

The relative importance of biotic and abiotic determinants of temporal occupancy for avian species in North America

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Abstract

Aim: We examined the relative importance of competitor abundance and environmental variables in determining the species distributions of 175 bird species across North America. Unlike previous studies, which tend to model distributions in terms of presence and absence, we take advantage of a geographically extensive dataset of community time series to model the temporal occupancy of species at sites throughout their expected range.

Location: North America.

Time period: 2001–2015.

Major taxa studied: One hundred and seventy-five bird species.

Methods: We calculated variation in temporal occupancy across species' geographic ranges and used variance partitioning and Bayesian hierarchical models to evaluate the relative importance of (a) the abundance of potential competitors and (b) the environment (elevation, temperature, precipitation, vegetation index) for determining temporal occupancy. We also created a null model to test whether designated competitor species predicted variation in temporal occupancy better than non-competitor species.

Results: On average, the environment explained more variance in temporal occupancy than competitor abundance, but this varied by species. For certain species, competitor abundance explained more variance than the environment. Migrant species with smaller range sizes and greater range overlap with competitors had a higher proportion of variance explained by competitor abundance than the environment. The abundance of competitor species had a stronger effect on focal species temporal occupancy than non-competitor species in the null model.

Main conclusions: Temporal occupancy represents an underutilized method for describing species distributions that is complementary to presence/absence or abundance. Geographic variation in temporal occupancy was explained by both biotic and abiotic drivers, and abiotic drivers explained more variation in temporal occupancy than abundance on average. Species traits also play a role in determining whether variation in temporal occupancy is best explained by biotic or abiotic drivers. The results of our study can improve species distribution models, particularly by accounting for competitive interactions.

KEYWORDS

competition, environmental filtering, spatial scale, species distribution, species interactions, temporal occupancy

1 | INTRODUCTION

Understanding what factors limit species distributions is critical for determining why species persist in their range and what habitat conditions they require (Andrewartha & Birch, 1954; Brown, 1984; Case, Holt, McPeck, & Keitt, 2005; Franklin, 2010; Guisan & Thuiller, 2005). Traditionally, species' distributions have been modelled based on presence/absence (Elith et al., 2006; Ferrier, Drielsma, Manion, & Watson, 2002; Phillips, Anderson, & Schapire, 2006) or as a snapshot in time of spatial abundance patterns (Bahn & McGill, 2007; Mönkkönen, Devictor, Forsman, Lehikoinen, & Elo, 2017). An alternative measure of occurrence is temporal occupancy, often measured as the proportion of years a species was observed at a given sampling site over time (Coyle, Hurlbert, & White, 2013; Snell Taylor, Evans, White, & Hurlbert, 2018). Temporal occupancy is distinct from traditional spatial measures of occupancy (e.g. Hanski & Gyllenberg, 1993; MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003) in that the focus is on the temporal persistence of a population at a given site rather than on the spatial prevalence. Temporal occupancy was highly variable when assessed across a species' geographic range, with species observed reliably at some sites within their range and only occasionally observed at others (Coyle et al., 2013). While temporal occupancy at a site is positively correlated with average abundance at that site for birds, many species maintain persistent populations at low density, making this correlation imperfect (Coyle et al., 2013). For this reason, temporal occupancy is a complementary metric to traditional measures for describing species distributions, although any interpretations of observed temporal occupancy values must consider how detectability might vary across species and environments to influence such patterns.

Generally, species require specific environmental conditions to succeed in a particular habitat, but often they do not occur everywhere the environment is suitable (Hutchinson, 1957; Chesson, 2000, Gaston, 2003). This distinction between the fundamental and realized niche is usually ascribed to interspecific interactions, such as where a species is outcompeted in parts of its suitable range by a superior competitor (Arif, Adams, & Wicknick, 2007; Connell, 1961; Cunningham, Rissler, Buckley, & Urban, 2016). Recent studies have demonstrated that including both positive and negative interspecific interactions can lead to more complete and accurate species distribution models (Belmaker et al., 2015; Blois, Zarnetske, Fitzpatrick, & Finnegan, 2013; Bruno, Stachowicz, & Bertness, 2003; Gotelli, Graves, & Rahbek, 2010; Guisan & Thuiller, 2005; Wisz et al., 2013). Interspecific competition for desirable habitat and resources may be the most relevant biotic interaction at large temporal and spatial scales of study and is the most studied biotic interaction for shaping species ranges (Sexton, McIntyre, Angert, & Rice, 2009). While many have argued for considering both environmental conditions and biotic factors in order to fully explain species distributions, there is not yet consensus on the relative importance of these two categories of

drivers, or on the types of species traits that might influence that relative importance.

Here, we seek to quantify the relative importance of biotic (competition-related) and abiotic drivers of temporal occupancy throughout the ranges of North American birds. Because temporal occupancy provides insight into the temporal persistence of populations that a snapshot of abundance cannot, we expect biotic and abiotic predictors to explain more variance in temporal occupancy than abundance. We also examine whether species migratory and foraging traits can help explain why temporal occupancy is better predicted by abiotic variables for some species and biotic interactions for others.

2 | METHODS

2.1 | Bird data

Birds are particularly suitable for modelling species ranges since they are well studied and there are ample data on their presence over time at large spatial extents (Bennett, Clarke, Thomson, & Mac Nally, 2015; Engler et al., 2017; Palacio & Girini, 2018). We used the North American Breeding Bird Survey (BBS) to characterize geographic variation in species presence and abundance. BBS surveys monitor breeding birds across the continent via a series of fifty 3-min point counts spaced at 0.8-km intervals along a roadside route (USGS Patuxent Wildlife Research Center, 2012). Each survey is conducted during the breeding season (typically June) by a single observer who records all avian species seen or heard along the route. We used the 953 BBS survey routes that were continuously surveyed from 2001 to 2015, and we excluded species that were poorly sampled by the survey design such as water birds, raptors, and nocturnal species (Butcher, Robbins, Bystrak, & Geissler, 1987). We identified 175 focal land bird species for analysis based on the following criteria: (a) species were present on at least 50 BBS routes over the 15 sampling years, and (b) species were observed at more than 30% of the survey sites within their geographic ranges (based on BirdLife International shapefiles, www.birdlife.org) over a 10-year period (Hurlbert & White, 2007). Each focal species was classified with respect to migratory class, family, and trophic group based on Hurlbert and White (2007). Breeding range centroids were calculated based on the BirdLife International shapefiles using the R package 'Gtools' (Warnes, Bolker, & Lumley, 2015).

2.2 | Biotic drivers

For each focal species, competitor species were identified as those species in the same family with any area of overlapping geographic range and within a twofold range of body mass (Dunning, 2007). These criteria are commonly used indicators of potential competitive

interactions in birds (Dhondt, 2012; Elsen, Tingley, Kalyanaraman, Ramesh, & Wilcove, 2017; Price, 1991; Yackulic, 2017). A comprehensive list of focal and associated competitor species is included in Supporting Information Table S1. In some cases, potential competitors from outside the focal species' family were included when such interactions were specifically described in natural history accounts (e.g. American redstart, *Setophaga ruticilla*, and least flycatcher, *Empidonax minimus*, Sherry, 1979). For each focal species, the competitor with the greatest percentage of breeding range overlap was also identified (hereafter, the most widespread competitor) based on BirdLife International shapefiles.

At each survey route r , we calculated an index of overall competitive pressure based on the summed abundance of all potential competitors relative to the focal species:

$$c_{sum,r} = \frac{\sum n_{j,r}}{\sum n_{j,r} + n_{i,r}} \quad (1)$$

where $n_{i,r}$ and $n_{j,r}$ are the abundances of focal species i and the j th competitor of species i , respectively, on route r . Given that some of the species listed as potential competitor species may not actually compete with the focal species, their inclusion may add noise to this metric of competitive pressure. As such, we conducted separate sets of analyses using only the scaled abundance of individual competitor species as the metric of competitive pressure, where:

$$c_{j,r} = \frac{n_{j,r}}{n_{j,r} + n_{i,r}} \quad (2)$$

For each focal species, we calculated $c_{j,r}$ based on the a priori identification of the most widespread competitor species with the greatest amount of breeding range overlap ($c_{widespread,r}$), as well as the a posteriori identification of the competitor species for which $c_{j,r}$ was most negatively correlated with focal occupancy (hereafter, most predictive competitor; $c_{max,r}$). We use these scaled indices of competitor abundance rather than raw abundances to account for variation in absolute densities over the broad geographic gradients examined.

2.3 | Abiotic drivers

Long term normals for mean annual temperature and mean annual precipitation were acquired from WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) at 2.5-min resolution, and a 30-m digital elevation model was acquired from the National Elevation Dataset (NED) from the United States Geological Survey (USGS). Normalized difference vegetation index (NDVI) was acquired from the Global Inventory Mapping and Monitoring Studies database (GIMMS). The NDVI data were 250-metre, monthly resolution, averaged over the summer months of June, July and August (<https://gimms.gsfc.nasa.gov/MODIS/>).

For each BBS route, the mean of each environmental variable was calculated within a 40-km buffer to ensure that the entire

40-km route was encompassed. For each species i , the environmental centroid or species' optimum, \bar{E} , for each environmental variable k was calculated by weighting the environmental value at each BBS route by the focal species' average abundance at that site ($n_{i,r}$):

$$\bar{E}_{ik} = \frac{\sum n_{i,r} E_{kr}}{\sum n_{i,r}} \quad (3)$$

Environmental values for each variable k were then transformed into z-scores describing the absolute deviation, D , from the optimum for species i at route r as follows:

$$D_{ikr} = \left| \frac{E_{kr} - \bar{E}_{ik}}{\sigma_{ik}} \right| \quad (4)$$

where σ_{ik} is the abundance-weighted standard deviation of environmental values across all routes at which species i is present. We took the absolute value of these environmental deviations because we are not concerned with the direction of deviations, simply their magnitude. Environmental deviation values were calculated for temperature, precipitation, elevation and NDVI across the set of BBS routes at which each focal species was expected to occur based on range map shapefiles. Higher values of this deviation metric indicate a greater deviation from the species' environmental optimum.

2.4 | Temporal occupancy and detectability

We measured temporal occupancy at each BBS survey route for each focal species as the fraction of sample years between 2001 and 2015 during which the species was observed at that site. Because it is possible for a species to be present at a site but go undetected, these values are minimum estimates of temporal occupancy. Ideally, repeat visits at each site within each survey season are needed to directly model imperfect detectability at the survey route scale (MacKenzie et al., 2003) and yet repeat visits at a site within a single survey season are not part of the BBS sampling protocol. Our analyses rely on the untested assumption that observed patterns of temporal occupancy are not driven simply by patterns in detectability, so we consider qualitatively how imperfect detectability is expected to impact our inferences. If detectability varies systematically with our covariates of interest then it may introduce bias, and if not, then it will simply add noise.

Of the environmental variables we examine, NDVI is the most likely to vary with detectability across broad geographic gradients, with more vegetated, higher NDVI sites having potentially smaller effective survey radii over which birds can be seen and heard (Hurlbert, 2004). Given such an effect of NDVI on detectability, observed occupancy may underestimate true occupancy to a greater degree at high NDVI compared to low NDVI sites. The premise of our analysis is that occupancy should decrease both above and below a species' NDVI centroid (Supporting Information Figure S1), and a monotonic decline in detectability with NDVI would be unlikely to produce such a pattern.

Nevertheless, we examined the relationship between occupancy and NDVI below the NDVI centroid for each species. If detectability decreases with increasing NDVI and if observed patterns are driven by variation in detectability, we expect a negative slope, as birds are detected less frequently at higher NDVI. Instead, we found that 86% of species had a positive slope, in opposition to any expected effect of detectability. Second, if detectability is lower above the NDVI centroid than below it, then we expect the slope of the occupancy and NDVI deviation relationship to be steeper above the centroid (Supporting Information Figure S1). For each species, we compared the occupancy and NDVI deviation relationships above and below the NDVI environmental centroid and found no systematic difference in which side had a steeper slope (Supporting Information Figure S2). This implies that while detectability is imperfect, it is not systematically varying within our dataset in a way that is generating the patterns we are testing. Nevertheless, the possibility exists that some fraction of variance explained in temporal occupancy could be attributable to unmeasured patterns of variation in detectability.

2.5 | Analysis

For each focal species, we used variance partitioning to quantify the amount of variance in temporal occupancy that could be uniquely explained by either the set of environmental variables (deviations from centroid) or scaled competitor abundance (c_{sum} , c_{max} or $c_{widespread}$), as well as the shared variance component that could not be uniquely ascribed to either variable class (Legendre & Legendre, 1998). When partitioning variance between two variable groups, the unique variance component for one variable group is defined as the increase in R^2 when that group is added to a model with the other variable group. We also developed a hierarchical Bayesian model to understand how competitor abundance and environmental deviation from the optimum influenced focal species temporal occupancy. The model used focal temporal occupancy as the response variable and scaled competitor abundance and deviation measures for each of the four abiotic variables, allowing for random slopes and intercepts by species:

$$\text{logit}(p_{i,r}) = \beta_0 + b_{0,i} + (\beta_1 + b_{1,i})c_{sum,ir} + (\beta_2 + b_{2,i})D_{temperature,ir} + (\beta_3 + b_{3,i})D_{elevation,ir} + (\beta_4 + b_{4,i})D_{precipitation,ir} + (\beta_5 + b_{5,i})D_{NDVI,ir} \quad (5)$$

where $p_{i,r}$ represents the probability of a given focal species i appearing in any given year at site r , β_j are the population level effect coefficients, and $b_{j,i}$ are the species level random effects. We assumed that the random effects were distributed $b_{j,i} \sim \text{Multivariate normal}(0, \Sigma)$, where Σ is an unstructured variance-covariance matrix. Observed occupancies we assumed were distributed $T_{i,r} \sim \text{Binomial}(p_{i,r}, n_r)$, where n_r were the number of years sampled at site r . The model was estimated using the brms package using the default priors in version 2.7.0 (Bürkner, 2017). We used this hierarchical Bayesian approach in order to estimate overall estimates for the effect of competitor abundance and abiotic variables across species, but used simple linear regression for within-species variance partitioning.

We quantified the extent to which temporal occupancy for a given species was better predicted by biotic or abiotic variables using the ratio R_C , defined as the competitor variance component divided by the sum of the competitor and abiotic environment variance components. Values of R_C above .5 indicate that of the variance in temporal occupancy explained, more variance is explained by competitor abundance than environment, while values below .5 indicate that more variance is explained by the environment than competitor abundance. We explored whether several species traits could explain interspecific variation in R_C using logit-transformed and arcsine-transformed regression models. First, we confirmed that variation in R_C was not simply due to phylogenetic relatedness by calculating Blomberg's K (Blomberg, Garland, & Ives, 2003) averaged across 100 trees sampled from the Jetz, Thomas, Joy, Hartmann, and Mooers (2012) pseudo-posterior distribution of phylogenetic trees for Aves from birdtree.org. Then, we examined how R_C varied with each species' environmental centroids for temperature, precipitation, elevation, NDVI, range size, proportional area of overlap with competitors, median temporal occupancy, migratory status, and trophic group categories, weighting each species in the analysis based on the total number of BBS routes on which it occurred over the 15-year period. The rationale for weighting species in this way is that species with larger ranges and hence larger spatial sample sizes should have better R^2 estimates. Competitor range overlap was calculated by summing the total area each focal species overlapped with a potential competitor species, divided by the focal range area. Because range overlap is summed across multiple competitor species, it may exceed 1. A list of focal species and the traits used in these analyses is provided in Supporting Information Table S2.

2.6 | Competitor null model

To better interpret the amount of variance in temporal occupancy explained by the abundance of individual competitors (most widespread or most predictive), we conducted a null model analysis examining the variance explained by the scaled abundance of non-competitor species. For our purposes, non-competitor species included the subset of all species in our dataset from a different family than the focal species (with some exceptions as noted), or from the same family but where body size differed from the focal species by twofold or more, and with some overlap in geographic range. For each focal species where the most widespread competitor abundance had a strong effect ($R^2 \geq 10\%$, $n = 61$), we conducted separate linear regressions predicting focal species temporal occupancy based on the scaled abundance of each non-competitor (based on Equation 1). The number of non-competitor species evaluated for each focal species varied between 116 and 274. Any variance explained by non-competitor species presumably reflects indirect habitat associations rather than competitive effects, and thus provides a benchmark for interpreting the variance explained and the effect size of the competitors on the focal species. We expected a stronger negative relationship between focal temporal occupancy

and abundance for the most widespread and most predictive competitors than for non-competitors, and we calculated the proportion of non-competitor species with a higher R^2 or more negative parameter estimate than either competitor.

3 | RESULTS

Species differed substantially in the total amount of variance in temporal occupancy explained and in whether competitor abundance or environmental factors explained more variance (Figure 1). The median total variance explained by both sets of predictors together was 31% across all 175 species, and abiotic factors uniquely explained more variance in temporal occupancy than summed competitor abundance on average (12% compared to 8%; Figure 1a, Supporting Information Table S3). The ratio R_c , which describes the relative amount of variance explained by competitor abundance, spanned a

wide range of values (0–.96). While a few species had high values, the bulk of the distribution fell under .5 (median = .34) indicating stronger predictive power of abiotic over biotic variables. Similar results were obtained using the abundance of the most predictive competitor rather than the summed abundance of all competitors (Supporting Information Table S4, Figure S3). Using the abundance of the most widespread competitor decreased the median variance explained by competitor abundance (3%, compared to 8% for all competitors), while the environmental median variance component increased (16%; Figure 1b, Supporting Information Table S5). Total variance and the ratio R_c decreased (28 and 18%, respectively). Unless otherwise specified, subsequent analyses refer to the summed abundance of all competitors to characterize competitive pressure.

The variance partitioning results for the 15 species that had the most variance in temporal occupancy explained by competitor abundance and by the environment, respectively, are shown in Figures 2 and 3 (full variance partitioning results and model output for all species are provided in Supporting Information Tables S3–S8). The range of unique variance explained for these top species was similar for competitor abundance (28–48%, Figure 2) and environment (29–43%, Figure 3) variance components, and species that were well explained by one variable category typically had little variance explained by the other. Shared variance that could not be uniquely ascribed to either competitors or the environment was higher for those species best explained by competitor abundance. Even though the median variance component explained by the environment was higher than the median variance component explained by competitors, the maximum variance component explained by competitors was higher than the maximum variance component explained by the environment.

Focal species temporal occupancy was lower at sites that deviated farther from the species' environmental optimum for all environmental variables, and temporal occupancy decreased as relative competitor abundance increased (Table 1). Across all variables, there was wide variation in the relationship between the environment, competitor abundance, and focal species temporal occupancy (Table 1). Deviations in temperature (slope = -0.45 [$-0.53, -0.37$]) and NDVI (slope = -0.27 [$-0.32, -0.21$]) had stronger negative relationships with focal temporal occupancy than elevation (slope = -0.15 [$-0.23, -0.07$]) or precipitation (slope = -0.16 [$-0.23, -0.09$]; Table 1). Competitor abundance (slope = -2.00 [$-2.56, -1.53$]) had a strong negative relationship with focal temporal occupancy, although its slope is not directly comparable to the slopes of environmental deviation since competitor abundance is scaled from 0 to 1. All values of \hat{R} , a potential scale reduction factor, were between 1.00 and 1.03 indicating model convergence. Full model output is available as Supporting Information (Table S9 for all competitors, Table S10 for widespread competitors).

We found that abiotic variables collectively explained approximately twice as much variance in temporal occupancy as they did in abundance across sites (Figure 4, green circles). In contrast, abundance was better predicted by summed competitor abundance

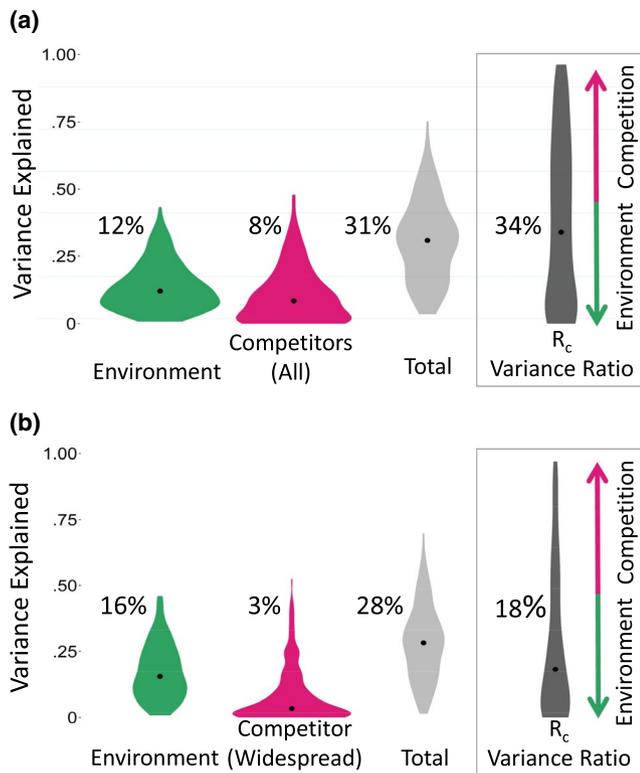


FIGURE 1 (a) Violin plots demonstrating the distribution of unique variance in focal temporal occupancy explained by environmental variables, the unique variance explained by the summed abundance of all competitors, the total variance explained by a model with both sets of variables, and R_c , the competitor variance component divided by the sum of the competitor and environment variance components. Points within each distribution represent the median. (b) Violin plots demonstrating the distribution of unique variance in focal temporal occupancy explained by environmental variables, the unique variance explained by the abundance of the most widespread competitor, the total variance explained by a model with both sets of variables, and the variance ratio, R_c [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 2 The top 15 focal species ranked by variance explained by scaled competitor abundance. Variance partitioning results illustrating the variance uniquely explained by competitor abundance (pink), uniquely explained by the environment (green) and the shared variance component that cannot be uniquely ascribed to either class of variables (blue) [Colour figure can be viewed at wileyonlinelibrary.com]

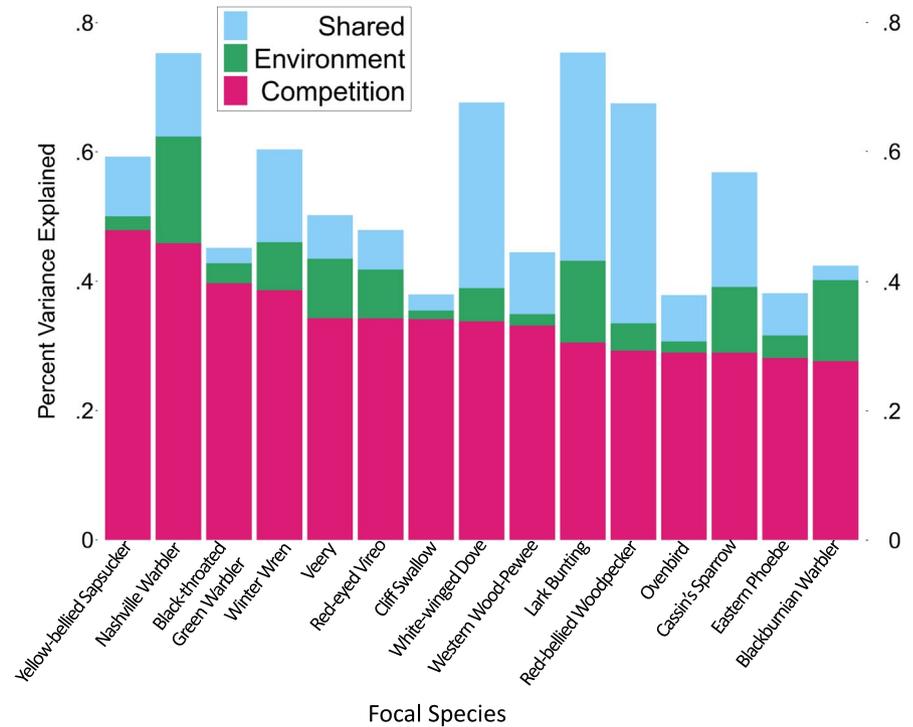
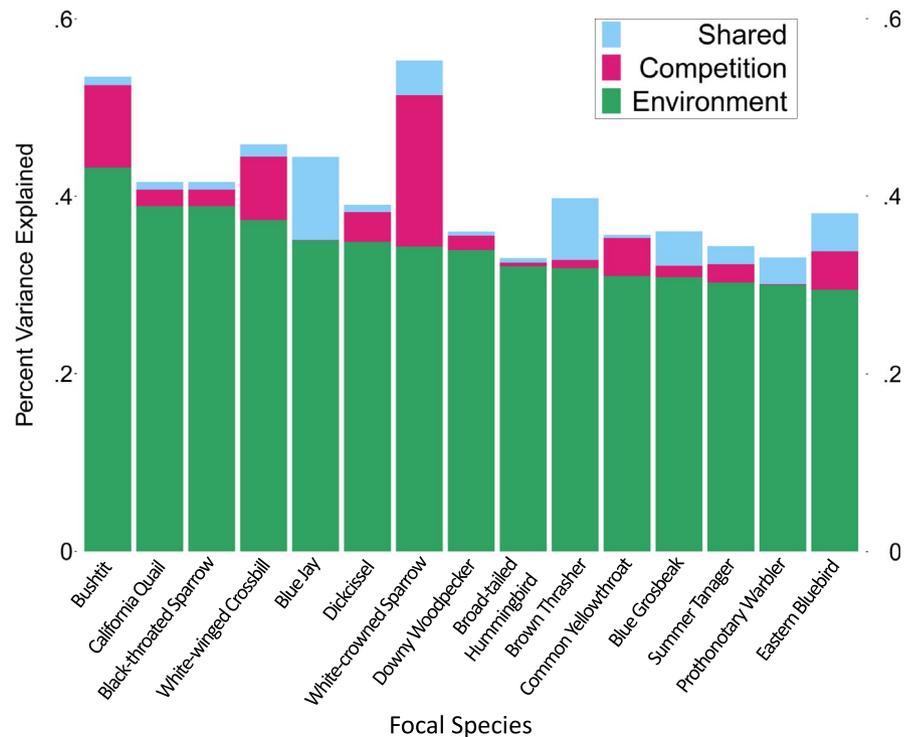


FIGURE 3 The top 15 focal species ranked by variance explained by deviation from optimal environmental conditions. Variance partitioning results illustrating the variance uniquely explained by the environment (green), competitor abundance (pink) and the shared variance component that cannot be uniquely ascribed to either class of variables (blue) [Colour figure can be viewed at wileyonlinelibrary.com]



on average, with the majority of points falling above the 1:1 line (Figure 4, pink triangles). However, using widespread or predictive competitor abundance rather than the summed abundance of all competitors, temporal occupancy and abundance were equally well predicted by competitor abundance (Supporting Information Figures S4–S5). The total variance explained by the combination of biotic and abiotic variables was only slightly greater on average when predicting abundance compared to temporal occupancy, although individual species differed substantially (Figure 4, grey crosses). Total

variance was slightly greater when predicting temporal occupancy compared to abundance when using the most widespread or the most predictive competitor abundance (Supporting Information Figures S4–S5). For example, 75% of the total variance in temporal occupancy could be explained for the lark bunting (*Calamospiza melanocorys*) compared to only 52% of the total variance in abundance, while for the worm-eating warbler (*Helmitheros vermivorum*), only 16% of the variance in temporal occupancy could be explained compared to 51% for abundance. Full variance partitioning results and

TABLE 1 Bayesian hierarchical model results for the fixed effects of the absolute value of the environmental z-score (deviation from the environmental centroid) and competitor abundance on focal species temporal occupancy. Species was included as a random effect allowing for random slopes and intercepts. σ^2 represents the posterior variance

	Mean	Credible interval		σ^2	Credible interval of σ	
		Lower 95%	Upper 95%		Lower 95%	Upper 95%
Intercept	3.26	2.75	3.88	3.74	3.35	4.18
Competitor abundance	-2.00	-2.56	-1.53	3.38	3.02	3.78
Temperature	-0.45	-0.53	-0.37	0.50	0.45	0.56
NDVI	-0.27	-0.32	-0.21	0.35	0.31	0.39
Elevation	-0.15	-0.23	-0.07	0.52	0.47	0.58
Precipitation	-0.16	-0.23	-0.09	0.48	0.43	0.54

NDVI = normalized difference vegetation index.

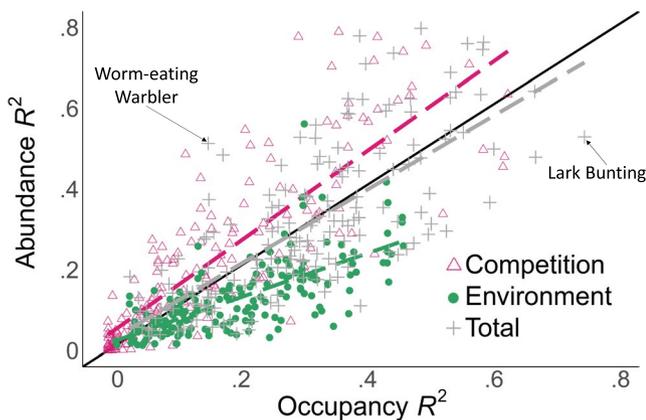


FIGURE 4 The ability of environmental variables (green circles), competitor abundance (pink triangles) or both combined (grey crosses) to predict spatial variation in temporal occupancy (x axis) compared to spatial variation in abundance (y axis) based on linear regression R^2 s (and not unique variance components, as portrayed in Figures 1–3). Black line represents the 1:1 line. Dashed lines indicate linear regressions through each of the three sets of predictor variables [Colour figure can be viewed at wileyonlinelibrary.com]

model output for all species predicting focal abundance rather than temporal occupancy are available in Supporting Information Tables S11–S16.

Species differed in the relative explanatory power of biotic or abiotic variables for predicting temporal occupancy, measured by the ratio R_C , and we examined whether species traits could explain this variation. The mean value of Blomberg's K was 0.105 (standard deviation = 0.013), indicating very little phylogenetic signal (Blomberg et al., 2003). Our model explained 29% of the variance in R_C . Species with smaller ranges ($\beta = -2.88, p < .001$) and higher median occupancy values ($\beta = 2.37, p < .001$) had a greater proportion of explained variance due to competitor abundance compared to the environment (Table 2). In addition, as range overlap between species and their competitors and median temporal occupancy increased, the proportion of explained variance due to competitors also increased ($\beta = 0.042, p = .003$). Mean temperature and NDVI across the range had a negative relationship

with R_C , meaning that species found at warmer and greener sites on average had a greater proportion of explained variance due to the environment ($\beta = -0.015, p < .001$; $\beta = -4.567, p = .011$, respectively). Mean precipitation across species range had a positive relationship with R_C , meaning that species in lower precipitation areas had a greater proportion of explained variance due to the environment ($\beta = 0.023, p = .001$). Mean elevation across the range had no strong effects on why some species are relatively better predicted by the environment than others ($p = .238$; Table 2).

As for categorical variables, R_C differed with trophic group and migratory guild. Insect/omnivores and insectivores had a greater proportion of explained variance due to competitor abundance than granivores or omnivores ($\beta = 0.676, p = .019$; $\beta = 0.52, p = .069$, respectively, Table 2). Short distance migrants had a greater proportion of explained variance due to competitor abundance than neotropical migrants ($\beta = 0.477, p < .001$), while residents had a greater proportion of explained variance due to the environment than neotropical migrants ($\beta = -0.458, p = .012$). Results were qualitatively similar using arcsine transformed linear models, with the exception that there was a smaller difference between residents and neotropical migrants ($p = .14$; Supporting Information Table S17).

In the null model, we modelled the temporal occupancy of each focal species as a function of the scaled abundance (Equation 1) of each non-competitor species in our dataset. As an example, the yellow-bellied sapsucker (*Sphyrapicus varius*) was compared to 154 non-competitors that were able to explain a median of 4% of the variance in temporal occupancy, compared to 51% explained by its most widespread and most predictive competitor, the hairy woodpecker (*Leuconotopicus villosus*; Figure 5a). In addition, the hairy woodpecker had a much stronger negative effect on yellow-bellied sapsucker temporal occupancy compared to the median effect size of non-competitors (-11.0 vs. -3.2, Figure 5b). For the 61 focal species with a strong ($R^2 \geq 10\%$) effect of widespread competitor abundance, only a small proportion of null non-competitors could explain more variance in temporal occupancy than the most widespread or most predictive competitors (Figure 5c).

TABLE 2 Regression model of the effect of continuous traits [range size, competitor range overlap between focal species and all competitors, median temporal occupancy, and abundance-weighted average temperature, precipitation, elevation, and normalized difference vegetation index (NDVI) calculated across each species' range] and categorical traits (trophic group, migratory status) on logit-transformed R_C , the competition variance component divided by the sum of the competition and environment variance components

	Estimate	Standard error	t value	p value
Intercept (granivore/neotropical migrant)	19.509	2.142	9.109	<.0001
Log10(focal range size)	-2.880	0.196	-14.671	<.0001
Median temporal occupancy	2.375	0.294	8.072	<.0001
Competitor range overlap	0.042	0.014	2.942	.003
Temperature	-0.015	0.004	-3.804	<.0001
Precipitation	0.023	0.007	3.396	.001
Elevation	3.59e-4	0.000	1.180	.238
NDVI	-4.567	1.802	-2.535	.011
Insectivore/omnivore	0.676	0.287	2.355	.019
Insectivore	0.520	0.285	1.820	.069
Omnivore	-0.602	0.379	-1.589	.112
Resident	-0.458	0.183	-2.504	.012
Short-distance migrant	0.477	0.125	3.824	<.0001

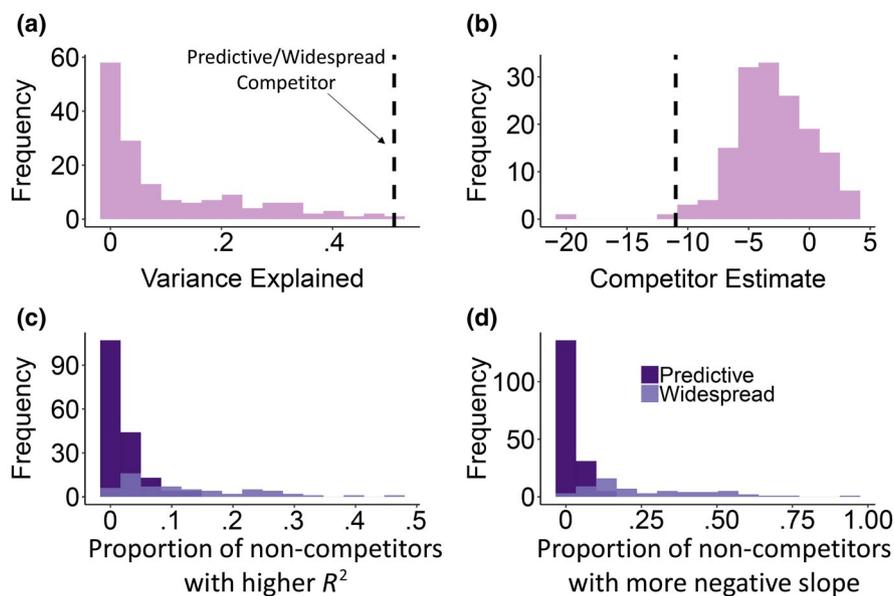


FIGURE 5 (a) Histogram of variance in temporal occupancy explained by 154 non-competitors of yellow-bellied sapsucker, *Sphyrapicus varius* (median = 0.04), in relation to the variance explained by the most widespread and most predictive competitor, hairy woodpecker (*Dryobates villosus*, dashed black line, $R^2 = .51$). (b) Histogram of the competitor abundance parameter estimate for 154 non-competitors of yellow-bellied sapsucker (median = -3.2) in relation to the estimate for hairy woodpecker (black dashed line; estimate = -11.0). (c) Histogram of the proportion of non-competitor species with R^2 values matching or exceeding the most widespread competitor R^2 (dark purple) or the most predictive competitor (light purple) when predicting focal species temporal occupancy. Low values indicate a stronger effect of the competitor species relative to non-competitors. (d) Histogram of the proportion of non-competitor species with estimates matching or exceeding the most widespread competitor estimate (dark purple) or the most predictive competitor estimate (light purple) when predicting focal species temporal occupancy [Colour figure can be viewed at wileyonlinelibrary.com]

Across these focal species, the explained variance of both the most widespread and most predictive competitor were much higher than the median variance explained by non-competitors (paired t test, $p < .001$). Similarly, we found that few non-competitors had effect sizes that were more negative than the effect size of the most widespread or most predictive competitors (paired t test, $p < .001$; Figure 5d).

4 | DISCUSSION

Temporal occupancy reflects the persistence of a population over time and varies broadly throughout a species' range. We found that both biotic and abiotic variables explain a large fraction of the geographic variation in temporal occupancy for any given species. While environmental variables typically explained more variation

than the abundance of interspecific competitors, there were many species for which the opposite was true, as well as some species whose temporal occupancy was poorly explained by all variables considered. For most species, environmental variables could better predict spatial patterns of temporal occupancy than they could spatial patterns of abundance, a traditionally examined metric. In addition, we found that traits help explain whether temporal occupancy is better predicted by biotic or abiotic variables: migrant species with smaller range sizes, higher median temporal occupancy, and greater range overlap with competitors had a higher proportion of variance explained by competitor abundance than the environment.

Abiotic factors have historically received the most attention in the literature for explaining species distributions (Andrewartha & Birch, 1954; Gaston, 2003; Sexton et al., 2009). Here, we found that species tend to have the highest temporal occupancy in environments that are closest to their range-wide environmental centroids, with decreasing temporal occupancy in environments that are most different from the centroid conditions. Overall, temperature had the strongest effect on temporal occupancy of the environmental variables considered, but no single variable consistently explained more variance in temporal occupancy compared to the other environmental variables in the single-species models. For example, the bushtit (*Psaltriparus minimus*) had the most variance in temporal occupancy explained by the environment (43%), with the strongest effects of temperature, followed by NDVI, and to a lesser extent elevation and precipitation. In contrast, temporal occupancy of the black-throated sparrow (*Amphispiza bilineata*) only exhibited a strong negative relationship with deviations in NDVI. These examples demonstrate variation in the exact environmental determinants of temporal occupancy for individual species, but collectively, environmental variables explained more variance in temporal occupancy than competitor abundance on average.

Ecologists increasingly recognize that biotic factors may also be important in shaping distributions over broad geographic scales (Araújo & Rozenfeld, 2014; Belmaker et al., 2015; Bruno et al., 2003; Mönkkönen et al., 2017). Even though abiotic variables generally explained more variance in temporal occupancy, the maximum amount of variance that could be explained by competitor abundance (48% for yellow-bellied sapsucker, *Sphyrapicus varius*) was greater than the maximum amount of variance that could be explained by the environment (43% for bushtit). The observed decline in temporal occupancy as competitor abundance increased is what we would expect if increasing competition made it more difficult for the focal species to persist at certain sites. We see these effects regardless of whether we used the abundance of the most widespread competitor species, the most predictive competitor species, or the summed abundance of all potential competitors, although effects were generally strongest using all competitors. In addition, these observed negative effects of competitor species were stronger and explained more variance than those of non-competitors, supporting the interpretation of competition (past or present) rather than associations due simply to differences in habitat preferences.

Nevertheless, there are some limitations to our approach and caveats in interpretation. We analysed patterns in observed temporal occupancy, which is by definition the product of true temporal occupancy and species' detectability. We have therefore assumed that detectability does not vary systematically with the environmental variables considered here. Because we scaled environmental variables separately for each species with respect to each species' environmental centroid, the most likely effect of variation in detectability is increased noise in the relationships we are trying to detect (Supporting Information Figure S1). Still, we cannot rule out the possibility that variation in detectability accounts for some fraction of the variance we are attempting to explain.

A second concern has to do with our assumptions about competitor species. Field studies quantifying the strength and consequences of interspecific competition in birds are time intensive (Dhondt, 2012) and have not been conducted for most species. To assign potential competitors to 175 focal species in a standardized fashion, we used a simple set of criteria: that they be from the same family (unless there was literature demonstrating a non-familial competitive relationship), that they be similar in body size and that their geographic ranges overlap. These selected species may include species that do not strongly compete with the focal species, introducing noise and potentially resulting in the low explained variance. Thus, our estimates of the explanatory power of competitor abundance may be conservative, and such interactions might actually be stronger when defining competitors based on finer-scale information such as foraging behaviour and morphological traits like bill, wing and leg dimensions. We encourage researchers to collect more experimental and observational data to augment existing compilations on the magnitude of pairwise competitive interactions (Martin, Desrochers, & Fahrig, 2017). Conversely, focal species may compete for resources with heterofamilial species that we did not consider, or even with other taxonomic groups (Brown, Davidson, & Reichman, 1979), such that we may have left out important potential competitors for some species.

Another limitation is that while negative effects of competitor abundance on focal species temporal occupancy are consistent with competitive interactions, they may also be consistent with divergent habitat preferences that lead to negative correlations in space. Such divergent habitat preferences may or may not result from past selection (Connell, 1980). Consider the yellow warbler (*Setophaga petechia*), whose broad geographic range leads to high range overlap – and therefore assignment of 'widespread competitor' status – with many other warbler species in our dataset (Supporting Information Table S1). Despite its broad geographic range, the yellow warbler preferentially breeds in wet, deciduous thickets and is commonly associated with willows (Lowther, Celada, Klein, Rimmer & Spector, 1999). For other warbler species, a negative correlation with yellow warbler abundance may simply reflect negative associations with yellow warbler's preferred habitat rather than evidence for ongoing competition. This is likely the case for most of the warbler species whose occupancies were strongly predicted by yellow warbler abundance, given the stated habitat preferences in their respective Birds

of North America species accounts (Rodewald, 2018). In some cases, the variance explained by abundance of the most widespread competitor may actually reflect finer-scale habitat associations rather than competition. That said, unless a species differs in habitat preference from all other members of its family, the use of the summed abundance of all potential competitors should minimize the influence of this alternative interpretation.

The scale at which we conducted our analyses likely affected observed temporal occupancy patterns and potentially the determinants of those patterns (Jenkins, White, & Hurlbert, 2018; Snell Taylor et al., 2018). Because we used environmental and community data collected at the scale of c. 40 km, we can only make inferences related to competition at the landscape scale. Competitive interactions have certainly been documented at these scales and larger (Belmaker et al., 2015; Gotelli et al., 2010; Wisz et al., 2013); however, our analysis was incapable of detecting the interspecific competition that occurs at much finer scales, as demonstrated in classic studies of local niche partitioning (Dhondt, 2012; MacArthur, 1957; Morse, 1980). As such, finding that competitor abundance explains little variation in temporal occupancy for any particular species clearly does not imply that competition is altogether unimportant for that species.

We examined temporal occupancy as a response that varied across a species' geographic range in contrast to previous studies that have examined spatial variation in abundance (Araújo & Rozenfeld, 2014; Bahn & McGill, 2007; Brown, 1984; Mehlman, 1997) or presence/absence (Elith et al., 2006; Ferrier et al., 2002; Phillips et al., 2006). Environmental variables were better able to predict spatial variation in temporal occupancy than spatial variation in abundance, while competitor abundance better predicted focal species abundance than focal species temporal occupancy. This difference in explanatory power based on the type of predictor highlights important differences in the ecological information encoded in temporal occupancy versus abundance. Because temporal occupancy integrates how a species interacts with its environment over time, it may produce a more accurate characterization of that species' fundamental niche. Temporal occupancy may also help distinguish between sites where a species shows up as a rare and infrequent transient species (Snell Taylor et al., 2018) as opposed to a rare but persistent member of the community. This further implies that species distribution models, which traditionally use environmental variables to predict presence or abundance, might have improved performance predicting temporal occupancy. Conversely, summed competitor abundance explained more variance in spatial abundance patterns than spatial occupancy patterns. Given that a species can persist under a given set of environmental conditions, the average population size it is able to obtain there may be in part due to the abundance of other competitors. Thus, temporal occupancy and abundance appear to be complementary measures of species distribution that may each help characterize a species' realized niche. More work is needed to understand what types of species and in which environmental contexts temporal occupancy will be most influenced by biotic and abiotic factors, and how such an understanding might ultimately inform habitat suitability models for conservation.

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DATA AVAILABILITY STATEMENT

The data and code associated with this study are available on Zenodo (<https://doi.org/10.1101/555227>) and the processed data and model outputs are available as a zip file in the Supporting Information (Tables S1-S17).

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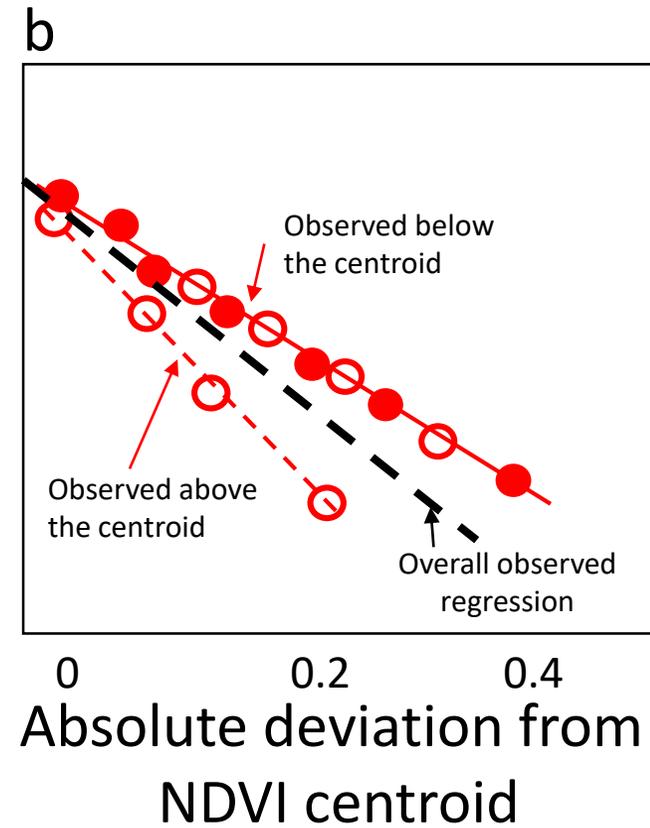
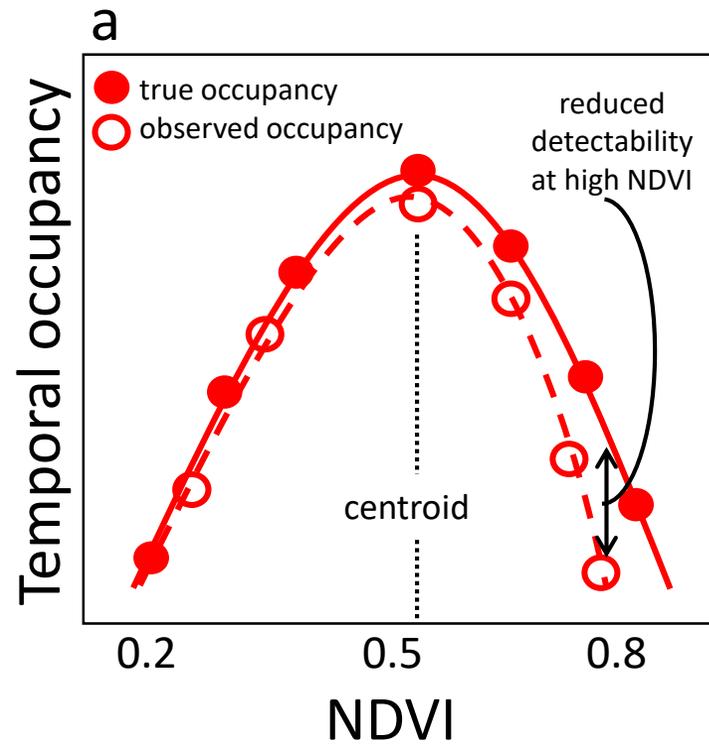
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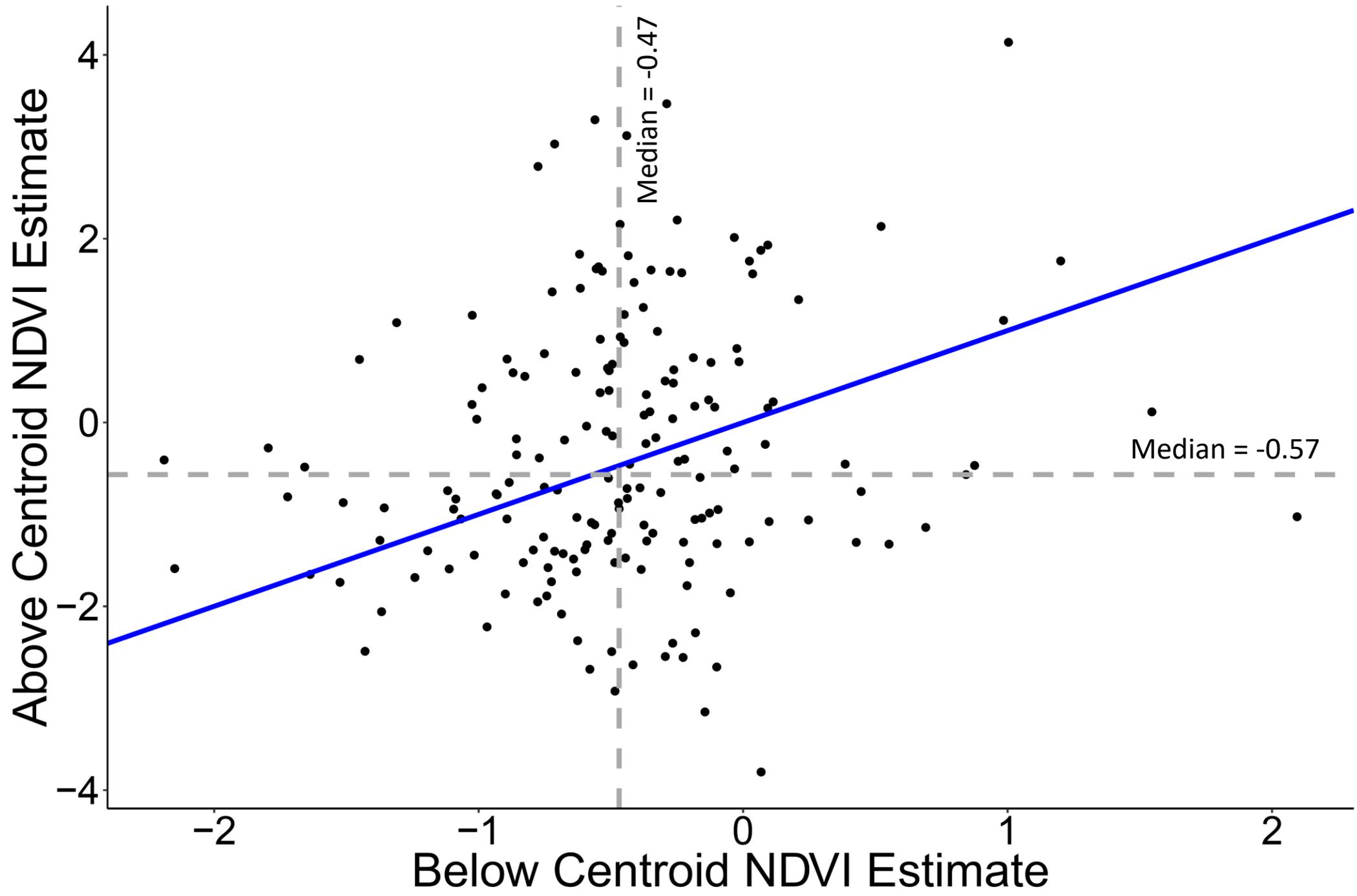
Sara Snell Taylor is a PhD candidate at the University of North Carolina. Her research considers how species interactions and the environment work to shape species distributions at large scales. **Allen Hurlbert** is interested in the processes governing the distribution of organisms in space and time.

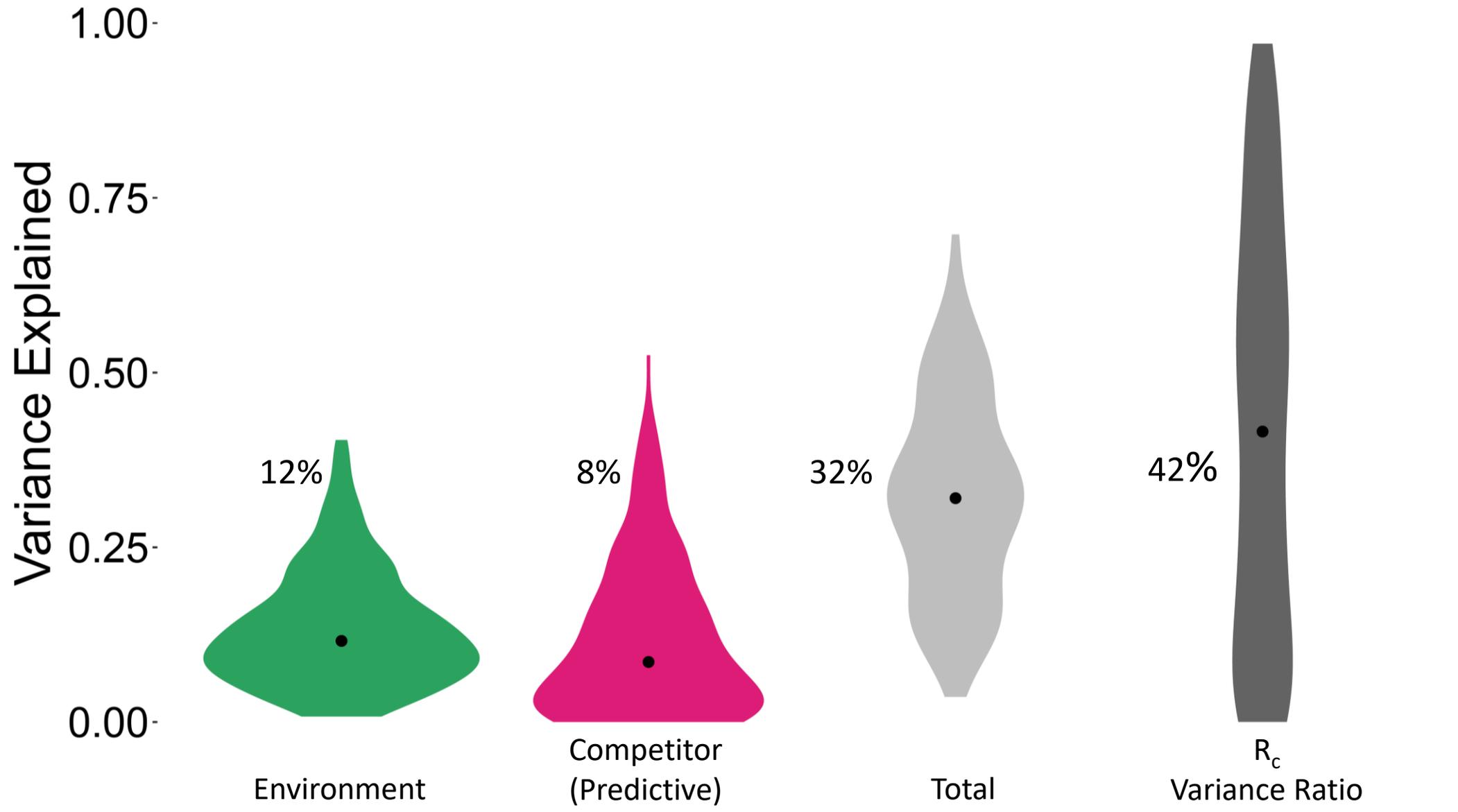
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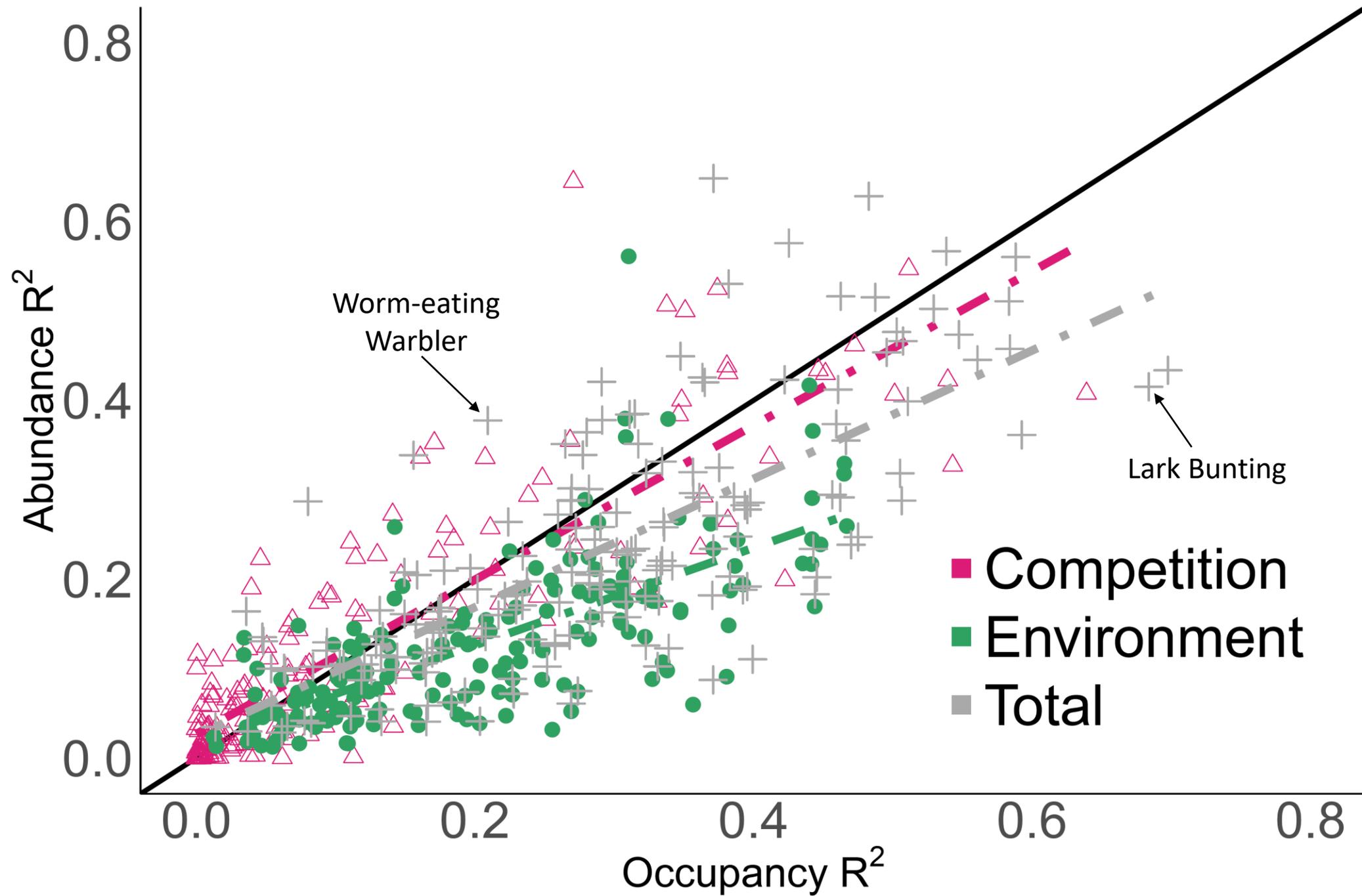
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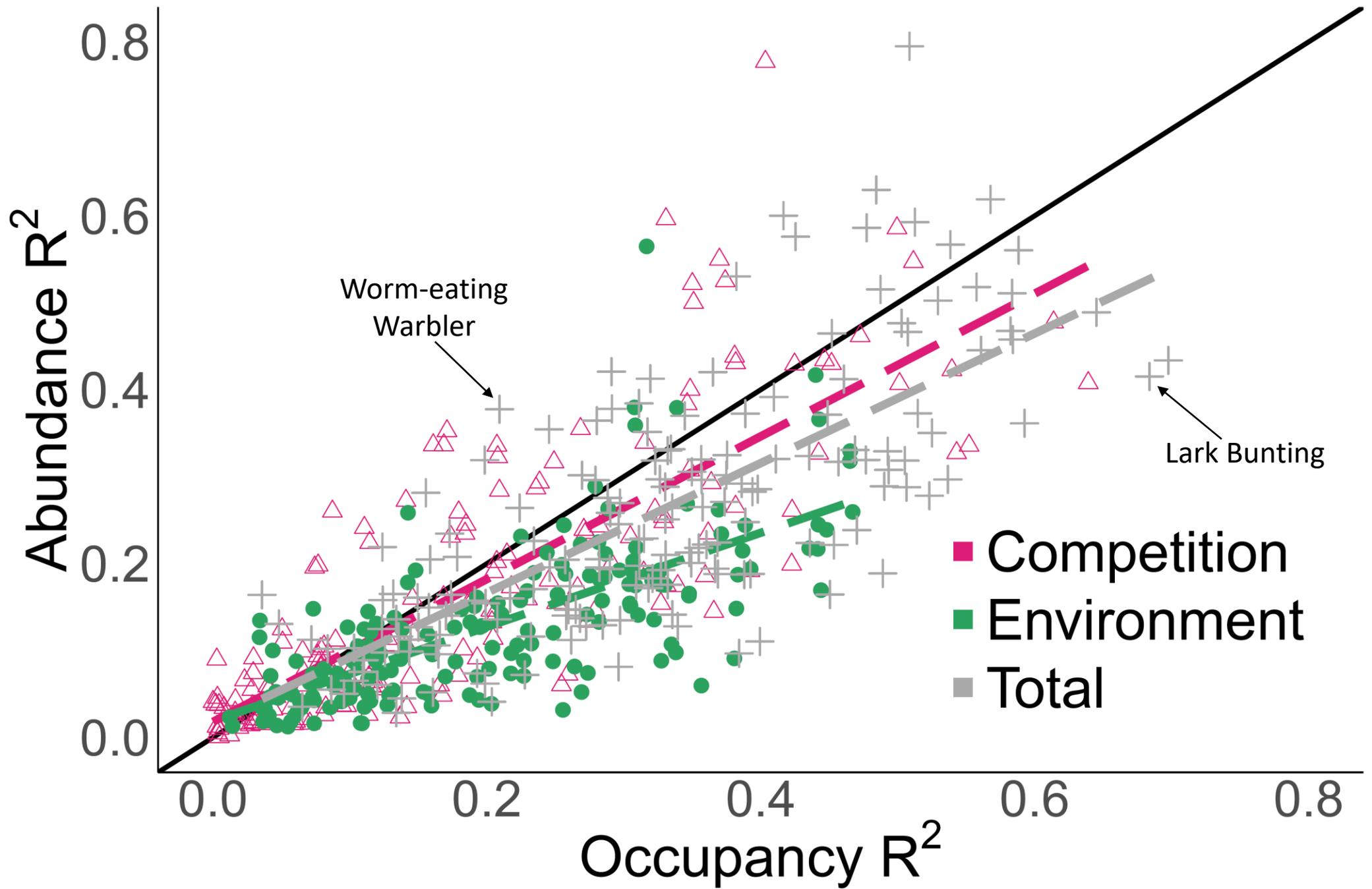
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The relative importance of biotic and abiotic determinants of temporal occupancy for avian species in North America. *Global Ecology and Biogeography*.

Data S1

List and descriptions of supplemental tables references in manuscript.

File list (files found within DataS1.zip)

DataS1.doc	TableS9.txt
TableS1.txt	TableS10.txt
TableS2.txt	TableS11.txt
TableS3.txt	TableS12.txt
TableS4.txt	TableS13.txt
TableS5.txt	TableS14.txt
TableS6.txt	TableS15.txt
TableS7.txt	TableS16.txt
TableS8.txt	TableS17.txt

Description

DataS1.doc – Document describing data included in supplemental tables.

TableS1.txt – Table of all focal species and assigned competitors considered in our analyses. Focal species common name, scientific name, id code (AOU), and family are listed, along with all competitors for each focal species, with the most widespread competitor or most predictive competitor denoted by a 1.

TableS2.txt – Table of all focal species and traits used in our analyses: focal species family, body mass, migratory class, trophic group, range size of focal species, proportion of overlap in range with competitors, mean optimal temperature, mean optimal precipitation, mean optimal elevation, mean optimal NDVI, number of routes a species was observed during the sampling period, and median, variance, minimum, and maximum occupancy during the sampling period.

TableS3.txt – Tabular output of temporal occupancy variance partitioning analysis using all competitors. Each row represents one focal species and the relative contribution of the environmental variables, competitor abundance, shared variance, total variance (environment plus competitor plus shared variance), number of sites (n), and the variance ratio (R_c) included in the analysis.

TableS4.txt – Tabular output of temporal occupancy variance partitioning analysis using the competitor that explained the most variance (most predictive). The linear regressions used to create the table are the same as for all competitors, however in this table the scaled competitor abundance only contains the most predictive competitor. Each row represents one focal species and the relative contribution of the environmental variables, competitor abundance, shared variance, total variance (environment plus competitor plus shared variance), number of sites (n), the variance ratio (R_c), and the most predictive competitor included in the analysis.

TableS5.txt – Tabular output of temporal occupancy variance partitioning analysis using the most widespread competitor. The linear regressions used to create the table are the same as for all competitors, however in this table the scaled competitor abundance only contains the competitor with the greatest amount of geographic overlap. Each row represents one focal species and the relative contribution of the environmental variables, competitor abundance, shared variance, total variance (environment plus competitor plus shared variance), number of sites (n), the variance ratio (R_c), and the most widespread competitor included in the analysis.

TableS6.txt – Tabular output of temporal occupancy variance partitioning analysis for all competitors. Each row contains the estimate, R^2 , and p-value for occupancy for each focal species.

TableS7.txt – Tabular output of temporal occupancy variance partitioning analysis for the most predictive competitor. Each row contains the estimate, R^2 , and p-value for occupancy for each focal species. Note that seven species did not have greater than two occurrences of having expected presence with the most predictive competitor, so their results are NA since we could not perform a linear regression on them. These species are included in other parts of the analysis.

TableS8.txt – Tabular output of temporal occupancy variance partitioning analysis for the most widespread competitor. Each row contains the estimate, R^2 , and p-value for occupancy for each focal species. Note that eight species did not have greater than two occurrences of having expected presence with the most widespread competitor, so their results are NA since we could not perform a linear regression on them. These species are included in other parts of the analysis.

TableS9.txt – Tabular output of Bayesian hierarchical model output of random slopes and intercepts grouped by family using all competitors. Each row represents a focal species intercept, environmental factor, and/or scaled competitor output.

TableS10.txt – Tabular output of Bayesian hierarchical model output of random slopes and intercepts grouped by family using the most widespread competitor. Each row represents a focal species intercept, environmental factor, and/or scaled competitor output.

TableS11.txt – Tabular output of abundance variance partitioning analysis using all competitors. Each row represents one focal species and the relative contribution of the environmental variables, competitor abundance, shared variance, total variance (environment plus competitor plus shared variance), number of sites (n), and the variance ratio (R_c) included in the analysis.

TableS12.txt – Tabular output of abundance variance partitioning analysis using most predictive competitor. The linear regressions used to create the table are the same as for all competitors, however in this table the scaled competitor abundance only contains the most predictive competitor. Each row represents one focal species and the relative contribution of the environmental variables, competitor abundance, shared variance, total variance (environment plus competitor plus shared variance), number of sites (n), and the variance ratio (R_c) included in the analysis.

TableS13.txt – Tabular output of abundance variance partitioning analysis using the most widespread competitor. Each row represents one focal species and the relative contribution of the environmental variables, competitor abundance, shared variance, total variance (environment plus competitor plus shared variance), number of sites (n), the variance ratio (R_c), and the most widespread competitor included in the analysis.

TableS14.txt – Tabular output of abundance variance partitioning analysis for all competitors. Each row contains the estimate, R^2 , and p-value for abundance for each focal species.

TableS15.txt – Tabular output of abundance variance partitioning analysis for the most predictive competitor. Each row contains the estimate, R^2 , and p-value for abundance for each focal species.

TableS16.txt – Tabular output of abundance variance partitioning analysis for the most widespread competitor. Each row contains the estimate, R^2 , and p-value for abundance for each focal species.

TableS17.txt – Tabular output of traits model (main manuscript Table 2) using an arcsine transformation instead of logit transformation.

Supplemental Figure Captions

Figure S1. (a) Hypothesized relationship between temporal occupancy and NDVI for a species, in which occupancy peaks at the average (centroid) NDVI within the species' range (solid line, filled symbols). If detectability decreases with NDVI, then observed occupancy (dotted line, open symbols) will exhibit increasingly negative deviations from the true occupancy line as NDVI increases. (b) Temporal occupancy is expected to decrease monotonically with the absolute value of deviations from the NDVI centroid. If detectability is lower at high NDVI sites above the centroid, then a regression through only those points should be steeper (dashed red line) than a regression through the points below the centroid (solid red line). A regression across all points will have a lower R^2 when detectability varies with NDVI (dashed black line, open symbols) compared to when detectability does not vary across the gradient (solid red line, filled symbols).

Figure S2. Comparison of estimates of below and above the Centroid NDVI. Each point represents a species, the dashed lines represent each axis' median, and the blue line is a 1:1 line.

Figure S3. Violin plots demonstrating the distribution of unique variance in focal temporal occupancy explained by environmental variables, the unique variance explained by the abundance of the maximum R^2 competitor, the total variance explained by a model with both sets of variables, and the variance ratio, R_c .

Figure S4. The ability of environmental variables (green circles), most widespread competitor abundance (pink triangles), or both combined (grey crosses) to predict spatial variation in temporal occupancy (x-axis) compared to spatial variation in abundance (y-axis) based on linear model R^2 s (and not unique variance components, as portrayed in Figures 1-3). Black line represents the 1:1 line. Dashed lines indicate linear regressions through each of the three sets of predictor variables.

Figure S5. The ability of environmental variables (green circles), most predictive competitor abundance (pink triangles), or both combined (grey crosses) to predict spatial variation in temporal occupancy (x-axis) compared to spatial variation in abundance (y-axis) based on linear model R^2 s (and not unique variance components, as portrayed in Figures 1-3). Black line represents the 1:1 line. Dashed lines indicate linear regressions through each of the three sets of predictor variables.