

# Community assembly in temperate forest birds: habitat filtering, interspecific interactions and priority effects

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**Abstract** Recent attempts to understand the processes governing community assembly have increasingly focused on patterns of phylogenetic relatedness and functional similarity among co-existing species. Considerations of the species pool, the number and identity of functional traits and the metrics used to identify patterns have come under scrutiny as possible influences on the detection of non-random patterns. Most mechanistic explanations of community assembly based on functional and phylogenetic approaches rely on deterministic explanations, while ignoring the role of stochastic processes and historical contingency, despite the prominent historical role of both types of explanations of species coexistence. We evaluated the phylogenetic and functional structure of 20 temperate forest bird assemblages in northeastern North America. We compared three approaches for characterizing the functional structure of assemblages. Regardless of approach, assemblages were generally no different than expected by chance. In contrast, phylogenetic structures of bird assemblages were overdispersed, clumped or consistent with random assembly depending on the site. Nonetheless, we found little evidence for differences in phylogenetic structure arising as a consequence of the identity of the species pool. We identified a strong relationship between the proportion of residents and phylogenetic relatedness that was unrelated to the species richness of assemblages. Our results suggest that different assembly mechanisms may structure resident and migratory subsets of temperate breeding bird communities. Resident assemblages are likely structured by interspecific interactions and habitat filtering prior to arrival of migrants. In contrast, the composition of migrant assemblages may be a consequence of priority effects in which the presence and abundance of residents and earliest arriving species affect the ability of

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subsequent migrants to colonize sites. This phenomenon enhances the likelihood of multiple alternative community structures in similar environments.

**Keywords** Avian · Functional trait · Niche · Neutral · Phylogenetic relatedness · Stochastic

## Introduction

A primary goal of ecology is to understand the processes governing species coexistence and the mechanisms underlying the assembly of communities. Ecologists have long debated the relative importance of deterministic factors (e.g., filtering with respect to environmental conditions and interspecific interactions) versus stochastic processes (e.g., chance colonizations, random extinctions, and ecological drift) for determining local species composition (recently discussed in Chase and Myers 2011; Vellend et al. 2014). In general, these opposing views lead to alternative predictions about the nature 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 processes should result in divergent communities that are dominated by different species. Putting to rest longstanding debates regarding community assembly may not be as simple as explicitly considering the spatial scale of inference, as some have suggested (Chase 2014). Nonetheless, a growing consensus suggests that processes operating at multiple spatiotemporal scales structure communities (HilleRisLambers et al. 2012) and that abandoning the stochastic versus deterministic dichotomy may be the most fruitful way forward (Vellend et al. 2014).

Recent attempts to understand mechanisms underlying the assembly of ecological communities have increasingly focused on patterns of phylogenetic relatedness among coexisting species (i.e., community phylogenetics; Webb et al. 2002; Cavender-Bares et al. 2009; Vamosi et al. 2009). The underlying rationale 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, such that patterns of relatedness among species in contemporary communities can be used to infer the processes governing assembly (Webb et al. 2002; Cavender-Bares et al. 2006, 2009; Swenson et al. 2006; Vamosi et al. 2009). A common approach for identifying patterns of coexistence, involves the comparison of metrics describing the distribution of phylogenetic distances between coexisting species in empirical communities to those of null communities that are assembled randomly from a regional species pool. Two mechanisms are frequently cited as explanations why empirical communities differ from randomly assembled ones. In the first, environmental characteristics play the dominant role. Habitats act as filters that select for a subset of species from a regional pool on the basis of functional traits associated with adaptations to the local environment (Webb et al. 2002). If closely related species are similar in function and have similar ecological requirements because of niche conservatism (Wiens and Graham 2005; Losos 2008), then environmental filtering leads to closely related species co-occurring more frequently than expected by chance (i.e., species in communities are clustered on a phylogenetic tree of the regional species pool; Webb et al. 2002; Cavender-Bares et al. 2009). Alternatively, species interactions could play a key role. If closely related species share more similar morphological and physiological traits as well as niche requirements,

they tend to compete more strongly for the same resources than do distantly related species, and this should result in patterns of phylogenetic overdispersion (i.e., communities comprise species that are evenly dispersed across the phylogenetic tree of the regional species pool; Webb et al. 2002; Cavender-Bares et al. 2009) as a consequence of limiting similarity (MacArthur and Wilson 1967).

Despite advances based on community phylogenetic approaches, contemporary coexistence theory also demonstrates that large fitness differences among populations and competitive exclusion can lead to clustering of closely related or functionally similar species, complicating interpretations of associations between processes and patterns at the scale of local communities (Mayfield and Levine 2010; HilleRisLambers et al. 2012). Moreover, a pattern of phylogenetic overdispersion (rather than clustering) may reflect environmental filtering of species with similar traits (if traits are convergent) or a lack of stabilizing niche differences between closely related species (if traits are conserved) rather than limiting similarity (Cavender-Bares et al. 2004, 2009; Kraft et al. 2007). Consequently, information on the phylogenetic structure of communities must be combined with information on functional traits of species, as well as considerations of the environmental conditions or the spatial relationships among communities, to more clearly distinguish among competing hypotheses that are responsible for community assembly (Cavender-Bares et al. 2006; Helmus et al. 2007; Cavender-Bares et al. 2009).

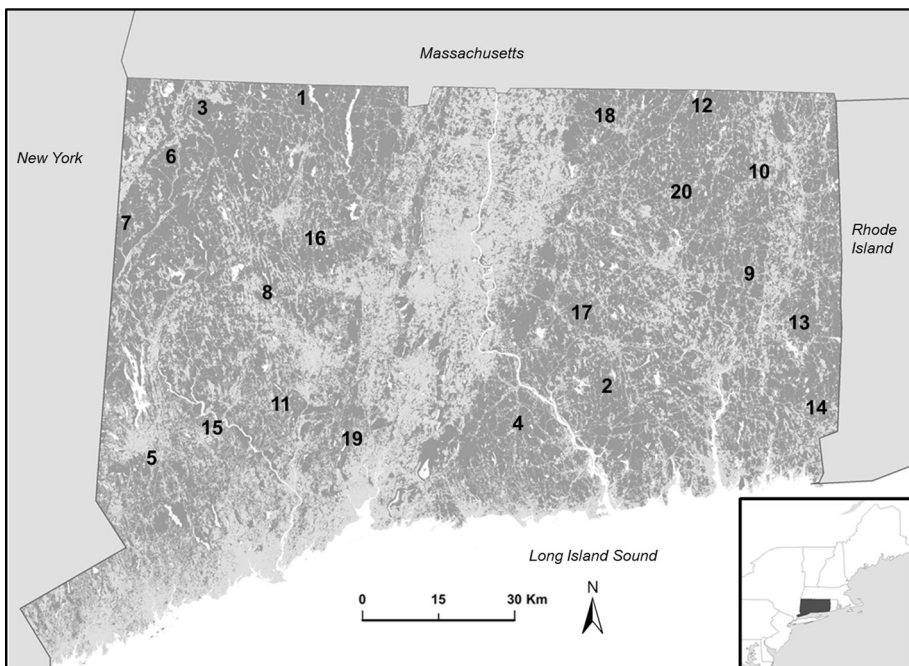
Community phylogenetic approaches have generally ignored the role of stochastic processes when identifying mechanisms of community assembly. Patterns of phylogenetic clumping or overdispersion are rarely attributed to stochastic processes, despite recognition that stochasticity in the order or timing of species colonizations can result in substantial differences in species composition among otherwise identical sites (e.g., Drake 1991; Chase 2003; Fukami 2004, 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). As such, priority effects can lead to high variability in community structure, among environmentally similar sites (Chase 2003, 2010; Fukami 2004). Nonetheless, the link between phylogenetic relatedness, community assembly, and priority effects has been explored only recently (Peay et al. 2012; Tan et al. 2012).

The issue of scale-dependence is a challenge in studies of phylogenetic community structure (Swenson et al. 2006; Kraft and Ackerly 2010; Trisos, et al. 2014). Interspecific competition is generally assumed to be strongest at the local scale (capturing direct interactions among individuals) with its effects on community structure becoming progressively weaker as spatial scale increases (Weiher and Keddy 1995; Vamosi et al. 2009; but see Gotelli et al. 2010). In contrast, habitat filtering should be stronger than competition at larger spatial scales because habitat heterogeneity allows species to coexist that may have been excluded from certain sites due to habitat-specific niche requirements (Swenson et al. 2007; Kraft and Ackerly 2010). 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 (Swenson et al. 2007; Cavender-Bares et al. 2009). However, the generality of such scale-dependent patterns is unknown, as previous studies have focused on only a few taxonomic groups and have produced mixed results (Vamosi et al. 2009; Münkemüller et al. 2014).

Most research on community assembly that incorporates phylogenetic relatedness has focused on plants, as these organisms are observed easily and are amenable to experimental manipulation (Vamosi et al. 2009). As a consequence, most of the ecological and

evolutionary patterns describing communities are based on systems in which interactions between individuals and the influence of the environment are likely to be greatly constrained from a spatial perspective. In contrast, birds are highly mobile with few natural barriers that impede their movement. Furthermore, species composition of temperate bird communities varies substantially in time and space (Holmes et al. 1986; Ricklefs 2011), enhancing the potential for interspecific interactions. 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). Nonetheless, research using phylogenetic approaches to study bird assemblages are few (Vamosi et al. 2009), most have focused on South America (Graham et al. 2009; Gomez et al. 2010; Gianuca et al. 2014; Dehling et al. 2014; Trisos et al. 2014; but see Lovette and Hochachka 2006; Price et al. 2014) and none have investigated the influence of residents and migrants on phylogenetic structure.

We used three complementary approaches to evaluate mechanisms of community assembly in temperate forest birds. First, we evaluated phylogenetic relatedness and functional trait structure in 20 interior forest bird assemblages to determine the relative influence of potential assembly mechanisms. Second, we determined the strength of the phylogenetic signal in functional traits that reflect important niche characteristics. Finally, we ascertained whether assembly mechanisms based on the phylogenetic structure of communities was dependent on the identity of the regional species pool or the proportion of residents in local assemblages.



**Fig. 1** Map of study area in Connecticut, USA represented by forest (dark gray), nonforest (light gray), and water (white). The locations of 20 interior forest sites are indicated by numbers (see Appendix 1, Table A1 for geographic coordinates). The location of Connecticut in northeastern North America is indicated by shaded area in lower right corner map. Land cover classification derived from CLEAR (2010)

## Materials and methods

### Study design

Birds were surveyed in deciduous and coniferous forests of Connecticut, USA (Fig. 1), with a combination of point counts (Ralph et al. 1995) and recordings from Autonomous Recording Units (ARUs). Twenty sites were established within interior forest patches of various sizes and shapes. A site consisted of 5 survey plots spaced approximately 250 m from each other and at least 100 m from forest edges. Spatial configuration of plots was consistent at all sites. Detailed description of site selection appears elsewhere (Klingbeil and Willig 2015).

For point counts, each plot within a site was visited on two occasions during the breeding season (May–August 2012) and sampled via a 10 min survey. Surveys were conducted within the first 4 h 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 h 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-min 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 min of point counts and 100 min 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 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 that were derived from both sampling approaches (Klingbeil and Willig 2015). 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 are the most species-rich orders in interior forests of the region and their constituent species 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 separately compared each assemblage to 999 randomly generated assemblages derived from each of two species pools. The first included only species observed in at least one of the 20 forest sites in the region. This sample-based approach reflects the species pool frequently applied in analyses of phylogenetic structure (Vamossi et al. 2009).

We refer to this species pool as the “filtered species pool” because it potentially reflects the consequences of habitat filtering, as all species were observed within a single habitat. We compare results of randomizations based on the filtered species pool to randomizations based on a more comprehensive species pool. This “unfiltered species pool” included all species identified at study sites as well as all species (from the orders Passeriformes and Piciformes) identified from Breeding Bird Survey routes in Connecticut during 2012. These two species pools share the same geographic and temporal extent, but differ in the richness and composition of species that could potentially colonize each site. We generated random assemblages from the filtered species pool using the independent swap algorithm. This approach constrains the frequency of occurrence of species and species richness in randomized assemblages to be the same as those in the empirical assemblages (Gotelli 2000). This null model has high power to detect niche-based community assembly and does not suffer from high Type I error rates associated with many other null models in community phylogenetics (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 among those 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 of multiple processes that act simultaneously but in opposite directions, obscuring any overall phylogenetic structure (Helmus et al. 2007).

We investigated two potential influences on patterns of phylogenetic structure; the identity of the species pool and proportion of resident versus migratory species at each site. To determine if the identity of the species pool had a significant effect on the outcome of tests of phylogenetic structure, we calculated the site-specific difference in values of NRI or NTI between unfiltered and filtered species pools. We used a paired *t* test to evaluate 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. To determine if the degree of clustering or overdispersion was a function of the proportion of residents in an assemblage, we used ordinary least squares regression. Similarly, we used least squares regression to evaluate if the pattern in phylogenetic structure was a function of the species richness of sites.

Phylogenetic comparisons were based on branch lengths extracted from a comprehensive phylogeny of the world's bird species (Jetz et al. 2012, 2014). 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 recalibrated “Stage 2 Mayr All Hackett” backbone (available at <http://birdtree.org>) and conducted all analyses based on this 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-based 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). 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 fly-catcher), 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 et al. 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 exhibit (Petchey and Gaston 2006). Consequently, selection of traits represents an effort to balance a desire for a comprehensive set of functional traits versus concerns about multicollinearity. To address this, 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 characterized functional attributes of species based on a subset of traits derived from morphological characteristics (e.g., NFRI-morph and NTFI-morph). Associations between morphological traits and ecological attributes are well established for birds. Avian bill measurements have long been used as surrogates for the trophic niche (Hutchinson 1959; Schoener 1965; Grant and Grant 2006; Trisos et al. 2014) and other

measurements such as tail and wing length can be related to foraging ability, microhabitat association, and substrate use (Miles and Ricklefs 1984; Trisos et al. 2014). Importantly, sets of traits often provide information about the same or non-independent 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 based on 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 each principal component axis (that accounted for a significant percent of the variation variation) 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 same randomization approach and comparison with filtered and unfiltered species pools that was used in assessments of phylogenetic relatedness. All analyses were executed using the Picante package in R (Kembel et al. 2010).

### Phylogenetic signal

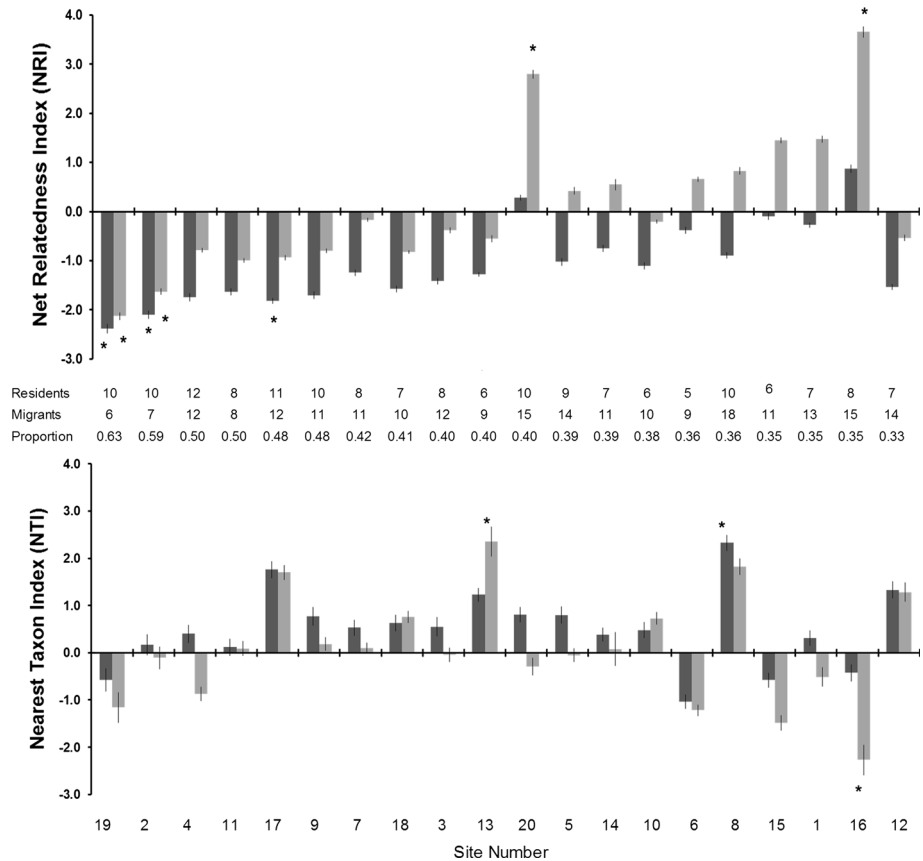
Determining the strength of phylogenetic signal is a critical step when using functional or phylogenetic information to infer mechanisms of community assembly (Losos 2008). Several methods have been developed for measuring the strength of phylogenetic signal in functional traits (i.e., a measure of the statistical dependence among trait values of species due to their phylogenetic relationships; Revell et al. 2008), and detailed assessments of the strengths and weaknesses of different measures exist (Münkemüller et al. 2012; Hardy and Pavoine 2012). Consequently, we used two methods to quantify the strength of phylogenetic signal. Pagel's  $\lambda$  (Freckleton et al. 2002; Pagel 1999) evaluated functional traits based on continuous data (e.g. mass, wing length), whereas the D-statistic (Fritz and Purvis 2010) evaluated functional traits based on 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.

Significance tests of phylogenetic signal are most frequently conducted via comparisons with a Brownian motion model of evolution, in which a continuous trait evolves according to a set of random steps with no preferred direction, roughly corresponding to a process of neutral drift over macroevolutionary time-scales. However, this may not be the most appropriate approach to characterize the evolution of quantitative characters on phylogenies (reviewed in Münkemüller et al. 2015). As an alternative, the Ornstein–Uhlenbeck model was introduced to model evolution towards a selective optimum (Hansen 1997; Butler and King 2004). This model is an extension of the Brownian motion model in which a term is added to effect attraction towards an optimal niche value and this may mimic patterns consistent with stabilizing selection, constrained evolution in bounded phenotypic space (Boucher et al. 2014) or evolution towards shifting niche optima (Hansen 2012). We evaluated the appropriateness of tests of phylogenetic signal that rely on a Brownian motion model by comparing patterns of continuous character evolution observed under a Brownian motion and an Ornstein–Uhlenbeck model with the “fitcontinuous” function in the R package Geiger (Harmon et al. 2009).



A maximum-likelihood approach was used to estimate Pagel’s  $\lambda$  for each continuous trait distribution and corresponding phylogeny. A maximum likelihood ratio test was used to determine whether estimated values of  $\lambda$  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  $\lambda$  indicate that traits have evolved according to a process in which the effect of phylogeny is weaker than predicted by 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 (Fig. 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 to the outcome of a Brownian



**Fig. 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. Site codes are defined in Table A1

threshold model (Fritz and 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  $\lambda$ ) and of a  $p$  value derived from 1000 phylogenetic trees. Tests of phylogenetic signal were executed with the R packages *Caper* (Orme 2013) and *phytools* (Revell 2012).

## Results

Forty-three species were identified with a combination of ARU and point count surveys. Most species were insectivores that obtain food by foraging on the ground or by gleaning insects from foliage (Table A2). Species richness of empirical assemblages ranged from 15 to 28 species. Based on breeding bird surveys, 88 species were identified as members of the unfiltered species pool, compared to only 43 species in the filtered species pool (Table A2).

Little variation characterized estimates of phylogenetic structure derived from 1000 trees, regardless of metric (i.e., error bars in Fig. 2). Variation in NRI was not related to variation in NTI. In contrast, metrics of phylogenetic structure derived from different species pools (filtered vs. unfiltered) were highly correlated for NRI and for NTI (Table 3). Nonetheless, 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  $t$  test:  $t = -8.38$ ,  $p < 0.001$ ). 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  $t$  test:  $t = 3.15$ ,  $p = 0.005$ ). Regardless of species pool, variation in NRI was associated with variation in the proportion of residents in assemblages (Table A4), but not with variation in the species richness of assemblages (NRI-unfiltered:  $\beta_1 = 0.050$   $R^2 = 0.001$ ,  $p$  value = 0.328; NRI-filtered:  $\beta_1 = 0.148$   $R^2 = 0.107$ ,  $p$  value = 0.087).

Comparison of Brownian motion and Ornstein–Uhlenbeck models of character evolution indicate that tests of phylogenetic signal based on Brownian models are generally appropriate (Table A4). Specifically, the added complexity with the Ornstein–Uhlenbeck model does not significantly enhance performance over that of the Brownian motion model. A strong signal characterized most continuous traits (Table 1), whereas a signal consistent with Brownian evolution characterized most categorical traits (Table 2). Patterns were consistent regardless of species pool, strongly suggesting that closely related species are more likely to be similar than expected by chance.

Functional structure of empirical assemblages generally did not differ significantly from that in randomly constructed assemblage regardless of metric or species pool (Tables A6, A7, and A8). Results of correlation analyses for functional estimates were generally consistent with patterns observed for phylogenetic comparisons (i.e., strong correlations between filtered and unfiltered estimates of each metric but weak correlations between estimates of NFRI and NTFI; Table 3). Principal components analysis of morphological traits identified one dominant axis, accounting for 92 (filtered species pool) and 88 % (unfiltered species pool) of the variation, representing an index of body size in both cases.

**Table 1** Evaluation of phylogenetic signal ( $\lambda$ ) for functional traits (continuous) of birds

Trait	Filtered		Unfiltered	
	$\lambda$	$\text{Pr}(\lambda) = 0$	$\lambda$	$\text{Pr}(\lambda) = 0$
Mass	1.039	< <b>0.001</b>	1.019	< <b>0.001</b>
Bill	0.775	< <b>0.001</b>	0.873	< <b>0.001</b>
Tail	1.045	< <b>0.001</b>	1.021	< <b>0.001</b>
Wing	1.040	< <b>0.001</b>	1.023	< <b>0.001</b>
Clutch size	0.982	< <b>0.001</b>	0.998	< <b>0.001</b>
Egg mass	1.025	< <b>0.001</b>	1.018	< <b>0.001</b>

Filtered and unfiltered designations refer to species pools used in analyses. Significance tests determine whether empirical values differed from 0 (i.e., those produced by random processes). Bold values indicate significance ( $p \leq 0.05$ )

**Table 2** Evaluation of phylogenetic signal (D) for categorical functional traits of birds

Functional component	Trait	Filtered			Unfiltered		
		D	$\text{Pr}(D) = 1$	$\text{Pr}(D) = 0$	D	$\text{Pr}(D) = 1$	$\text{Pr}(D) = 0$
Diet	Insectivore	-0.138	<b>0.014</b>	0.822	-0.069	< <b>0.001</b>	0.850
	Omnivore	-0.136	<b>0.014</b>	0.825	0.053	< <b>0.001</b>	0.953
	Granivore	–	–	–	-0.895	<b>0.034</b>	0.402
	Herbivore	–	–	–	-2.432	<b>0.005</b>	0.149
Foraging	Ground	-0.056	< <b>0.001</b>	0.886	-0.242	< <b>0.001</b>	0.464
	Flycatching	-1.083	< <b>0.001</b>	0.225	-1.093	< <b>0.001</b>	0.222
	Foliage	-0.516	< <b>0.001</b>	0.285	-0.307	< <b>0.001</b>	0.366
	Bark	0.023	<b>0.006</b>	0.951	-0.236	< <b>0.001</b>	0.620
	Aerial	–	–	–	-1.823	< <b>0.001</b>	<b>0.027</b>
Migratory	Resident	-0.140	< <b>0.001</b>	0.739	0.056	< <b>0.001</b>	0.901
	Migrant	-0.139	< <b>0.001</b>	0.739	0.056	< <b>0.001</b>	0.899

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 [ $\text{Pr}(D) = 1$ ] or with trait allocation based on Brownian motion [ $\text{Pr}(D) = 0$ ]. Bold values indicate significance ( $p \leq 0.05$ ). A dash indicates a trait was not present in a particular species pool

As a consequence, other axes are not discussed further (Table A9). Regardless of species pool or estimate of NFRI, variation in NFRI was not significantly associated with variation in the proportion of residents in assemblages (Table A4).

## Discussion

### Functional structure of assemblages

The functional structure of most assemblages was not different from that expected by chance, regardless of species pool, suggesting that stochastic processes play a dominant role in community assembly. Metrics that combine traits from multiple niche axes have the

**Table 3** Spearman rank correlations (Rho) and associated  $p$  values for comparisons between estimates of functional structure (NTFI-) and comparisons between estimates of phylogenetic structure (NRI-)

Comparison	Rho	$p$ value
<b>Phylogenetic</b>		
NRI <sub>filtered</sub> – NTI <sub>filtered</sub>	–0.344	0.137
NRI <sub>unfiltered</sub> – NTI <sub>unfiltered</sub>	–0.140	0.555
NRI <sub>filtered</sub> – NRI <sub>unfiltered</sub>	0.970	<b>&lt;0.001</b>
NTI <sub>filtered</sub> – NTI <sub>unfiltered</sub>	0.802	<b>&lt;0.001</b>
<b>Functional</b>		
NFRI-all <sub>filtered</sub> – NTFI-all <sub>filtered</sub>	0.388	0.092
NFRI-all <sub>unfiltered</sub> – NTFI-all <sub>unfiltered</sub>	0.783	<b>&lt;0.001</b>
NFRI-all <sub>filtered</sub> – NFRI-all <sub>unfiltered</sub>	0.997	<b>&lt;0.001</b>
NTFI-all <sub>filtered</sub> – NTFI-all <sub>unfiltered</sub>	0.417	0.069
NFRI-morph <sub>filtered</sub> – NTFI-morph <sub>filtered</sub>	0.156	0.509
NFRI-morph <sub>unfiltered</sub> – NTFI-morph <sub>unfiltered</sub>	0.179	0.449
NFRI-morph <sub>filtered</sub> – NFRI-morph <sub>unfiltered</sub>	0.989	<b>&lt;0.001</b>
NTFI-morph <sub>filtered</sub> – NTFI-morph <sub>unfiltered</sub>	0.962	<b>&lt;0.001</b>
NFRI-size <sub>filtered</sub> – NTFI-size <sub>filtered</sub>	–0.008	0.975
NFRI-size <sub>unfiltered</sub> – NTFI-size <sub>unfiltered</sub>	0.018	0.942
NFRI-size <sub>filtered</sub> – NFRI-size <sub>unfiltered</sub>	0.994	<b>&lt;0.001</b>
NTFI-size <sub>filtered</sub> – NTFI-size <sub>unfiltered</sub>	0.995	<b>&lt;0.001</b>

See text for descriptions of species pool (i.e., filtered and unfiltered) and functional characteristics (i.e., all, morph, size and shape) that are associated with particular metrics. Bold values indicate significance ( $p \leq 0.05$ )

advantage of providing an integrated overview of community structure. Nonetheless, a drawback of such metrics is that they may combine signals of opposing processes (Swenson and Enquist 2009) that could obscure identification of niche-based assembly mechanisms and erroneously suggest neutral dynamics (Kraft et al. 2007; Weiher 2011; Trisos et al. 2014). We evaluated if this was the case by employing three functional classifications that differed in the number and identity of niche axes. Regardless of classification or metric (i.e., NFRI or NTFI) results were consistent with random assembly, strongly suggesting that empirical patterns of functional composition were not an artifact of the functional classification scheme (e.g., Trisos et al. 2014).

Application of relatedness metrics to functional rather than phylogenetic information as an approach to determine assemblage structure is rare. We are aware of only one other study (Dehling et al. 2014) that has evaluated variation in patterns of functional structure in bird assemblages using approaches that are similar to those used herein. Dehling et al. (2014) evaluated functional structure along an extensive elevational gradient in the tropics, and found strong evidence of clustering, overdispersion, and random structure. Variation in functional structure generally corresponded to variation in habitat types, with functional overdispersion present in more structurally complex lowlands, functional clustering in less structurally complex highlands, and random structure in middle elevations. Random functional structure may be a dominant pattern in bird communities from this study as a consequence of the habitat type. Temperate interior forests in the current study are likely to be similar to the middle elevation forests of Dehling et al. (2014) that were not significantly different from random. Consequently, forest of this type may offer a sufficiently general array of resources to birds that preclude specialization or competition. Most of the birds in the study are either insectivorous or omnivorous during the breeding season and can exhibit dietary flexibility that takes advantage of increased availability of resources during the summer months in temperate climates. As a result, the identity of species (and

consequently the functional structure of an assemblage) at a particular site may be strongly influenced by stochastic processes, such as annual fluctuations in population sizes, arrival times of migrants, or the composition of residents that occupy sites year-long.

Alternatively, the sensitivity of functional classifications or the selection of traits may have influenced empirical patterns. Fine scale differences in species niches or resource requirements may not be captured by general dietary classifications (e.g., insectivore omnivore) or morphological correlates of function (e.g., mass, bill length). Furthermore, characteristics not included (e.g., nesting location, territory size) in this study may show different patterns than those based on foraging location, residency or others included in this study.

### Phylogenetic structure of assemblages

The nature of the species pool, and the domain from which it is constructed, can play a critical role in determining the apparent strength and direction of environmental signals in interpretation of phylogenetic patterns (Cavender-Bares et al. 2006; Swenson et al. 2006; Kraft and Ackerly 2010). We anticipated that the species pool may affect identification of patterns because we assessed phylogenetic structure of assemblages in a single habitat type that is dispersed throughout a regional matrix of multiple land cover types (agriculture, suburban, urban). We hypothesized that the species pool identified from our sampling was a non-random subset of the regional pool that had been “filtered” by species adapted to forest. If this was true, then phylogenetic clustering should be most apparent in analyses derived from an unfiltered (or regional pool comprised of species observed in multiple habitats) rather than a filtered species pool (Cavender-Bares et al. 2006; Swenson et al. 2006; Kraft et al. 2007; Swenson et al. 2007). Our results contradict such expectations. Phylogenetic structure of assemblages (based on NRI) was more frequently indicative of overdispersion based on an unfiltered species pool than when based on a filtered species pool.

We explore two mechanisms that could lead to differences between empirical results and expectations, given that functional traits show a phylogenetic signal, suggesting that closely related species are more similar than expected by chance (Tables 1, 2; Cavender-Bares et al. 2009). One possibility is that habitat filtering is occurring, but it results in multiple small (2 or 3 species) clusters of closely related species within sites that are distributed evenly across the phylogeny, or eliminates complete clades in the center of the phylogeny. Alternatively, competition between closely-related species could structure assemblages, so that phylogenetic structure is more evident when species from multiple habitats are included in species pools. If the latter is true, then species in the unfiltered species pool that were not observed at any of the sites should be closely related to species that were observed at the sites, but simply occur more frequently in habitats other than interior forest (e.g., edge habitats, agriculture, suburbs). This could indicate that either unobserved species were historically outcompeted in forested habitat, or that habitat specificity is less constrained by evolutionary history. A suggestion that species niches in general are not conserved seems unlikely, considering results from tests of phylogenetic signal (Tables 1, 2). However we did not explicitly test for a phylogenetic signal in habitat specificity and previous studies suggest that habitat selection or specificity in vertebrates 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 visually inspecting the phylogenies for each site, testing for clustering and overdispersion of particular nodes, and by comparing relationships between NRI and NTI. 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 differences in sensitivity, 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 results in several small clusters of closely related species within assemblages that are evenly distributed across the phylogeny, or in the absence of clades, then estimates of NRI and NTI should be uncorrelated and estimates of NTI should generally be indicative of clustering, even when NRI is not. Results for NRI and NTI suggest that phylogenetic structure in interior forest bird assemblages is more strongly influenced by habitat filtering rather than by competition. Moreover, visual inspection of the phylogenies and analysis of nodes that contribute disproportionately to patterns of phylogenetic structure (Figure A1) suggest that birds in the wood warbler genus *Setophaga* are strong contributors to patterns of overdispersion. This leads us to believe that something more than habitat filtering may be influencing the phylogenetic structure of assemblages. This is particularly evident when considering variation in strength of phylogenetic patterns among sites, metrics, and species pools (Fig. 2). Uncertainty regarding the dominant mechanism structuring assemblages is not unusual (Vamosi et al. 2009). This uncertainty often is attributed to environmental differences among sites or to the consequences of competition and filtering that act at different scales (e.g., Lovette and Hochachka 2006). Although these explanations are reasonable, another mechanism may be 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 (Fig. 2). Nonetheless, 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 broad biogeographic regions, 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 represents a single biogeographic region. Moreover, all assemblages were located in a single habitat type (interior forest), with species likely colonizing from the same source pool. Consequently, the idea that multiple assembly processes exert highly divergent degrees of influence and lead to multiple phylogenetic patterns is less compelling in this environmental context.

We offer an alternative explanation that posits variation in the phylogenetic structure of forest interior bird assemblages in this study is the consequence of priority effects exerted by residents and by the first arriving migrants that influence subsequent colonization of sites by later-arriving migrants. Priority effects can cause unexpectedly high variability in community structure even among environmentally similar sites (Chase 2003, 2010; Fukami 2004), rather than cause a single pervasive structure (e.g. Drake 1991; Chase 2003; Fukami 2004, 2010; Tan et al. 2012).

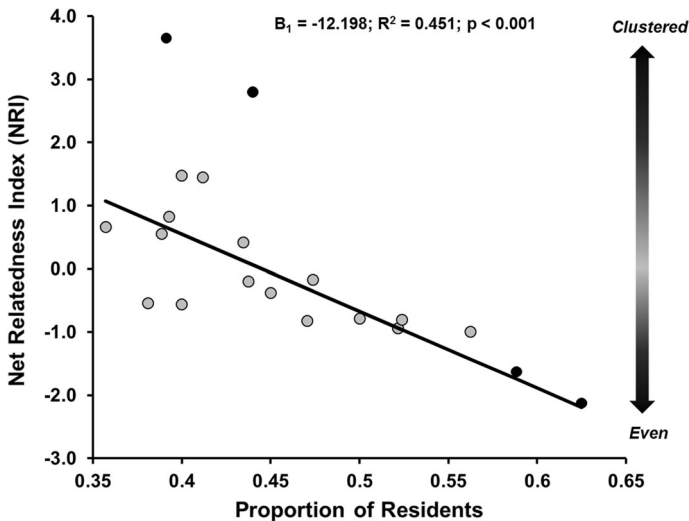
In general, temperate bird communities annually assemble and disassemble, with only a portion of the inhabitants (i.e., migrants) participating in yearly colonization. Consequently, the phylogenetic structure of assemblages likely reflects the influence of assembly processes acting on two distinct groups of birds. In situ assembly processes that have



determined the presence of resident species operate year-round, resulting in assemblage structure of residents being relatively similar over time. In contrast, assembly processes influence colonization by migrant species in an episodic manner (in the spring of each year), potentially enhancing variation among sites and years. Consequently, sites with similar environmental conditions can be quite variable in 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 during the non-breeding season (Lack 1966; Forsman and Monkkonen 2003), suggesting that environmental characteristics of local sites play a dominant role in determining the location resident territories. In contrast, migrants are more time-constrained in their decisions, as habitat selection, pairing, nest building, and reproduction must be accomplished within a few weeks of arrival on the breeding grounds. Moreover, migrants exhibit a range of natal philopatry and adults may change breeding sites from year to year (Weatherhead and Forbes 1994; Schlossberg 2009), suggesting that environmental characteristics of local sites play less of a role in site selection and that 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; Fig. 3), and these relationships were unrelated to the species richness of assemblages. Assemblages comprising a greater proportion of residents than migrants were phylogenetically overdispersed (Fig. 2) and generally lacked members of the genus *Setophaga*. In contrast, assemblages with relatively equal numbers of residents and migrants were generally either phylogenetically clustered or indistinguishable from random.



**Fig. 3** Variation in phylogenetic relatedness (NRI) in relation to the proportion of resident 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 expectation. *Gray circles* represent structure consistent with random assembly. *Solid line* represents significant linear relationship ( $p \leq 0.05$ ) from ordinary least squares regression ( $B_1 =$  slope) and  $R^2$  indicates the fit of the model

Assemblages with many more migrants than residents were not observed in the study, so we could not ascertain if such 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 evince greater phylogenetic overdispersion as a consequence of interspecific interactions (i.e., residents prevent migrants with similar niches from colonizing a site—niche preemption; Fukami 2015). Alternatively, it has been suggested that resident bird densities in northern environments (i.e., boreal and temperate forests) rarely reach high enough densities to result in competitive exclusion (Thomson et al. 2003). In fact, migrants may 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 by migrants (i.e., heterospecific attraction, Monkkonen et al. 1990, 1997; Monkkonen and Forsman 2002). If this were occurring, we would expect to see few assemblages with disproportionately high numbers of residents and would expect to see evidence of assemblages that were more functionally similar than expected due to chance; this was not the case (Table A5).

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, 1997; 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 (winter). In contrast, 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 1958; Herrera 1978; Hurlbert and Haskell 2003; Mönkkönen et al. 2006). Akin to priority effects leading to unexpectedly high variability in community structure even among environmentally similar sites, 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

Independent assembly mechanisms may structure resident and migratory subsets of temperate breeding bird communities. More specifically, 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. Temperate breeding bird communities offer a unique opportunity to study this mechanism, as colonization occurs on an annual basis. We hypothesize that priority effects may influence bird assemblages and lead to unexpectedly high variability in community structure even among environmentally similar sites based on results from spatial replicates with similar environmental conditions, but this hypothesis can only be tested by employing temporal replicates, or long-term data from sites with little environmental variation. Most studies examining the phylogenetic structure of communities focus on the relative role of environmental filtering versus competition (Vamosi et al. 2009). An important avenue for future research is to incorporate colonization history and historical contingency when considering the relative roles of filtering and competition in structuring assemblages.

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