046
12	Nipmuck	42.025	-72.176
13	PachaugN	41.595	-71.887
14	PachaugS	41.484	-71.859
15	Paugusset	41.405	-73.197
16	Roraback	41.732	-73.059
17	Salmon	41.618	-72.378
18	Shenipsit	42.000	-72.399
19	Sleeping	41.436	-72.889
20	Uconn	41.820	-72.236

Table S2. List of species included in regional species pool. Names followed by an asterisk indicate species that were also included the study-based species pool.

Scientific name	Common name
<i>Melanerpes erythrocephalus</i>	Red-headed Woodpecker*
<i>Melanerpes carolinus</i>	Red-bellied Woodpecker*
<i>Sphyrapicus varius</i>	Yellow-bellied Sapsucker*
<i>Picoides pubescens</i>	Downy Woodpecker*
<i>Picoides villosus</i>	Hairy Woodpecker*
<i>Colaptes auratus</i>	Northern Flicker*
<i>Dryocopus pileatus</i>	Pileated Woodpecker*
<i>Contopus virens</i>	Eastern Wood-Pewee*
<i>Empidonax virescens</i>	Acadian Flycatcher
<i>Empidonax alnorum</i>	Alder Flycatcher
<i>Empidonax traillii</i>	Willow Flycatcher
<i>Empidonax minimus</i>	Least Flycatcher
<i>Sayornis phoebe</i>	Eastern Phoebe*
<i>Myiarchus crinitus</i>	Great Crested Flycatcher*
<i>Tyrannus tyrannus</i>	Eastern Kingbird
<i>Vireo griseus</i>	White-eyed Vireo
<i>Vireo flavifrons</i>	Yellow-throated Vireo*
<i>Vireo solitarius</i>	Blue-headed Vireo
<i>Vireo gilvus</i>	Warbling Vireo
<i>Vireo olivaceus</i>	Red-eyed Vireo*
<i>Cyanocitta cristata</i>	Blue Jay*
<i>Corvus brachyrhynchos</i>	American Crow*
<i>Corvus ossifragus</i>	Fish Crow
<i>Corvus corax</i>	Common Raven*
<i>Progne subis</i>	Purple Martin
<i>Tachycineta bicolor</i>	Tree Swallow
<i>Stelgidopteryx serripennis</i>	Northern Rough-winged Swallow
<i>Riparia riparia</i>	Bank Swallow
<i>Hirundo rustica</i>	Barn Swallow
<i>Parus atricapillus</i>	Black-capped Chickadee*
<i>Baeolophus bicolor</i>	Tufted Titmouse*
<i>Sitta canadensis</i>	Red-breasted Nuthatch*
<i>Sitta carolinensis</i>	White-breasted Nuthatch*
<i>Troglodytes troglodytes</i>	Winter Wren*
<i>Thryothorus ludovicianus</i>	Carolina Wren
<i>Troglodytes aedon</i>	House Wren
<i>Cistothorus palustris</i>	Marsh Wren
<i>Poliophtila caerulea</i>	Blue-gray Gnatcatcher
<i>Sialia sialis</i>	Eastern Bluebird

Table S2 (continued)

<i>Catharus fuscescens</i>	Veery*
<i>Catharus guttatus</i>	Hermit Thrush*
<i>Hylocichla mustelina</i>	Wood Thrush*
<i>Turdus migratorius</i>	American Robin*
<i>Dumetella carolinensis</i>	Gray Catbird*
<i>Mimus polyglottos</i>	Northern Mockingbird
<i>Toxostoma rufum</i>	Brown Thrasher
<i>Sturnus vulgaris</i>	European Starling
<i>Bombycilla cedrorum</i>	Cedar Waxwing
<i>Seiurus aurocapilla</i>	Ovenbird*
<i>Helmitheros vermivorum</i>	Worm-eating Warbler
<i>Seiurus motacilla</i>	Louisiana Waterthrush*
<i>Seiurus noveboracensis</i>	Northern Waterthrush*
<i>Vermivora pinus</i>	Blue-winged Warbler
<i>Mniotilta varia</i>	Black-and-white Warbler*
<i>Geothlypis trichas</i>	Common Yellowthroat*
<i>Wilsonia citrina</i>	Hooded Warbler*
<i>Setophaga ruticilla</i>	American Redstart*
<i>Parula americana</i>	Northern Parula
<i>Dendroica fusca</i>	Blackburnian Warbler
<i>Dendroica coronata</i>	Yellow Warbler
<i>Dendroica pensylvanica</i>	Chestnut-sided Warbler
<i>Dendroica cerulea</i>	Cerulean Warbler*
<i>Dendroica magnolia</i>	Magnolia Warbler*
<i>Dendroica caerulescens</i>	Black-throated Blue Warbler*
<i>Dendroica pinus</i>	Pine Warbler*
<i>Dendroica discolor</i>	Prairie Warbler
<i>Dendroica virens</i>	Black-throated Green Warbler*
<i>Wilsonia canadensis</i>	Canada Warbler*
<i>Pipilo erythrophthalmus</i>	Eastern Towhee*
<i>Spizella passerina</i>	Chipping Sparrow*
<i>Spizella pusilla</i>	Field Sparrow
<i>Passerculus sandwichensis</i>	Savannah Sparrow
<i>Melospiza melodia</i>	Song Sparrow
<i>Melospiza georgiana</i>	Swamp Sparrow
<i>Piranga olivacea</i>	Scarlet Tanager*
<i>Cardinalis cardinalis</i>	Northern Cardinal*
<i>Pheucticus ludovicianus</i>	Rose-breasted Grosbeak*
<i>Passerina cyanea</i>	Indigo Bunting
<i>Dolichonyx oryzivorus</i>	Bobolink
<i>Agelaius phoeniceus</i>	Red-winged Blackbird
<i>Sturnella magna</i>	Eastern Meadowlark
<i>Quiscalus quiscula</i>	Common Grackle
<i>Molothrus ater</i>	Brown-headed Cowbird
<i>Icterus galbula</i>	Baltimore Oriole
<i>Carpodacus purpureus</i>	Purple Finch
<i>Carpodacus mexicanus</i>	House Finch
<i>Carduelis tristis</i>	American Goldfinch
<i>Passer domesticus</i>	House Sparrow

Table S3. Results of principal components analysis on four morphological characteristics of birds and percent of variation explained by each axis.

Traits	Principal component axis			
	1	2	3	4
Mass	-0.516	0.060	-0.445	0.730
Wing length	-0.515	-0.034	-0.521	-0.680
Bill length	-0.483	-0.721	0.497	0.021
Tail length	-0.485	0.690	0.532	-0.075
% Variance	0.918	0.063	0.014	0.005

Table S4. Net Relatedness Index (NRI), Nearest Taxon Index (NTI) and associated p-values for 20 forest interior bird assemblages. Filtered and unfiltered designations refer to species pools used in analyses. Bold values indicate significance ($p \leq 0.05$) determined via a randomization approach (see text for details). Site number refers to location in study area (Figure 1).

Site number	Site	Richness	NRI-filtered	p-value	NRI-unfiltered	p-value	NTI-filtered	p-value	NTI-unfiltered	p-value
1	Algonquin	20	1.476	0.151	-0.274	0.829	-0.518	0.590	0.317	0.782
2	Babcock	17	-1.626	0.035	-2.093	0.013	-0.106	0.826	0.171	0.889
3	Canaan	20	-0.375	0.775	-1.413	0.140	-0.048	0.970	0.559	0.608
4	Cockaponsett	24	-0.782	0.446	-1.742	0.059	-0.873	0.402	0.410	0.715
5	Collis	23	0.419	0.619	-1.026	0.311	-0.047	0.934	0.806	0.443
6	Housatonic	14	0.660	0.394	-0.387	0.750	-1.216	0.261	-1.029	0.321
7	Macedonia	19	-0.167	0.975	-1.246	0.204	0.106	0.862	0.534	0.623
8	Mattatuck	28	0.824	0.400	-0.892	0.385	1.813	0.063	2.334	0.014
9	Mohegan	21	-0.802	0.410	-1.701	0.065	0.185	0.742	0.772	0.466
10	Natchaug	16	-0.201	0.844	-1.111	0.268	0.733	0.415	0.482	0.659
11	Naugatuck	16	-0.996	0.333	-1.632	0.076	0.096	0.963	0.123	0.922
12	Nipmuck	21	-0.539	0.659	-1.542	0.102	1.285	0.246	1.344	0.182
13	PachaugN	15	-0.557	0.548	-1.275	0.192	2.306	0.028	1.231	0.230
14	PachaugS	18	0.557	0.547	-0.740	0.486	0.037	0.982	0.383	0.729
15	Paugusset	17	1.447	0.190	-0.104	0.965	-1.490	0.185	-0.575	0.574
16	Roraback	23	3.654	0.006	0.874	0.385	-2.283	0.015	-0.417	0.673
17	Salmon	23	-0.940	0.355	-1.819	0.045	1.717	0.133	1.773	0.069
18	Shenipsit	17	-0.826	0.398	-1.577	0.090	0.748	0.373	0.632	0.556
19	Sleeping	16	-2.123	0.002	-2.376	0.002	-1.142	0.308	-0.562	0.588
20	UConn	25	2.798	0.020	0.280	0.748	-0.303	0.855	0.809	0.440

Table S5. Net Functional Relatedness Index (NFDI), Nearest Taxon Functional Index (NTFI) and associated p-values for analyses based on all functional characteristics (NFDI-all, NTFI-all) and the first two axes derived from principal components analysis of four morphological characteristics (NFDI-morph, NTFI-morph). Bold values indicate significance ($p \leq 0.05$) determined via a randomization approach (see text for details). Site number refers to location in study area (Figure 1).

Site number	Site	Richness	NFDI-all	p-value	NTFI-all	p-value	NFDI-morph	p-value	NTFI-morph	p-value
1	Algonquin	20	0.674	0.468	0.018	0.862	0.164	0.918	0.046	0.912
2	Babcock	17	-0.999	0.260	-0.624	0.736	-1.434	0.160	1.216	0.268
3	Canaan	20	1.003	0.323	0.445	0.550	0.297	0.768	-0.202	0.842
4	Cockaponsett	24	-0.668	0.394	-0.565	0.664	-0.423	0.648	0.558	0.622
5	Collis	23	0.051	0.976	-0.986	0.202	0.624	0.542	-0.355	0.730
6	Housatonic	14	-0.664	0.572	-1.306	0.194	-1.055	0.288	-1.467	0.120
7	Macedonia	19	-1.101	0.182	-0.209	0.942	-1.400	0.160	0.389	0.666
8	Mattatuck	28	-1.380	0.262	-0.846	0.308	-1.149	0.330	-0.638	0.530
9	Mohegan	21	0.240	0.808	-0.874	0.338	0.417	0.688	0.267	0.784
10	Natchaug	16	-0.977	0.310	-0.419	0.890	-0.246	0.848	-0.609	0.608
11	Naugatuck	16	1.437	0.120	1.702	0.086	0.755	0.492	0.721	0.540
12	Nipmuck	21	1.367	0.204	0.397	0.572	0.650	0.464	-1.688	0.098
13	PachaugN	15	1.723	0.056	1.068	0.486	1.623	0.080	0.412	0.762
14	PachaugS	18	1.529	0.140	2.051	0.072	1.637	0.112	2.098	0.034
15	Paugusset	17	-0.374	0.732	-0.888	0.436	-0.011	0.941	-0.493	0.688
16	Roraback	23	1.146	0.204	-1.071	0.154	1.268	0.164	-1.092	0.274
17	Salmon	23	0.213	0.814	-0.732	0.492	0.920	0.330	0.200	0.858
18	Shenipsit	17	0.861	0.452	-0.163	0.906	0.550	0.608	-1.084	0.268
19	Sleeping	16	-1.248	0.184	-0.829	0.566	-1.456	0.154	-0.792	0.518
20	UConn	25	-1.246	0.250	2.047	0.080	-0.648	0.448	-0.495	0.644

Table S6. Net Functional Relatedness Index (NFI), Nearest Taxon Functional Index (NTFI) and associated p-values for analyses based on size and shape axes derived from principal components of morphological characteristics. First principal component axis reflects body size and shape (NFI-size, NTFI-size). Second principal component axis reflects foraging location and prey selection (NFI-shape, NTFI-shape). Bold values indicate significance ($p \leq 0.05$) determined via randomization approach (see text for details). Site number refers to location in study area (Figure 1).

Site number	Site	Richness	NFI-size	p-value	NTFI-size	p-value	NFI-shape	p-value	NTFI-shape	p-value
1	Algonquin	20	0.112	0.932	-0.763	0.414	0.737	0.432	-0.768	0.442
2	Babcock	17	-1.434	0.148	1.034	0.466	0.353	0.732	0.483	0.704
3	Canaan	20	0.077	0.964	-0.484	0.816	1.669	0.082	-0.051	0.904
4	Cockaponsett	24	-0.285	0.784	1.072	0.370	-1.480	0.144	0.996	0.398
5	Collis	23	0.565	0.598	-0.639	0.628	-0.072	0.946	0.893	0.468
6	Housatonic	14	-1.104	0.238	-0.446	0.778	-0.232	0.782	0.972	0.408
7	Macedonia	19	-1.420	0.166	0.754	0.656	1.400	0.134	-0.274	0.738
8	Mattatuck	28	-1.367	0.278	-0.390	0.794	2.481	0.022	2.310	0.008
9	Mohegan	21	0.395	0.670	-0.699	0.542	0.042	0.978	-1.236	0.226
10	Natchaug	16	-0.285	0.832	-0.667	0.552	0.119	0.924	0.064	0.992
11	Naugatuck	16	0.773	0.548	1.024	0.452	-1.863	0.078	-0.701	0.450
12	Nipmuck	21	0.511	0.548	-1.480	0.100	0.271	0.824	-0.574	0.552
13	PachaugN	15	1.808	0.020	0.925	0.538	-1.087	0.276	0.042	0.964
14	PachaugS	18	1.714	0.094	1.598	0.086	-1.102	0.286	0.218	0.902
15	Paugusset	17	-0.039	0.998	-0.588	0.683	0.278	0.758	1.265	0.180
16	Roraback	23	1.446	0.146	-1.672	0.076	-0.229	0.864	0.807	0.500
17	Salmon	23	1.169	0.220	-0.330	0.952	-1.008	0.342	0.241	0.854
18	Shenipsit	17	0.519	0.583	-0.625	0.620	0.956	0.332	0.833	0.466
19	Sleeping	16	-1.277	0.198	-1.157	0.286	-2.593	0.012	-0.547	0.584
20	UConn	25	-0.706	0.380	-0.737	0.564	1.018	0.340	-0.952	0.366

CHAPTER FOUR

HABITAT CONFIGURATION STRUCTURES TEMPERATE FOREST BIRD METACOMMUNITIES

Abstract

Community assembly involves multiple processes acting at a number of different spatial scales, often resulting in complex patterns of species distributions within a region. The metacommunity framework has been advanced as an approach to link processes across scales to identify mechanisms that lead to patterns of species distributions. We apply two complementary approaches for the study of metacommunities that have rarely been applied together in order to determine empirical patterns and the relative importance of structuring mechanisms in a temperate forest bird metacommunity. The first approach combines an analysis of the elements of metacommunity structure (coherence, turnover, and boundary clumping) with ordination methods to evaluate if bird metacommunities in temperate interior forest are structured along a landscape structure gradient. The second approach uses variance partitioning to distinguish the roles of spatial structure and environmental filtering in community assembly. We separately assessed metacommunity structure for (1) all bird species, (2) resident species, and (3) migratory species.

Metacommunity structure of all birds and migrants was consistent with a Clementsian pattern of species distributions. In contrast, metacommunity structure of residents was Gleasonian. Metacommunities were structured along the same gradient associated with the spatial configuration of core forest patches at a single scale for all three groups of birds. Results of variance partitioning indicated that bird metacommunities are structured by a mix of local and regional processes but that neither process exerts a strong independent influence. This suggests that the structure of bird metacommunities in temperate forests, likely represent a combination of dispersal-mediated and environmentally structured processes. The relative influence of these processes may be affected by the severity of human influences on landscapes.

Introduction

A fundamental challenge in ecology is to understand the relative roles of local and regional determinants of community composition. The metacommunity framework, in which a set of communities are potentially connected through dispersal, has been advanced as an approach to link processes across scales (Leibold et al. 2004; Cottenie 2005; Holyoak et al. 2005). This requires the identification of empirical patterns of species distributions across communities, as well as the ability to disentangle the relative roles of dispersal and environmental filtering in determining the regional coexistence of species within empirical landscapes (Cottenie 2005; Munkemuller et al. 2012). To address this, recent studies have suggested the use of multiple approaches and multiple scales in metacommunity analysis (Logue et al. 2011; Munkemuller et al. 2012). Indeed, two complementary approaches for the study of metacommunities are popular (Logue et al. 2011), yet they rarely have been applied in concert to identify empirical patterns and the relative importance of structuring mechanisms that may determine them (but see Meynard et al. 2013 and Bonthoux and Balent 2015).

The first approach (elements of metacommunity structure; EMS) involves the identification of multi-species distributional patterns along latent environmental gradients and seeks to identify the processes and underlying biotic or abiotic characteristics that account for different types of non-random species associations within metacommunities (Leibold and Mikkelsen 2002, Presley et al. 2010). In this approach, a metacommunity may be characterized by one of six idealized structures (Leibold & Mikkelsen 2002; Presley et al. 2010). Random (or non-coherent) structure suggests that distributions of species cannot be characterized by a single environmental gradient, possibly because the focal taxa represent a diversity of life-history strategies or because of interspecific differences in the environmental characteristics that mold

distributions. A Gleasonian pattern reflects individualistic turnover of species along an environmental gradient, whereas a Clementsian pattern indicates that distinct groups of species with similar environmental affinities replace each other along the gradient. Nested patterns may indicate a gradient in the quality of habitats, and consequently, the number of species that they can support, as species-poor sites contain distributions of species that are a subset of species-rich sites. Both checkerboard and evenly spaced patterns suggest strong interspecific competition, but may also reflect large differences in the habitat requirements or environmental tolerances of species. By identifying how empirical patterns of species distributions correspond to these six idealized patterns, we can gain insight into the mechanisms that determine the distributions of species.

The second approach, variance partitioning, is used to tease apart the roles of spatial structure and environmental filtering in community assembly (Cottenie 2005). This approach quantifies variation in community composition that is uniquely attributable to different predictor matrices (e.g. environment and space), after controlling for their shared effects, facilitating inferences regarding the relative influence of competing mechanisms that may have independent, complementary, or redundant effects. The explained variance that can be linked solely to environmental variables is usually attributed to environmental filtering; the part that is linked to spatial structure and is non-environmentally driven is usually attributed to dispersal limitations; and the interaction term between environment and spatial structure represents spatially structured environmental variation (Borcard et al. 1992; Cottenie 2005). Variance partitioning was initially considered to be a way to distinguish among four competing paradigms (i.e., patch dynamics, species sorting, mass effects and neutral dynamics). Nonetheless, recent evaluations suggest that it would be more beneficial to view metacommunities as being structured by either neutral

processes or environmentally driven species sorting (i.e., environmental filtering) with various degrees of dispersal limitation (Weingard et al. 2012).

Community assembly involves multiple processes acting at a number of different spatial scales, often resulting in complex patterns of species distributions within a region. Identification of mechanisms that structure temperate breeding bird assemblages may be particularly difficult if processes are affecting two distinct groups of birds, residents and migrants (e.g., Monkkonen et al. 2006; Chapter 3). Residents can invest more time and energy in assessing the relative quality of available habitat patches, and populations are likely to be limited or strongly affected by the conditions during the non-breeding season (Lack, 1966; Fretwell, 1972; Forsman & Monkkonen, 2003). This suggests that environmental characteristics play a dominant role in determining where residents reside. In contrast, migrants are more time-constrained in their decisions, because habitat selection, pairing, nest building, and reproduction must be accomplished within a few weeks after arrival. Migrants generally exhibit low natal philopatry and adults may change breeding sites from year to year (Weatherhead & Forbes 1994; Paradis et al. 1998; Schlossberg 2009), suggesting that environmental characteristics may play less of a role in site selection and that colonization may be more strongly influenced by stochastic effects or by interspecific interactions.

Landscape modification has a strong influence on patterns of avian biodiversity (e.g. Villard et al. 1999; Flynn *et al.* 2009; Meynard *et al.* 2011; Smith et al. 2011; Chapter 2) and may influence metacommunity structure (Ozkan et al. 2013; Bonthoux and Balent 2015). In many human-dominated landscapes, natural habitats are reduced and fragmented, influencing the distributions of species (Hanski 1998, Holyoak et al. 2005). Consequently, several aspects of landscape heterogeneity may be relevant for metacommunity dynamics, including the

composition and configuration of land cover types, connectivity, and the diversity of habitat patches, yet these are rarely considered explicitly (Biswas and Wagner 2012; but see Cisneros et al. 2014). Accordingly, we evaluate the degree to which bird metacommunities in temperate interior forest are structured along a gradient in landscape structure. Moreover, we evaluate relationships at multiple spatial scales, because the scale at which patterns of metacommunity structure are most strongly associated with variation in landscape structure is not well understood. We examine this relationship separately for residents and migrants under the assumption that the former will be associated more strongly with landscape structure at smaller spatial scales compared to the latter. This prediction reflects the idea that residents may select sites by making a series of local-scale movements, accumulating information about habitat features at increasingly larger spatial scales, ultimately reflecting landscape structure (i.e., bottom-up evaluation). In contrast, selection of sites by migrants entails individuals flying at a relatively high altitude and assessing landscape-scale features before descending to make increasingly finer habitat selection decisions at local local-scales (i.e., top-down evaluation; Hutto 1985; Kristan 2006; Tavernia 2010).

We use tests of coherence, turnover and boundary clumping (i.e., EMS) to identify dominant features characterizing the distributions of bird species in temperate forest landscapes and determine if that pattern is consistent with the distributions of two distinct subsets of the biota (i.e., residents and migrants). Specifically, we predict that species distributions in the resident metacommunity will more strongly reflect the influence of environmental characteristics and be consistent with a Clementsian pattern. In contrast, we expect species distributions of the migrant metacommunity to reflect a Gleasonian pattern because it is likely that characteristics of the local environment play less of a role in colonization of sites by migrants, and species

interactions or stochastic processes will play a stronger role, leading to idiosyncratic distributions of species. Due to differences among these groups of birds we expect that the metacommunity comprising all birds will reflect characteristics of both groups but will be dominated by the group with higher species richness, resulting in either a quasi-Clementsian or quasi-Gleasonian pattern.

Environmental filtering and spatial factors jointly determine metacommunity structure of previously studied temperate forest bird assemblages (Meynard and Quinn 2008; Meynard et al. 2011; Ozkan et al. 2013; Bonthoux and Balent 2015). Within a metacommunity framework, most studies have evaluated mechanisms of community assembly along a combination of steep environmental or isolation gradients, often in human modified forest landscapes. This has identified that dispersal-driven spatial processes have a more pronounced role in structuring communities when environmental gradients are not steep but isolation enhances dispersal limitation, whereas environmental filtering dominates along steep gradients with low dispersal limitation. We evaluate the relative roles of environmental filtering and spatial processes in structuring a temperate forest bird metacommunity where intermediate levels of environmental variation are present and predicted relationships are less clear. We evaluate this separately with two groups that generally differ in their dispersal distances (Paradis et al. 1998).

Methods

Study Area

Research was conducted in eastern deciduous and coniferous forests of Connecticut, USA, excluding coastal areas. Currently, 60% of land cover in the state is forest, dominated by oak-hickory and northern hardwood forest types, although pine forests are common along the northern border of the state (Butler et al., 2012). Like many areas, Connecticut has experienced profound anthropogenic alteration of landscapes (Drummond & Loveland 2010), so that forest

currently exists as patches or fragmented parcels of various sizes and ages, interwoven with various types of human-altered land covers (i.e., urban and suburban developments, agricultural fields, road networks, and power line rights of way; Figure 1A).

Approximately one-third of the forests in the lower 48 states are on public lands, supporting 45% of the U.S. distribution of 149 obligate forest bird species, and representing the largest unfragmented forests in many regions (NABCI, 2011). Consequently, twenty sites were established on public land within interior forest patches of various sizes and shapes. Sites were selected by processing a 2010 land cover map (CLEAR, 2010a) with the Landscape Fragmentation Tool (LFT v2.0; CLEAR 2010b) add-on to Arc Toolbox to identify suitable locations with sufficient area of interior forest (i.e., forest pixels located at least 100 m from non-forest pixels) to contain 5 plots spaced at least 250 m apart. Plots were separated by at least 250 m to reduce the potential of counting the same birds in multiple samples. Sites were separated from other sites and from the coast of Long Island Sound by least 10 km. Prospective sites were visited and ground-truthed to evaluate accuracy of land cover maps and to ensure accessibility.

Landscapes corresponding to 6 spatial scales (i.e. circles of 1, 1.5, 2, 2.5, 3 and 5 km radius) were centered on each site, and described by eight characteristics of landscape structure (Table 1). Landscape characteristics quantify focal habitat composition, focal habitat configuration, matrix composition, and landscape heterogeneity. Relationships between these aspects of landscape structure and variation in composition of populations and communities are well described (e.g., Fahrig 2003 for review) but their relationship to metacommunity structure is not well understood. Landscape characteristics were quantified at multiple spatial scales because species may perceive their environment at multiple spatio-temporal scales and differ from each other in this regard as a consequence of species-specific life-history, dispersal, resource

acquisition, and predator avoidance characteristics (Kotliar & Wiens 1990; Andrén 1994; With & Crist 1995). Furthermore, as the scale at which avian metacommunities respond to landscape structure is unknown, we hope to avoid the pitfalls of previous multi-scale research at the community level that may have relied on either too few or too narrow a range of scales to determine effects of landscape structure on species (Jackson and Fahrig 2014). Landscape characteristics were estimated with Fragstats 4.1 (McGarigal et al. 2012) from the same land cover map that was used in site selection.

Avian Surveys

Birds were surveyed with a combination of point counts (Ralph et al. 1995) and recordings from Autonomous Recording Units (ARUs; Wildlife Acoustics Song Meter Sm2 +). Using a combination of ARU and point count approaches enhances the likelihood of identifying species present at sites when compared to using either method on its own (Venier et al. 2011; Tegeler et al. 2012; Chapter 2). For point counts, each plot within a site (Fig. 2B) was visited on two occasions during the breeding season (May - August 2012) and sampled via a 10 minute unlimited distance survey. Surveys were conducted within the first 4 hours of local sunrise, and all species that were heard or seen were considered to be present. In addition to point counts, each of the 5 plots within a site contained an ARU and was surveyed for 4 hours on a daily basis, beginning at local sunrise during the same time period as point counts. To supplement point-count data, recordings from ARUs were sampled randomly by selecting a plot and 2-minute time period on each of 50 days (exclusive of those days when point counts were conducted). This approach results in equal sample effort for acoustic surveys and point count surveys for each site (i.e. 100 minutes of point counts and 100 minutes of ARU recordings). Recordings were analyzed and sonograms were viewed with Song Scope software (Wildlife Acoustics Inc.). To

assist in identification of species, field recordings were compared with sonograms of previously identified species obtained from the Macaulay Library at the Cornell Lab of Ornithology.

Statistical analyses were based on the incidence of bird species identified from both sampling approaches. We followed the nomenclature and taxonomic recommendations of the North American Classification Committee of the American Ornithologists' Union (Chesser *et al.* 2013). Analyses were restricted to birds from the Passeriformes and Piciformes as these two orders are the most species-rich in temperate interior forests of the region.

Elements of metacommunity structure

The analytical methods of Leibold and Mikkelsen (2002) and the conceptual framework of Presley et al. (2010) were used to identify the best fit metacommunity structure for (1) all bird species, (2) resident species, and (3) migratory species. Three characteristics of species distributions (coherence, species range turnover and boundary clumping) were evaluated from an ordinated site-by-species incidence matrix created for each group of birds. Matrices were ordered using the primary axis extracted via reciprocal averaging, which optimizes the proximity of species with similar distributions and the proximity of sites with similar species compositions. Reciprocal averaging is appropriate for identifying patterns in response to latent gradients because similarities in species occurrences determine the positions of sites along the axis of correspondence without a priori knowledge of or assumptions about the particular factors that govern species responses (Gauch, 1982; Leibold & Mikkelsen, 2002). For each analysis of coherence, 1000 randomly generated matrices were created using a null model that constrained site richnesses to equal observed values and that had equiprobable species occurrences. This null model creates a biologically realistic null space for evaluation of coherence in which the number of species at each site is fixed, but the number of sites at which a species occurs is random

(Presley et al. 2009, 2010). Furthermore, this level of constraint has a desirable combination of Type I and Type II error properties when applied to small matrices (i.e. those with fewer than 30 species and sites) compared to alternative models.

Each randomly generated matrix was also subjected to reciprocal averaging. Embedded absences of the randomly generated matrices were counted and used to create a null distribution, and a z-test based on the mean and variance of that null distribution was used to determine significance based on a two-tailed test. A metacommunity was considered significantly and positively coherent if the likelihood of having fewer embedded absences than expected was ≤ 0.025 . A metacommunity was considered significantly and negatively coherent if the likelihood of having more embedded absences than expected was ≤ 0.025 . Negative coherence is characteristic of checkerboards, whereas positive coherence is characteristic of coherent structures (Fig. 1). Nonsignificant coherence suggests that the distributions of the preponderance of species are not shaped by the same environmental gradient.

Species range turnover was evaluated if a metacommunity was positively coherent. To quantify turnover, the number of times one species was replaced by another between each possible pair of sites was counted in the ordinated empirical matrix. To ensure that the number of replacements was an accurate estimate of species turnover along the latent environmental gradient, species ranges were made coherent by filling in embedded absences prior to analysis (Leibold and Mikkelsen 2002). To determine significance, the empirical number of replacements was compared to a null distribution of replacement values created from 1000 matrices that contained randomly shifted species ranges (Leibold and Mikkelsen 2002). Positive species turnover occurs when the likelihood of randomly generating more replacements than observed

was ≤ 0.025 , and negative species turnover is when the likelihood of randomly generating fewer replacements than observed was ≤ 0.025 .

If positive coherence and positive turnover were identified, Morisita's index (I) was used to determine degree of range boundary clumping by counting the number of terminal boundaries at each site. Significance was determined via a χ^2 goodness of fit test that compared the observed distribution of range boundaries to an expected uniform distribution. Range boundaries that occurred at random have a Morisita's index of ~ 1.0 and a non-significant χ^2 test. Index values > 1.0 with a significant χ^2 test indicate clumped boundaries, whereas index values < 1.0 with a significant χ^2 test indicate hyper-dispersed boundaries.

These metacommunity types are broad idealizations of nature, and hence, a number of subtypes can also be distinguished. We followed Presley et al. (2010) and recognized quasi-structures (shaded area of Fig. 1) in cases of significant positive coherence followed by nonsignificant turnover along an ordination axis. Nonsignificant negative turnover indicates quasi-nestedness, whereas nonsignificant positive turnover can lead to either quasi-evenly spaced, quasi-Gleasonian, or quasi-Clementsian structure metacommunity. These three quasi-structures can be distinguished via boundary clumping as described above (Leibold and Mikkelsen 2002). Elements of metacommunity structure were quantified with the metacom package (Dallas 2014) in R version 3.1.2 (R Development Core Team 2014).

To determine the scale at which landscape characteristics were associated with gradients along which metacommunities were structured, we used principal components analysis (PCA) followed by canonical correspondence analysis. We conducted a separate principal components analysis on landscape characteristics (Table 1) for each of the six spatial scales. The first PC axis from each analysis accounted for at least 80% of the variation in landscape structure at each

scale. Consequently, we used these six PC axes to represent scale-specific landscape structure rather than the 48 variables (i.e., 8 characteristics x 6 scales). Next, we determined the scale at which landscape variation was most strongly associated with each metacommunity. We used Canonical Correspondence Analysis (CCA; Ter Braak 1986) for this because it is a combination of correspondence analysis and multiple regression (Palmer 1993). Therefore CCA axes are defined by a similar ordination as used in EMS, resulting in a parallel method for determining associations of environmental factors with metacommunity structure (de la Sancha et al. 2014). We used CCA to determine which scale metacommunities were most strongly associated with landscape structure by analyzing the relationship between scores from the reciprocal averaging (that ordinated each site by species matrix) and the 6 PC axes, each of which describe landscape structure at a different spatial scale.

After determining which spatial scale was most strongly related to metacommunity structure, we explored which of the landscape characteristics measured at that scale, were most strongly associated with the environmental gradient structuring each metacommunity. This was determined by using CCA to analyze the relationship between site scores from reciprocal averaging ordination and the eight landscape characteristics quantified at the scale that was selected with the approach described above.

Variance partitioning

A suite of full and partial redundancy analyses were used to assess the joint and unique effects of spatial variables and landscape structure on the composition of avian assemblages (Borcard et al. 1992; Legendre & Legendre 1998; Cottenie 2005). This approach enables partitioning variance in species composition into additive components. Variation explained by landscape structure after controlling for spatial structure [LS|SS], variation explained by spatial

structure after controlling for landscape structure [SS|LS], and inseparable variation accounted for by landscape structure and spatial structure [LS∩SS], sum to form variation accounted for by the model [LS + SS]. [LS] and [SS] describe the amount of variation accounted for by landscape structure and spatial variables, respectively, without taking into account their correlated effects. The percentage of the variation attributed to each fraction was assessed with the adjusted R^2 because fractions are influenced by the number of environmental and spatial predictors and by sample size (Peres-Neto et al. 2006). If a fraction was negative, which is often the case for adjusted values of non-significant shared fractions, we did not assess its significance (Peres-Neto et al. 2006; Legendre et al. 2012). The significance of each fraction was tested by an ANOVA permutation test using 999 random permutations.

Species-by-site incidence matrices for all birds, residents and migrants were used for variance partitioning. In addition, an environmental and a spatial matrix were created. The spatial matrix contained the latitude and longitude of each site. The environmental matrix contained the six PC axes that describe landscape structure at each of six spatial scales. Variance partitioning analyses were conducted with the vegan package (Oksanen et al. 2013) in R version 3.1.2 (R Development Core Team 2014).

Results

Forty-three species, twenty-seven of which were migrants, were identified with the combination of ARU and point count methods (Table 2). Richness of sites ranged from 15 to 28 species. Seven species (i.e. Black-capped Chickadee, Eastern Wood-Pewee, Ovenbird, Red-eyed Vireo, Scarlet Tanager, White-breasted Nuthatch, and Wood Thrush) occurred at all 20 sites, and seven species (i.e. Canada Warbler, Gray Catbird, Great Crested Flycatcher, Hooded Warbler, Louisiana Waterthrush, Northern Waterthrush) occurred exclusively at a single site (Table 2;

Figure 3). Landscapes encompassing sites were dominated by forest, regardless of spatial scale. Minimum percent cover of core forest was less extensive, and ranged from 77% (mean = 95.78% \pm 6.0) at the 1 km scale to 51% (mean = 67.1% \pm 9.2) at the 5 km scale. In general, landscapes were more diverse and heterogeneous at larger scales than at smaller scales. For example, mean contagion was lowest and mean Shannon diversity of land cover types was greatest in the 5 km scale (Table S1). Geographic distance between sites spanned more than an order of magnitude ranging from 10 to 138 km.

Along the primary axis of correspondence (from reciprocal averaging), each metacommunity exhibited positive coherence (Table 2). Positive coherence indicates that distributions of species within each metacommunity (Figure 3) were molded by the same latent environmental gradient. All birds exhibited positive turnover and positive boundary clumping, consistent with a Clementsian structure. Residents exhibited positive turnover and non-significant boundary clumping consistent with a Gleasonian structure. Migrants did not exhibit significant turnover, but did show significant and positive boundary clumping, indicating that distributions were consistent with a quasi-Clementsian structure. Landscape structure at a 3 km focal scale was most strongly associated with metacommunity structure for all three groups of birds (Table 4). Furthermore, the first axis from reciprocal averaging and the first CCA axis of landscape characteristics quantified at 3 km were highly correlated for each group of birds (all birds $\rho = 0.95$, $P < 0.001$; residents $\rho = -0.97$, $P < 0.001$; migrants $\rho = -0.83$, $P < 0.001$). This suggests that axes from both analyses represent variation in the same latent environmental gradient. The latent environmental gradient was most strongly associated with the spatial arrangement of core forest patches in a landscape (Table 5).

Landscape characteristics and spatial factors accounted for less than 15% of the variation in bird species composition among sites for each group of birds, and this relationship was significant for all birds and residents (Table 6). Landscape characteristics and spatial factors accounted for a similar amount of variation for each group of birds (Figure 4). In general, variance explained by landscape structure after controlling for spatial structure [LS|SS] accounted for a larger proportion of variation than did spatial structure after accounting for landscape structure [SS|LS]. However, neither relationship was significant for any group of birds (Table 6). Landscape structure and spatial structure (i.e., [LS] and [SS]) accounted for significant proportions of the variance in all birds and residents. However, no partition was significant for migrants.

Discussion

Metacommunity characteristics of all birds and migrants were similar in temperate forest landscapes but differed from residents. Distributions of species in metacommunities comprising all birds and migrants were consistent with a Clementsian pattern (although the pattern was weaker in migrants leading to a quasi-Clementsian pattern). In contrast, residents evinced a Gleasonian structure. We expected to see a difference in metacommunity structure between groups and hypothesized that resident distributions may be influenced more strongly by environmental characteristics as a consequence of their year-round occupancy, whereas distributions of migrants may be influenced by a mix of environmental characteristics and interspecific interactions. The migrant metacommunity was consistent with a quasi-Clementsian pattern, suggesting that environmental characteristics may play a weak role in structuring distributions of migrants. However, this patterns still suggests that groups of species share similar environmental tolerances that differ from other groups within the metacommunity. In

contrast, distributions of residents respond idiosyncratically to the latent environmental gradient. Consequently, resident distributions may reflect species-specific differences in sensitivity to environmental characteristics. Metacommunity structure characterizing all birds was similar to other studies evaluating metacommunity structure of birds with the EMS approach. A quasi-Clementsian pattern characterized a tropical bird metacommunity along an extensive elevational gradient in the Andes (Presley et al. 2012). Clementsian patterns also characterized temperate bird metacommunities separated by 25 years in a highly fragmented forest landscape in France (Bonthoux and Balent 2015). The preponderance of Clementsian patterns (although based on few studies to date) and the lack of any alternative patterns in the literature would suggest that environmental characteristics play a dominant role in driving the assembly of forest bird communities. However, in this study, subsets of the metacommunity that differ in life history characteristics (i.e., residents and migrants) did not evince the same pattern (Clementsian) as detected for the entire fauna.

Relationships between landscape structure and species composition are well established for bird communities (e.g. Andren 1994; McGarigal and McComb 1995; Villard et al. 1999; Fahrig et al. 2003; Smith et al. 2011; Chapter 2). In contrast, relationships between landscape structure and metacommunity structure have just begun to be explored (Ozkan et al. 2013; Bonthoux and Balent 2015). This may reflect the fact that ecologists have been reluctant to abandon a local concept of the community (Ricklefs 1987; Harrison & Cornell 2008) and have only recently begun to broadly focus on the role regional processes play in determining the composition of local assemblages (Ricklefs 2008 and cited works). In this study, patterns of species distributions were strongly related to the configuration of core forest patches. Variation in the size, shape and distance between core forest patches (characterized by a proximity index)

was strongly associated with the latent environmental gradient structuring each of the three metacommunities. The area of core forest (also referred to as interior forest) and its configuration was quantified independently of edge forest because edges may increase vulnerability of some species to nest predation or brood parasitism, and represent lower quality habitats that are only used when higher quality habitats (i.e., core forest) are occupied (Ries et al. 2004). Failure to separate forest into core and edge components and evaluate them separately may result in misleading conclusions about the nature of relationships between communities or metacommunities and landscape structure (Fahrig 2013). Birds are highly mobile and the degree to which habitat configuration affects species or communities above and beyond habitat amount remains unclear (Trzcinski et al. 1999; Smith et al. 2011; Villard and Metzger et al. 2014). However, forest birds may be more affected by habitat fragmentation than would be expected based on their volant nature because some species show a reluctance to cross gaps in forest habitat (reviewed by Harris and Reed 2002). Many birds are sensitive to habitat area (Bayard and Elphick 2010), however the size and distance between patches of core forest, rather than simply the area, may play a strong role in determining which sites species will persist in landscapes. Specifically, this could alter distribution patterns if some species are more adept or willing to cross gaps in forest than others are. To the best of our knowledge, the role that habitat configuration may play in determining the structure of bird metacommunities has not been explored previously. This precludes comparisons that may provide insight into whether our findings are influenced by the makeup of the regional species pool or by the amount of variation in landscape structure. Although other studies have evaluated the influence of landscape composition (e.g., percent of land cover types) or heterogeneity (e.g., landscape diversity), they

have not assessed the effects of configuration, which we found to play a stronger role than other landscape characteristics in determining metacommunity structure.

Variance partitioning indicated that bird metacommunities are structured by a mix of local and regional processes but that neither process exerts a strong independent influence (Table 6). Indeed, landscape structure and spatial structure account for a similar amount of variation in all three groups of birds. This may indicate that there are not large differences in dispersal capabilities between residents and migrants in the study and supports results suggesting that these groups do not differ in their sensitivity to landscape structure (Tables 4 and 5). We found no significant effect of landscape structure or spatial structure when their correlated effects were accounted for. This could be an artifact of using landscape characteristics, which are inherently spatial and may exhibit spatial autocorrelation (Wagner and Fortin 2005). This is frequently the case if the region from which they are estimated shows a strong spatial gradient (e.g., urban to forest or forest to grassland). However, this was not the case in the current study, as all sites were located within interior forest, and landscapes encompassing sites were dominated by forest (Table S1). In contrast, results of variance partitioning may reflect the strong influence of habitat configuration on metacommunity structure, as was observed with the EMS approach. The proximity metric that was related to the underlying gradient structuring species distributions of all three groups reflects a combination of spatial and environmental characteristics. Larger patches are likely to contain a greater area of core forest that may represent higher habitat quality to many of the bird species. Moreover, if larger patches are closer together then a greater opportunity exists for individuals to satisfy their foraging and nesting requirements, and dispersal distances will be shorter, positively influencing species persistence. Ultimately, the structure of bird metacommunities in temperate forests likely represents a combination of dispersal-mediated

and environmentally structured processes. However, the relative influence of these processes may be a consequence of the severity of human influences (Ozkan et al. 2013; Bonthoux and Balent 2015).

The spatial scale at which landscape characteristics were most strongly related to the latent environmental gradient structuring metacommunities did not differ among groups of birds. This was surprising because hypotheses regarding differences in the way that migrants and residents evaluate the suitability of habitats (i.e., bottom up vs. top-down) suggest that they view the landscape at different scales (Hutto 1985; Kristan 2006; Tavernia 2010). Furthermore, differences exist between migrants and residents with respect to level of habitat specialization, territory size and average dispersal distance (Paradis et al. 1998; Bowman 2003). However, it is possible that the variation within each of these groups may be sufficient to mask mean differences between groups when the number of individuals is low, or the scale of inquiry (e.g., distribution of a species vs. a territory or a home range) is coarse. Furthermore, any differences that exist between residents and migrants as a group, is highly dependent on the species composition of each group, as some resident and migratory species have very similar habitat affinities and dispersal capabilities.

Our multi-scale approach was motivated in part by recent criticisms of research that evaluates the influence of landscape structure on species and assemblages. Previous research has been criticized for relying on either too few or too narrow a range of scales to determine the most appropriate “scales of effect” (Jackson and Fahrig 2014). Furthermore, failure to evaluate if scales differ between groups that differ in life history characteristics is another important criticism. We evaluated relationships at a wide range of scales, and the scale with the strongest relationship was neither the smallest nor largest, suggesting that relationships were evaluated at

an appropriate scale (Jackson and Fahrig 2014). Furthermore, we separately evaluated relationships for groups that may respond differently (i.e., migrants and residents), and determined in this case, they respond to landscape structure at the same spatial scale.

Conclusions

Ongoing refinement of metacommunity theory is dependent on empirical studies that compare predictions from a range of metacommunity models, approaches, taxa, and systems (McGill et al. 2006; Logue et al. 2011; Mihaljevic 2012; Weingard et al 2012). In particular, the types of habitat and ecological characteristics of biotas included in empirical approaches need to be extended to enhance generality. Most empirical studies have addressed permanent habitat patches with discrete boundaries, or focused on insular habitats that restrict dispersal (e.g. lakes, ponds, islands or moss patches; Logue et al. 2011). This may not reflect the dominant types of metacommunity observed in nature. Many natural and human-modified systems are hierarchically structured, have indistinct boundaries, or are spatially and temporally variable. A recent review of the literature suggests that environmental filtering is the predominant structuring force of metacommunities (Soininen 2014). However, the veracity of this conclusion remains uncertain. In particular, the role of landscape structure and consequences of human activities on dispersal will require greater attention as these forces are likely to exert strong influences on the spatial and environmental structure of metacommunities.

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Table 1. Description of landscape characteristics quantified at each of 6 focal scales for 20 interior forest sites. See McGarigal et al. 2012 for details on calculation of characteristics.

Landscape Characteristic	What it quantifies	Description
Percent core forest	Habitat composition	Percent of the focal scale that is core forest (i.e., forest > 100 m from any non forest cover type).
Percent edge forest	Habitat composition	Percent of the focal scale that is edge forest (i.e., forest < 100 m from any non forest cover type).
Mean core forest patch density	Habitat configuration	Number of forest patches per unit area within a focal scale.
Mean core forest proximity	Habitat configuration	An average measurement of core forest patch isolation, weighted by the size each patch. A scale with many large patches in close proximity will have a large index value (i.e., high proximity, low isolation).
Percent Agriculture	Matrix composition	Percent of the focal scale that is agriculture land cover (includes fields for grazing, hay, corn, and tobacco).
Percent Developed	Matrix composition	Percent of the focal scale that is developed land cover (includes roads, urban and suburban developments, and buildings).
Contagion	Landscape heterogeneity	Measures the dispersion and interspersion of land cover types. Contagion approaches 0 when the patch types are maximally disaggregated (i.e., every cell is a different patch type) and interspersed. Contagion = 100 when all patch types are maximally aggregated or there is only one patch type in the focal scale.
Shannon diversity	Landscape heterogeneity	Diversity index that quantifies the relative proportion of nine land cover types in each focal scale.

Table 2. Scientific and common names of bird species identified at each of 20 temperate interior forest sites (indicated by an X). Site numbers correspond to locations in Figure 2.

No.	Order	Family	Scientific name	Common name	Residency	Site																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																						
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1	Piciformes	Picidae	<i>Melanerpes erythrocephalus</i>	Red-headed Woodpecker	Migratory																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																							</

Table 3. Results from analysis of three elements of metacommunity structure (coherence, turnover, and clumping; Liebold and Mikkelsen 2002) for all birds, residents and migrants. Mean and standard deviation (SD) were calculated from 10,000 matrices that were randomized based on a null model that constrained row totals (site richness) to equal the empirical richness and that had equal probabilities of species occurrence. Significant results ($p \leq 0.05$) are bold. Abs = number of embedded absences, Rep = number of replacements, I = Morisita's index.

Group	Coherence			Turnover		Clumping		Metacommunity	
	Abs	Mean (SD)	p-value	Rep	Mean (SD)	I	p-value	Structure	
All birds	260	385 (13.6)	<0.001	3600	1264 (559.6)	2.28	<0.001	Clementsian	
Residents	64	96 (6.7)	< 0.001	613	248 (116.7)	1.18	0.13	Gleasonian	
Migrants	132	245 (12.3)	< 0.001	2361	1406 (513.9)	1.96	< 0.001	Quasi-Clementsian	

Table 4. Loadings of the first axis from canonical correspondence analysis (CCA) for metacommunities comprising all birds, residents or migrants. CCA was based on the first axis of principal components describing landscape structure at a particular scale. The strongest association for each metacommunity is indicated in bold.

Scale	All birds	Residents	Migrants
1 km	-0.370	-0.318	0.295
1.5 km	-0.256	-0.529	0.108
2 km	0.013	-0.151	-0.017
2.5 km	-0.298	-0.367	0.108
3 km	0.850	0.571	-0.921
5 km	-0.254	-0.414	0.072

Table 5. Loadings of the first axis from canonical correspondence analysis (CCA) for metacommunities comprising all birds, residents or migrants based on 8 landscape characteristics estimated at a 3 km spatial scale. The strongest association for each metacommunity is indicated in bold.

Landscape metric	All birds	Residents	Migrants
Core forest	-0.301	-0.385	-0.204
Edge forest	0.352	0.476	0.204
Core forest density	0.384	0.627	0.162
Core forest proximity	0.811	0.691	0.835
Agriculture	0.156	0.133	0.081
Developed	0.111	-0.005	0.171
Diversity	0.194	0.285	0.165
Contagion	-0.121	-0.275	-0.084

Table 6. Adjusted R^2 and associated p-values from variance partitioning of three groups (i.e., all birds, residents or migrants). Variation explained by landscape structure after controlling for spatial structure [LS|SS], variation explained by spatial structure after controlling for landscape structure [SS|LS], and inseparable variation accounted for by landscape structure and spatial structure [LS \cap SS], sum to form variation accounted for by the model [LS + SS]. [LS] and [SS] refer to amount of variation accounted for by habitat and spatial variables, respectively, without taking into account their correlated effects. Unexplained indicates residual variation unaccounted for in the model. NA refers to partitions that are not able to be tested for significance. Significant partitions ($p \leq 0.05$) are bold.

Partition	All birds		Residents		Migrants	
	adj. R^2	p-value	adj. R^2	p-value	adj. R^2	p-value
[LS + SS]	0.123	0.015	0.148	0.026	0.105	0.07
[LS]	0.083	0.034	0.135	0.005	0.045	0.222
[SS]	0.048	0.029	0.062	0.036	0.039	0.113
[LS SS]	0.074	0.081	0.086	0.102	0.065	0.179
[SS LS]	0.040	0.143	0.014	0.356	0.059	0.116
[LS \cap SS]	0.009	NA	0.049	NA	-0.020	NA
Unexplained	0.877	NA	0.852	NA	0.895	NA

Figure Legends

Figure 1. A diagrammatic representation (after Presley et al. 2010) of the combinations of distributional characteristics (i.e., three elements of metacommunity structure indicate with shaded ovals) that differentiate among six idealized metacommunity structures and four quasi-structures (in shaded area). Illustrative incidence matrices that depict distributional patterns (grey boxes) of idealized structures are included for each of the six metacommunity structures (shaded columns indicate a species distribution across sites, which are indicated by rows). Results that are consistent with particular structures are within circles (+, positive significance; NS, nonsignificant; —, negative significance). For non-significant analyses of turnover, < indicates that the observed number of replacements was less than the average number based on randomizations, and > indicates that the observed number of replacements was greater than the average number based on randomizations.

Figure 2. Map of study area illustrating major land cover types derived from 2010 land cover data. Gridded area indicates land outside the study area that was not classified into land cover types. Location of study area in northeastern North America is delimited with a rectangle in the lower left corner. Location of 20 sites (indicated by number; see Table S1 for geographic coordinates) within the study area appear in the lower right corner.

Figure 3. Distributional profiles of each species (numbers refer to species in Table 2) across 20 temperate forest sites (numbers refer to sites in Figure 2) as ordered via the first axis of reciprocal averaging. Matrices depict (A) all bird species, (B) resident species (black bars), and (c) migratory species (grey bars).

Figure 1

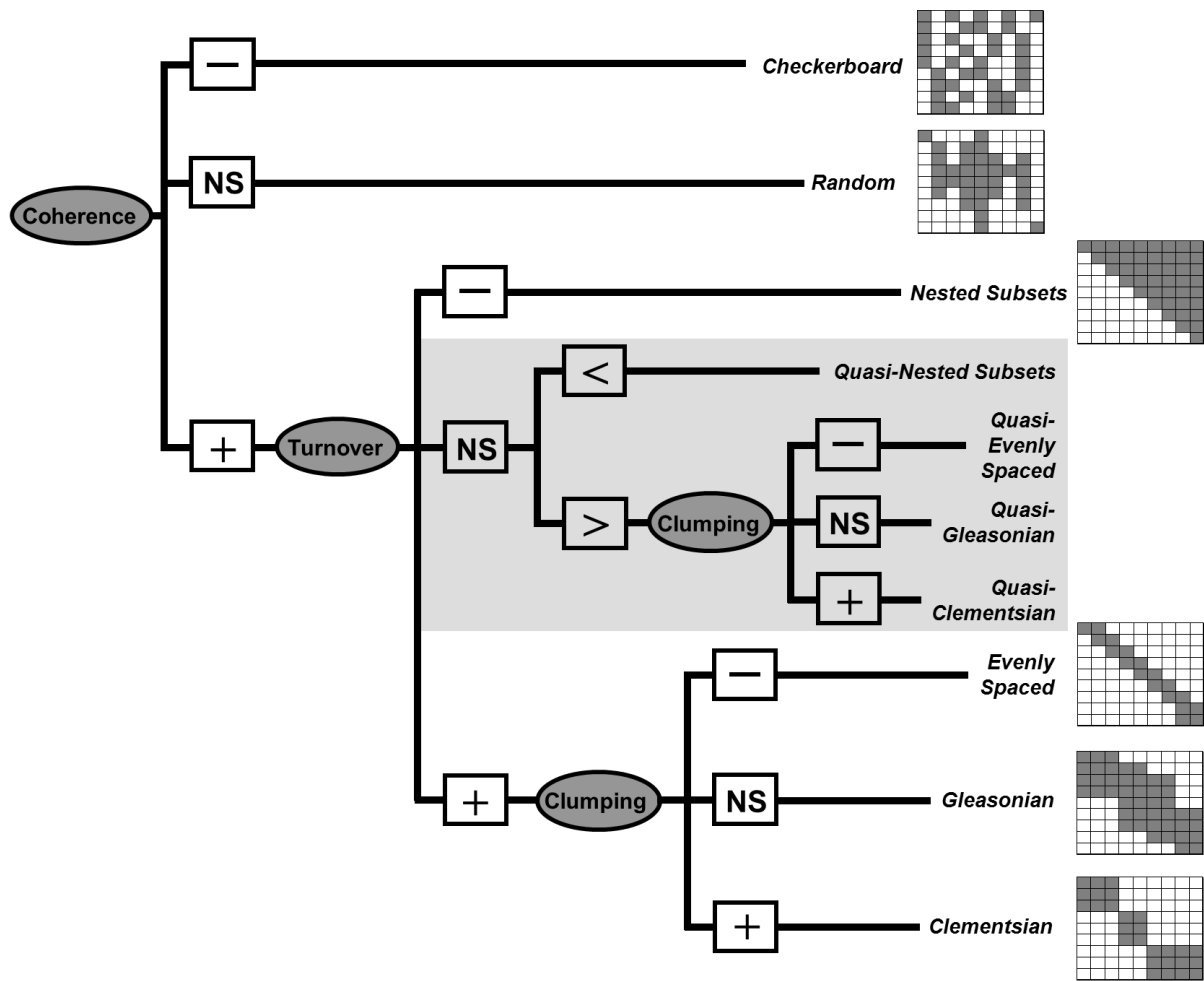


Figure 2

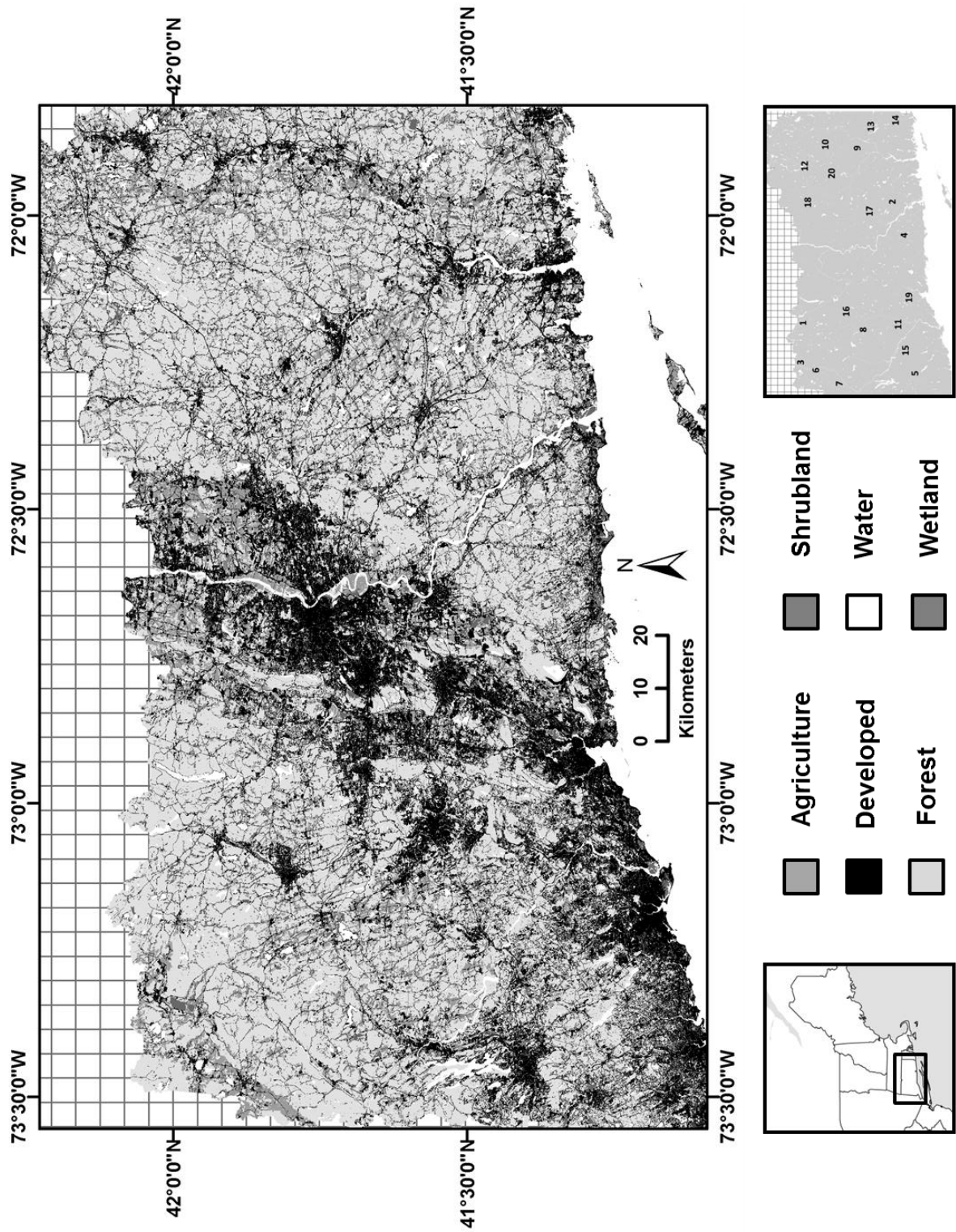
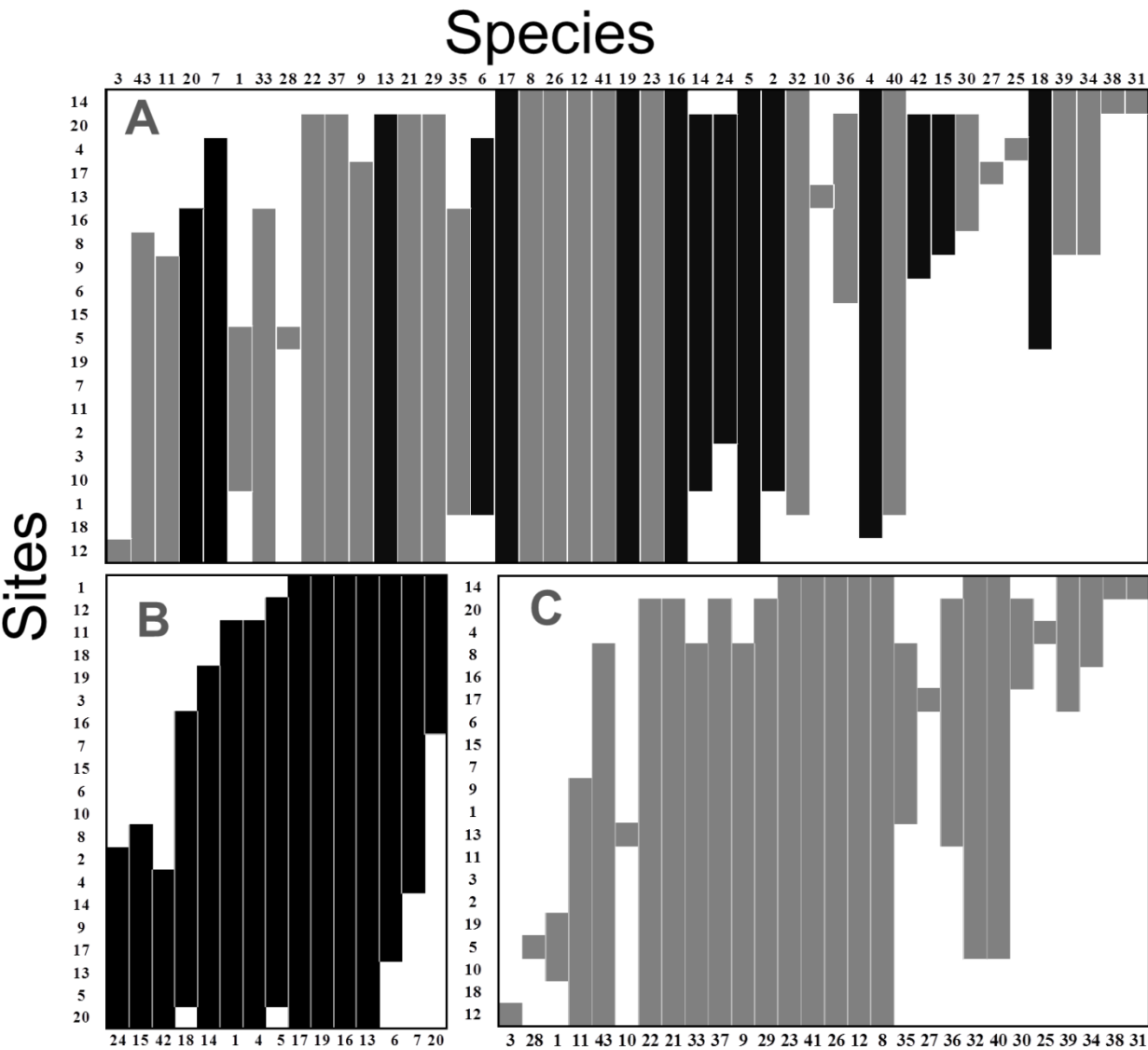


Figure 3



Supporting Information

Table S1. Geographic locations of 20 interior forest sites. Latitude and longitude (decimal degrees) represent the approximate center of each site. Numbers correspond to site locations indicated on inset map of Figure 1.

Site number	Site name	Latitude	Longitude
1	Algonquin	41.988	-73.058
2	Babcock	41.522	-72.405
3	Canaan	42.005	-73.296
4	Cockaponsett	41.473	-72.536
5	Collis	41.346	-73.349
6	Housatonic	41.905	-73.406
7	Macedonia	41.775	-73.488
8	Mattatuck	41.646	-73.089
9	Mohegan	41.670	-72.069
10	Natchaug	41.856	-72.057
11	Naugatuck	41.461	-73.046
12	Nipmuck	42.025	-72.176
13	PachaugN	41.595	-71.887
14	PachaugS	41.484	-71.859
15	Paugusset	41.405	-73.197
16	Roraback	41.732	-73.059
17	Salmon	41.618	-72.378
18	Shenipsit	42.000	-72.399
19	Sleeping	41.436	-72.889
20	Uconn	41.820	-72.236

Table S2. Descriptive statistics of landscape characteristics for 20 sites at each of 6 spatial scales. Landscape characteristics estimated from 2010 land cover data (CLEAR 2010b) with Fragstats 4.1 (McGarigal, Cushman & Ene 2012).

Spatial scale	Descriptive statistic	Percent core forest	Percent edge forest	Percent agriculture	Percent developed	Core patch density	Core proximity	Diversity	Contagion
1 km	Mean \pm SD	95.78 \pm 5.96	1.42 \pm 2.42	0.00 \pm 0.00	0.01 \pm 0.04	0.32 \pm 0.00	0.00 \pm 0.00	0.06 \pm 0.08	94.77 \pm 7.6
	Range	77.19 - 100.00	0.00 - 9.43	0.00 - 0.00	0.00 - 0.17	0.32 - 0.32	0.00 - 0.00	0.00 - 0.29	72.93 - 100.00
1.5 km	Mean \pm SD	91.44 \pm 6.20	3.15 \pm 2.57	0.33 \pm 1.13	0.57 \pm 1.13	0.16 \pm 0.06	4.19 \pm 18.75	0.17 \pm 0.13	90.32 \pm 6.56
	Range	81.14 - 100.00	0.00 - 8.67	0.00 - 4.85	0.00 - 4.14	0.14 - 0.40	0.00 - 83.85	0.00 - 0.47	76.00 - 100.00
2 km	Mean \pm SD	86.33 \pm 8.41	5.21 \pm 3.22	1.01 \pm 2.96	1.83 \pm 2.70	0.13 \pm 0.08	27.47 \pm 37.28	0.30 \pm 0.18	88.92 \pm 6.26
	Range	70.97 - 98.18	0.53 - 11.32	0.00 - 11.07	0.00 - 11.63	0.08 - 0.41	0.00 - 120.82	0.02 - 0.67	78.29 - 98.97
2.5 km	Mean \pm SD	81.58 \pm 9.11	6.80 \pm 3.50	1.54 \pm 3.57	2.94 \pm 3.74	0.15 \pm 0.09	276.83 \pm 239.73	0.38 \pm 0.17	87.2 \pm 5.36
	Range	60.78 - 93.72	1.54 - 15.09	0.00 - 12.07	0.00 - 15.84	0.05 - 0.41	15.65 - 899.21	0.13 - 0.73	75.95 - 94.12
3 km	Mean \pm SD	77.43 \pm 10.32	8.10 \pm 3.44	2.00 \pm 4.02	4.19 \pm 4.20	0.19 \pm 0.08	190.77 \pm 125.42	0.51 \pm 0.22	84.26 \pm 6.43
	Range	56.31 - 91.84	2.61 - 16.16	0.00 - 14.02	0.59 - 18.26	0.07 - 0.32	40.34 - 591.85	0.18 - 0.98	69.04 - 93.83
5 km	Mean \pm SD	67.13 \pm 9.17	10.93 \pm 2.40	3.75 \pm 4.57	6.77 \pm 4.97	0.22 \pm 0.09	493.17 \pm 432.92	0.77 \pm 0.22	78.42 \pm 5.74
	Range	50.98 - 81.28	5.95 - 14.29	0.00 - 15.43	2.54 - 20.27	0.09 - 0.40	110.00 - 1999.75	0.44 - 1.25	66.78 - 87.75