

ARTICLE

Substituting space for time: Bird responses to forest loss in space provide a general picture of responses over time

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Abstract

The practice of space-for-time substitution assumes that the responses of species or communities to land-use change over space represents how they will respond to that same change over time. Space-for-time substitution is commonly used in both ecology and conservation, but whether the assumption produces reliable insights remains inconclusive. Here, we tested space-for-time substitution using data from the North American Breeding Bird Survey (BBS) and Global Forest Change (GFC) to compare the effects of landscape-scale forest cover on bird richness and abundance over time and space, for 25 space–time comparisons. Each comparison consisted of a landscape that experienced at least 20% forest loss over 19 years (temporal site) and a set of 15–19 landscapes (spatial sites) that represented the same forest cover gradient over space in 2019 as experienced over time in their corresponding temporal site. Across the 25 comparisons, the observed responses of forest and open-habitat birds to forest cover over time generally aligned with their responses to forest cover over space, but with comparatively higher variability in the magnitude and direction of effect across the 25 temporal slopes than across the 25 spatial slopes. On average, the mean differences between the spatial and temporal slopes across the 25 space–time comparisons frequently overlapped with zero, suggesting that the spatial slopes are generally informative of the temporal slopes. However, we observed high variability around these mean differences, indicating that a single spatial slope is not strongly predictive of its corresponding temporal slope. We suggest that our results may be explained by annual variability in other relevant environmental factors that combine to produce complex effects on population abundances over time that are not easily captured by snapshots in space. While not being a 1:1 proxy, measuring bird responses to changes in habitat amount in space provides an idea on how birds might be expected to eventually equilibrate to similar changes in habitat amount over time. Further, analyses such as this could be potentially used to screen for cases of regional space–time mismatches where population-limiting factors other than habitat could be playing a more important role in the population trends observed there.

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KEYWORDS

Breeding Bird Survey, habitat amount, habitat loss, habitat use, population change, population prediction, population trend, species abundance, species richness

INTRODUCTION

The use of long time series to study the causes of wildlife population change is frequently encouraged as a “gold standard” (Kratz et al., 2003) but is often not possible because time series data are lacking for most taxa (McGarigal & Cushman, 2002; Strayer et al., 1988). This is because time series data are effort- and time-intensive to collect and costly, especially at the broad spatial scales most relevant for assessing population change (McGarigal & Cushman, 2002). As a result, ecologists frequently use a so-called space-for-time substitution approach by studying wildlife responses along altitude, precipitation, temperature, and/or land-cover gradients in space to predict how they would respond along similar gradients over time (De Palma et al., 2018; Lemoine et al., 2007; Pickett, 1989; Rustad, 2008).

Historically, space-for-time substitution has been used in chronosequence studies of vegetation succession and soil development (Cowles, 1899; Pickett, 1989) and is still commonly used in those contexts (Miao et al., 2018). In recent decades, space-for-time substitution has been used to provide improved guidance for conservation decisions and land management by predicting species responses to gradients of climate and different types of land cover (De Palma et al., 2018; Endenburg et al., 2019). For example, Frey-Ehrenbold et al. (2013) suggest that measures to increase future landscape connectivity could promote bat diversity, based on their comparisons across landscapes in Switzerland. Fahrig (2015) and Martin et al. (2020) suggest that new policies aimed at reducing crop field sizes would increase biodiversity, based on comparisons across agricultural landscapes containing different crop field sizes in Canada. Such recommendations assume that patterns of landscape composition and/or configuration across space provide valid information for predicting what would happen over time under a given policy.

Space-for-time substitution remains a popular strategy despite a persistent lack of evidence that it produces accurate predictions. The inherent assumption that landscapes studied across space represent different stages of a population undergoing a land-cover change over time may be problematic (Johnson & Miyanishi, 2008; Pickett, 1989). Indeed, due to inconsistencies between population-landscape relationships predicted from spatial patterns and those observed in time, some studies have advised caution when using space-for-time substitutions in landscape

ecology, for example, studies on bird population dynamics in response to land cover (Bonthoux et al., 2013; La Sorte et al., 2009); butterfly abundance in response to climate change (Isaac et al., 2011); tropical insect species richness, species composition, and biomass in response to Amazonian logging (França et al., 2016); and plant community composition in response to changes in various environmental factors such as soil conditions and climate (De Lombaerde et al., 2018). On the other hand, some studies have found moderate support for space-for-time substitutions. For example, space-for-time substitution was found to work well for predicting bluefin killifish density in response to seasonal changes in the Florida Everglades (Banet & Trexler, 2013). Guittar et al. (2016) found that plant functional traits that are associated with temperature gradients in space were predictive of grassland community responses to warming climate over time. Following the shrub restoration of a sand dune, Miao et al. (2018) showed that space-for-time substitution accurately predicted species diversity and evenness of the recovering system over time, though it did not reliably predict density, coverage, or biomass. Finally, Blois et al. (2013) found that space-for-time predictions of eastern North American plant compositional turnover in response to climate change during the Late Quaternary were 72% as accurate as predictions based on observed temporal turnover.

Birds are an important and feasible group for testing the space-for-time substitution. Space-for-time substitution is commonly used when evaluating the effects of habitat and landscape change on bird richness and abundance (e.g., Cushman & McGarigal, 2003; Quinn et al., 2012; Rodewald & Yahner, 2012), and therefore, it is important to determine whether the inferences made from these studies are likely to be valid. Birds are also a feasible group for this test because we have extensive publicly available temporal and spatial bird data, thanks to volunteer-based citizen science databases in North America and Europe (Harris et al., 2020; National Audubon Society, 2020; Sullivan et al., 2014). The North American Breeding Bird Survey (BBS) is an exceptional example in both its spatial and temporal coverage. Conducted since the 1970s, it is one of the longest-running continent-scale programs and is frequently used both for population trend estimation (Environment and Climate Change Canada [ECCC], 2021; Sauer et al., 2017) and testing a variety of ecological hypotheses (e.g., Rushing et al., 2016; Tittler et al., 2006; Vance et al., 2003).

Spatial analyses have demonstrated that conversion of forest to farmland is a threat to forest birds and a benefit to open-habitat birds (Endenburg et al., 2019; Wilson et al., 2017). Landscape-scale forest cover is a strong, positive predictor of forest bird abundance and richness in space (Bélisle et al., 2001; Trzcinski et al., 1999). This association suggests that a similar change in forest cover over time would cause similar changes in forest bird abundance and richness over time. We also expect that such a change in forest cover would cause the opposite change in open-habitat birds, which use landscapes dominated by crops, grasses, and pastures (Wright et al., 2011).

Our objective was to test the space-for-time substitution using the responses of North American forest-breeding and open-habitat-breeding birds to forest-cover change over time and space. If responses over time can be predicted from responses over space, then bird

richness and abundance should respond to changes in forest cover similarly over time and space. Specifically, if it is valid to infer bird responses to land-cover change over time from those effects in space, as is the current practice, then the slopes of the bird–forest cover relationships over time and space should be equal or nearly equal.

METHODS

Overview

We compared temporal and spatial responses of birds to forest cover for 25 separate comparisons between a single landscape over time and a set of many landscapes in a single year (Figure 1). Each comparison contained one “temporal” site and multiple nearby (within 300 km)

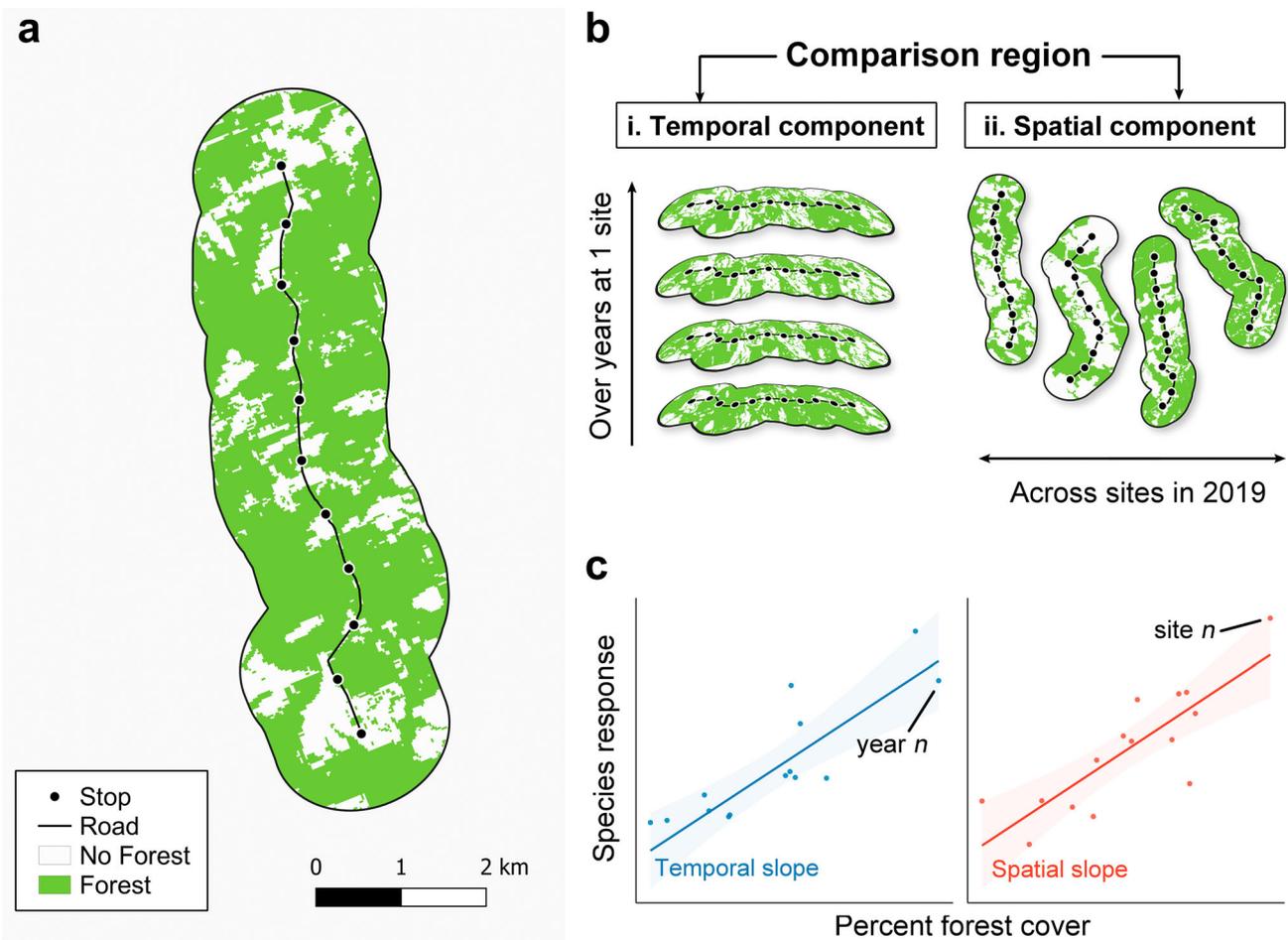


FIGURE 1 Visual description of space–time comparison study design where (a) a site consisted of the first 11 “stops” of a North American Breeding Bird Survey (BBS) route, along with the landscape within 1 km, within which forest cover was measured. (b) Sites were organized into “space–time comparisons” consisting of a single “temporal site,” with bird and forest information from 2000 to 2019, and multiple “spatial sites” covering the same forest gradient over space in 2019 as the forest gradient over time at the associated temporal site. (c) The relationship between bird species responses and percent forest cover was estimated as a slope over time at the temporal site and over space across corresponding spatial sites.

“spatial” sites. We asked whether a relationship across spatial sites between bird richness and abundance and forest cover in 2019 accurately predicted the actual change over time in bird richness and abundance over the same gradient in forest cover during the previous 19 years. In this way, our study mimicked 25 hypothetical field studies, each of which would have measured effects on bird richness and abundance of forest cover across space and used the resulting relationship to infer changes in bird responses to an equivalent change in forest cover over time.

Bird surveys

The BBS is a long-running bird-monitoring program (1966–present) consisting of over 4000 roadside survey routes containing regular stops where birds are counted annually by volunteers (ECCC, 2021; Pardieck et al., 2015; Sauer et al., 2017). These standardized surveys are conducted in Canada, the United States, and northern Mexico during peak breeding season between late May and early July (Sauer et al., 2018). Each 39.5-km-long route contains 50 stops spaced ~800 m apart along the road. At each stop, volunteers spend 3 min counting all individuals, identified to species, that are heard or seen within 400 m of the stop (Sauer et al., 2018). For our analysis, we extracted bird occurrence data from routes in Canada and the continental United States because the survey has not been running long enough in Mexico to analyze the long-term effects of changing forest cover (ECCC, 2021).

We obtained an up-to-date Canadian BBS route geodatabase with stop-level location information from the ECCC BBS administration team. A similar geodatabase was not available from the USGS and was instead obtained from a publicly available online source (Patuxent Wildlife Research Center, 1999). This US data set contained geospatial data for whole routes but lacked individual stop locations. We estimated stop locations for the US routes by placing points 800 m apart along the length of the routes using R version 4.0.3 (R Core Team, 2020) and ArcMap version 10.8. We removed any routes where the estimated stop locations would be highly uncertain due to irregularly branching roads, incomplete roads, or digitized routes that did not agree with the route’s known start point coordinates.

Site characteristics

Our sites consisted of the area within 1 km of the road segment defined by the first 11 stops of each BBS route, creating oblong landscapes ~8 km long and 18 km² in

area (Figure 1a). We chose a 1-km width because the BBS includes observations out to 400 m from each survey point and therefore a 1-km buffer on either side of the road would likely cover the territories, and thus the main land covers, that the species detected are using. We used only the first 11 stops of the BBS routes (similar to Endenburg et al., 2019) to establish the boundary of our sites so that we could limit their length and irregularity. This also increased the likelihood of finding candidate sites that experienced forest cover change across their landscape that would be substantial enough to produce measurable effects in birds over the 2000–2019 period.

Forest cover

We obtained forest-cover information for 2000 to 2019 from the University of Maryland’s Global Forest Change (GFC) data set (version 1.7; Hansen et al., 2013). This data set consisted of three 30-m-resolution raster layers summarizing global tree-cover extent in 2000, annual tree-cover loss from 2001 to 2019, and tree-cover gain in 2012 compared to 2000. Like Rushing et al. (2016), we used a 50% canopy-closure threshold to distinguish forest from nonforest habitat (see Supplementary Materials of Rushing et al., 2016). The transition from savannas to woodlands has been defined by, or around, a threshold of 40%–50% canopy closure (Hanberry & Thompson, 2019). Using the R package *gfcanalysis* (version 1.6.0; Cooper & Zvoleff, 2020) and raster (Hijmans et al., 2021), we processed all three raster layers such that pixels containing tree stands with $\geq 50\%$ canopy closure in 2000 were considered forest and pixels with $< 50\%$ canopy closure were considered open-habitat matrix.

For each site, we calculated forest cover from 2001 to 2019 in oblong landscapes surrounding the first 11 stops of each BBS route (see above). To do this, we extracted the number of forested pixels that were lost in each year and iteratively subtracted them from the number of forested pixels in the year before, starting with the layer of forest cover in 2000. In 2012, we added the number of pixels gained within the 2000–2012 period before subtracting lost pixels for that year. We then calculated our final land-cover metric, percent forest cover, as the proportion of forested pixels in the landscape of each site in each year.

Site selection

To create multiple space–time comparisons, we carried out site selection in two distinct steps. First, we found sites that (1) had experienced more than 20% net forest-cover change between 2000 and 2019 (as either loss

or gain) and (2) contained at least 15 years of bird occurrence data over the same time. These were potential temporal sites. We needed one temporal site for each evaluation of the space-for-time substitution. The 20% net change threshold was chosen as a trade-off between ensuring the forest-cover gradients were large enough to detect changes in bird species richness and abundance that could be associated with that change in forest and maximizing the number of space–time comparisons we could make. In preliminary analyses, higher thresholds for net change in percent forest cover resulted in sparse candidate site pools, which would have limited our statistical power.

Second, for each temporal site, we selected a set of spatial sites with forest and bird data available in 2019. The spatial sites associated with a given temporal site had to cover a similar range ($\pm 5\%$) in percent forest cover over space as the range in percent forest cover over time at that corresponding temporal site.

A margin of $\pm 5\%$ was used to ease data limitations experienced during preliminary site selection trials. In addition, the spatial sites had to fall within the same North American Level I Ecoregion (U.S. Environmental Protection Agency, 2020) as the matching temporal site and had to be within 300 km of the matching temporal site. These criteria were assumed to result in similar species pools among the spatial sites and the temporal site for a given space–time comparison. We chose 300 km to increase the number of space–time comparisons that could be made and to ensure at least 15 spatial sites could be found for each comparison’s spatial relationship. To evaluate the impact of this decision on the results, we repeated the analyses using a 200-km buffer to define the boundary for each space–time comparison (Appendix S1). Notably, this re-analysis (1) reduced our sample size of space-for-time comparisons by almost half and (2) did not result in any changes to our conclusions.

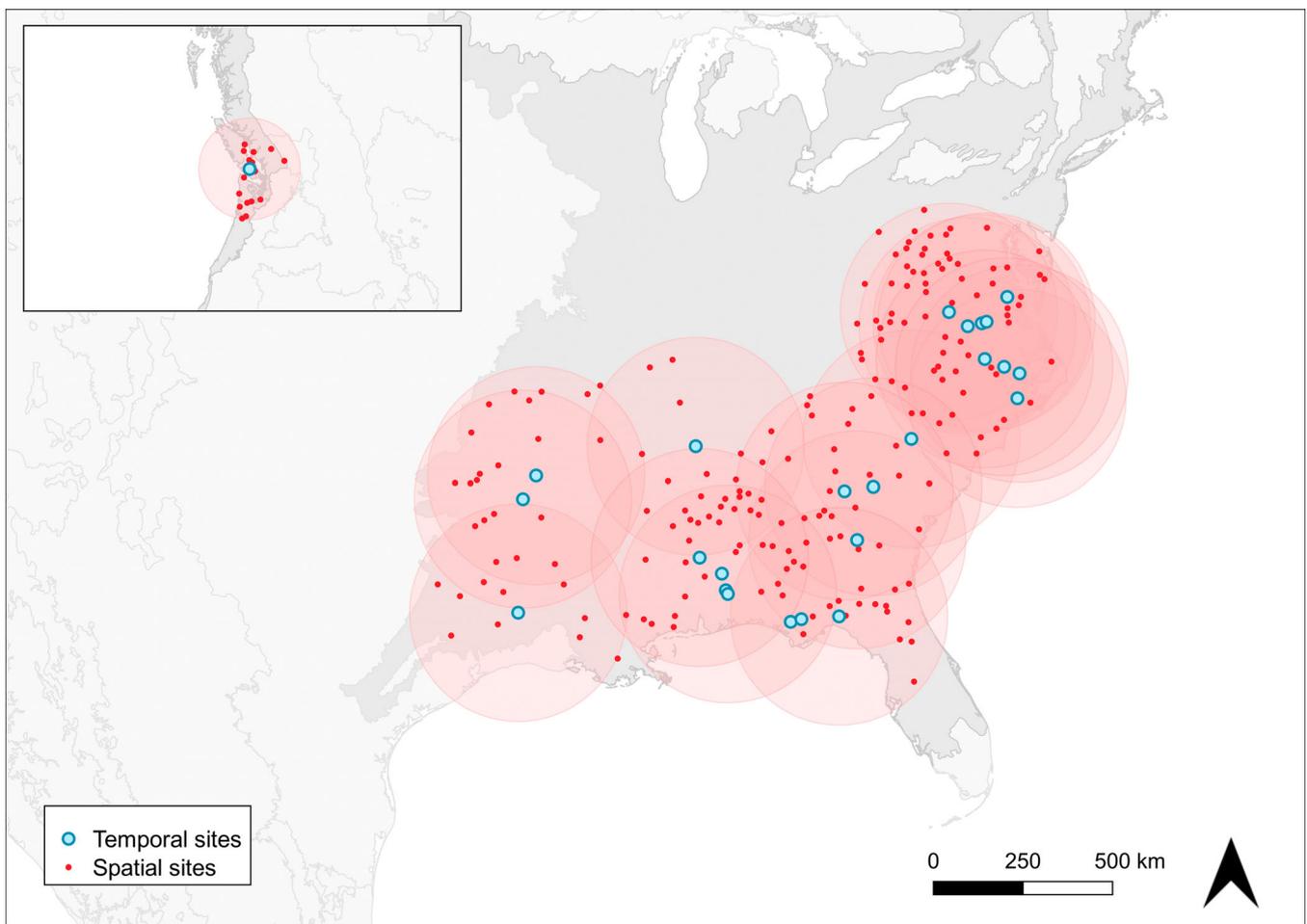


FIGURE 2 Locations of 25 space–time comparisons within continental United States (US) and Canada, each consisting of a single temporal site (gradient of forest cover over time) and a series of matched spatial sites (gradient of forest cover across space) located within 300 km of temporal site. Comparison regions fell in two Level I Ecoregions: the Marine West Coastal Forest (leftmost dark gray area in inset map) and the Eastern Temperate Forests (rightmost dark gray area in main map area).

The final set of space–time comparisons fell within two Level I Ecoregions: 24 in the Eastern Temperate Forests of the eastern and southeastern United States and one in the Marine West Coastal Forests on Vancouver Island, Canada (Figure 2). The proximity between most eligible temporal sites meant that the spatial sites selected for each space–time comparison sometimes overlapped between space–time comparisons (on average 1.5 shared sites between spatial site sets, ranging from 0 to 12). We selected a subset of spatial sites to match the number of years of bird data in the corresponding temporal site for each comparison. This ultimately resulted in 15–20 sites or years in space and time, respectively, for each space–time comparison. The selection prioritized creating a spatial site subset where the gradient of percent forest cover values most closely matched the forest cover values across years at the temporal site.

Data analysis

For our bird response variables, we calculated total species richness and total abundance separately for two bird guilds: species that breed in forests and species that breed in open grasslands (so-called “forest” and “open-habitat” birds, respectively; North America Bird Conservation Initiative, 2016; Rodewald, 2018). Species richness at a site was the total number of forest (or open-habitat) species present across all 11 stops in the site. Similarly, bird abundance at a site was the total number of forest (or open-habitat) individuals recorded at all 11 stops in the site. In all models, forest cover was the percent forest cover in the landscape, that is, the proportion of forested pixels in the 1-km-radius buffer out from the road segment for the first 11 stops at a site (see *Forest cover* above).

For each of the 25 space–time comparisons, we estimated linear slopes relating bird responses to forest cover (1) at the temporal site over time (“temporal slopes”) and (2) across the spatial sites (“spatial slopes”) using Bayesian general linear models. There were four temporal slopes estimated per temporal site, one for each of species richness and abundance for each of forest and open-habitat species. The same four spatial slopes were estimated across the set of spatial sites associated with each temporal site. For each of the four “scenarios” (the four combinations of species richness or abundance and forest species or open-habitat species), both the temporal and spatial slopes for all 25 comparisons were fit using a single multiple-regression model.

Models were compiled and run with Stan’s Hamiltonian Monte Carlo samplers using the R wrapper packages cmdstanR and rstan (Stan Development Team, 2020) using weakly informative priors (i.e., \sim Normal [0, 1] and \sim Student_t[4, 0, 1]). The models consisted of an intercept and slope parameter that varied by slope type (spatial or temporal) and by space–time comparison ($n = 25$). Importantly, the models did not share or pool information across space–time comparisons for any parameter estimates. Intercepts and slopes were independently estimated within their grouping levels (space or time for each individual space–time comparison) and were not shrunk toward any grouping-level mean. Because the BBS is conducted by many observers, we also included an individual observer effect (Sauer et al., 1994) and a first-year-of-observation effect (Kendall et al., 1996) in the models.

The site-level total species richness or total abundance in a given site-year, i , was modeled using a Poisson distribution and a log-link, where the intercept (α) was grouped by space–time comparison, c (from 1 to 25), and slope type, d (1 = temporal or 2 = spatial). An observation is the site-level total species richness or total abundance in a given year. The effects of percent forest cover in the site-level landscape (i.e., within 1-km buffer surrounding the 11 stops; F) for space and time were measured by two separate slope coefficients, β_{space} and β_{time} , which were controlled by two dummy variables, D_{space} and D_{time} :

$$\lambda_i = \begin{cases} \log\left(\alpha_{c,d} + \left(\beta_{\text{space}} \times 0 \times F_i\right) + \left(\beta_{\text{time}} \times 1 \times F_i\right) + \omega_j + \nu_k + \sigma\right) & \text{if } D_{\text{time}} = 1 \text{ and } D_{\text{space}} = 0, \\ \log\left(\alpha_{c,d} + \left(\beta_{\text{space}} \times 1 \times F_i\right) + \left(\beta_{\text{time}} \times 0 \times F_i\right) + \omega_j + \nu_k + \sigma\right) & \text{if } D_{\text{time}} = 0 \text{ and } D_{\text{space}} = 1 \end{cases} \quad (1)$$

where ω_j measures the relative effect of each observer, j (from 1 to 225 observers), on bird richness or abundance; ν_k measures the relative effect of observations being an observer’s first survey in the BBS or not, k ; and σ is a noise term for extra Poisson variance. The species richness or total abundance, rounded to the nearest whole number, was modeled assuming

$$y \sim \text{Poisson}(\lambda) \quad (2)$$

We assessed posterior model convergence using traceplots, the Gelman-Reuben statistic (R-hat; Gelman & Rubin, 1992), the number of effective samples (N_{eff}), and posterior predictive checks. In addition, we performed a model validation step using a fake data simulation to test

whether our model would be capable of detecting equal and unequal effects of forest cover on birds in space and time.

Lastly, for each of the four scenarios, we evaluated the space-for-time substitution by calculating the comparison-level difference between temporal slopes and spatial slopes ($\Delta\beta_c = \beta_{\text{time}_c} - \beta_{\text{space}_c}$) across all iterations and the mean difference between the mean temporal slope and the mean spatial slope, each averaged across all 25 space–time comparisons ($\Delta\bar{\beta} = \frac{\sum\beta_{\text{time}}}{25} - \frac{\sum\beta_{\text{space}}}{25}$).

RESULTS

Overall, the 25 space–time comparisons included 118 forest species and 55 open-habitat species. Species richness and bird abundances summed across the data set of all 25 sets of sites in space and 25 sites in time were very similar (Table 1). All 25 temporal sites in our analysis experienced net forest loss over the 19 years, from a minimum of 20% loss to a maximum of 49% loss. The 25 sets of spatial sites each captured a similar range of forest loss across space as their corresponding temporal site experienced over time. The mean number of shared spatial sites between any two space–time comparisons was 1.5 and ranged from 0 to 12 shared sites (Appendix S2: Figure S7). Our model was capable of determining whether space and time coefficients were equal or unequal to each other (Appendix S2).

The observed bird responses to forest cover over time generally aligned with the observed bird responses to forest cover over space (Figures 3 and 4; Appendix S3), but with high uncertainty (Figure 5). In forest birds, on average, the difference between spatial slope coefficients and

temporal slope coefficients overlapped with zero (mean of temporal–spatial slopes = $\Delta\bar{\beta} = -0.100$ [95% CI $-0.398, 0.192$] and 0.224 [95% CI $-0.516, 0.071$] for forest species richness and abundance, respectively; Figures 3 and 5). In space, forest bird richness and abundance were consistently predicted to decrease with forest loss in space across all comparisons, with the exception of one, at similar magnitudes. Conversely, in time, forest bird richness and abundance declined with loss of forest in six and seven comparisons, respectively (Figure 3). Further, the uncertainty surrounding these effects in time for each of the 25 comparisons was often higher than the uncertainty around the corresponding effects predicted in space (Figure 4).

For the most part, open-habitat species richness and abundance in space and time were weakly positively associated with forest loss in the landscape, although there were some negative slopes. For open-habitat species there was little difference across comparisons between the mean spatial and temporal slope coefficients (mean of temporal–spatial slopes = $\Delta\bar{\beta} = 0.299$ [95% CI $-0.052, 0.651$] and 0.081 [95% CI $-0.283, 0.446$] for richness and abundance, respectively; Figures 3 and 5). Notably, open-habitat bird richness was predicted to decrease with forest loss (contrary to our expectations) at about 30% of the temporal sites compared to only 10% of spatial site sets. Open-habitat bird abundances were predicted to decrease with forest loss just as often in time as in space.

Importantly, for all four scenarios, the variability in slope coefficients across the temporal comparisons was higher than the variability in slopes across the spatial comparisons, as shown by the spread of points in Figure 3 and of the regression lines in Figure 4 between space and time. This higher variability in time compared to space was observed in both the direction and the magnitude of the effect (Figure 4). Further, the high

TABLE 1 Bird metrics summarized across 25 sets of spatial sites in 2019 (at least 15 sites per set) and across 25 temporal sites observed over time (at least 15 years per site).

Response metric	Bird guild	Minimum	Maximum	Median
Spatial sites				
Species richness	Forest	3	28	16
	Open habitat	0	14	5
Total abundance	Forest	5	164	55
	Open habitat	0	211	14
Temporal sites				
Species richness	Forest	7	36	17
	Open habitat	0	13	4
Total abundance	Forest	16	164	54
	Open habitat	0	112	14

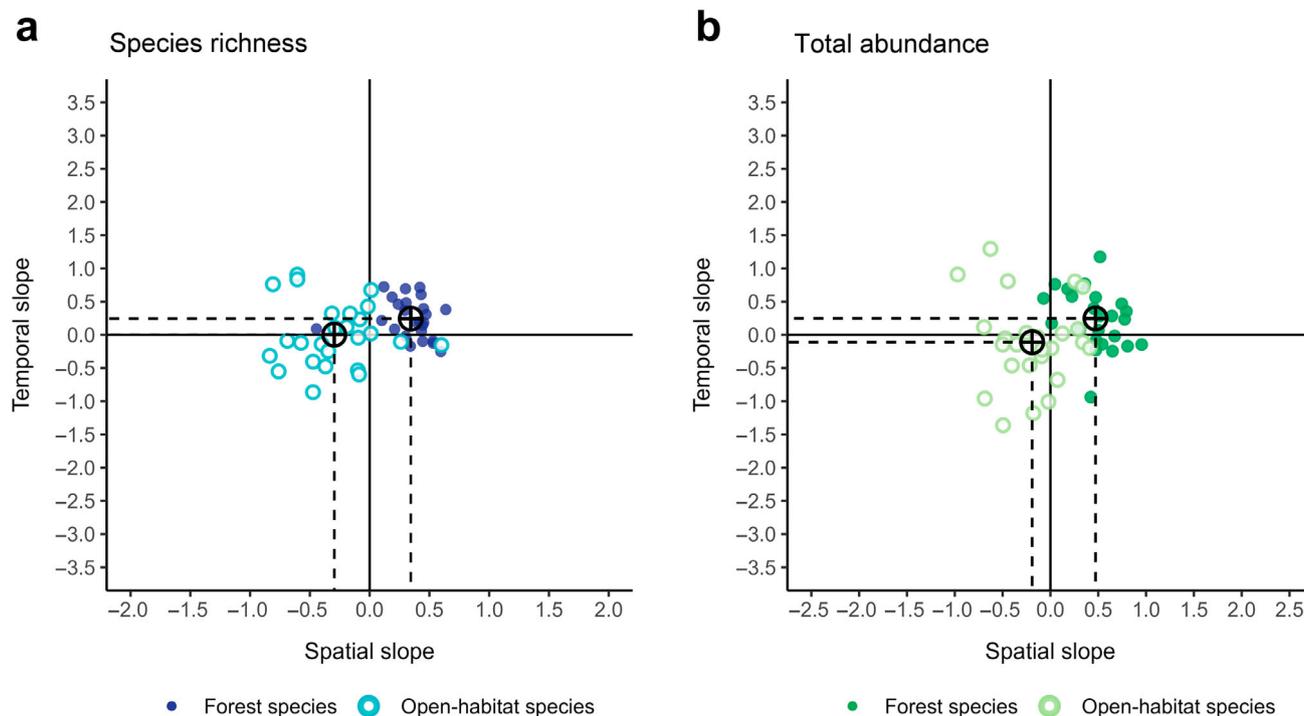


FIGURE 3 Temporal versus spatial slope values between forest and birds for each of the 25 space–time comparisons (small dots) in each of the four scenarios: species richness (blue) or abundance (green), each for forest birds (a) or open-habitat birds (b). The large crosshair associated with each scenario indicates the mean slope coefficients across the 25 comparisons, and the clouds of points indicate the variability around those means.

variability around the mean differences between the spatial and temporal slopes (Figure 5) indicates that while, on average, the spatial slopes are informative of the temporal slopes, a single spatial slope is not strongly predictive of its corresponding temporal slope.

DISCUSSION

Our study provides general support for space-for-time substitution in predicting the effects of forest loss on bird richness and abundance in North America. However, while the mean bird–forest slopes across time were similar to the mean bird–forest slopes across space, there was high variability both between temporal slopes of different comparisons and in the difference between the spatial and temporal slopes across comparisons. This high variability in both cases indicates that the response of bird richness or abundance to forest cover loss over time is likely to differ from the same response over space within individual comparisons, even though space-for-time substitution does hold for these relationships with forest cover on average.

The high uncertainty in the space-for-time predictions we observed could be related to inherent variability in the relationship between forest habitat and birds through time.

This variability would reduce the correspondence between the spatial slope and the temporal slope for a given comparison and is supported by our observation of higher variability of bird–forest slopes in time than in space. One mechanism underlying this possibility is that many of the birds in our data set are migratory, so that their populations are limited by a host of factors operating simultaneously and heterogeneously across their annual distributional range, with evidence pointing toward migration (Hewson et al., 2016; Klaassen et al., 2014; Lok et al., 2014; Sillett & Holmes, 2002) and nonbreeding ground threats (Dokter et al., 2018; La Sorte et al., 2017; Taylor & Stutchbury, 2016; Wilson, Saracco, et al., 2018) being the most relevant for many species. These other limiting factors may weaken the predictions of richness and abundance from habitat loss over time on the breeding grounds alone and contribute to the greater temporal compared to spatial variability in relationships with forest cover observed in our study. Interestingly, cases where temporal predictions of relationships with breeding ground habitat do not match spatial predictions in the same region could provide insight into other factors underlying change in richness or abundance, such as those discussed earlier (e.g., carryover effects from changes in nonbreeding ground habitat [Taylor & Stutchbury, 2016] and/or stopover habitat [Mehlman et al., 2005]), as well as factors relating to rapid

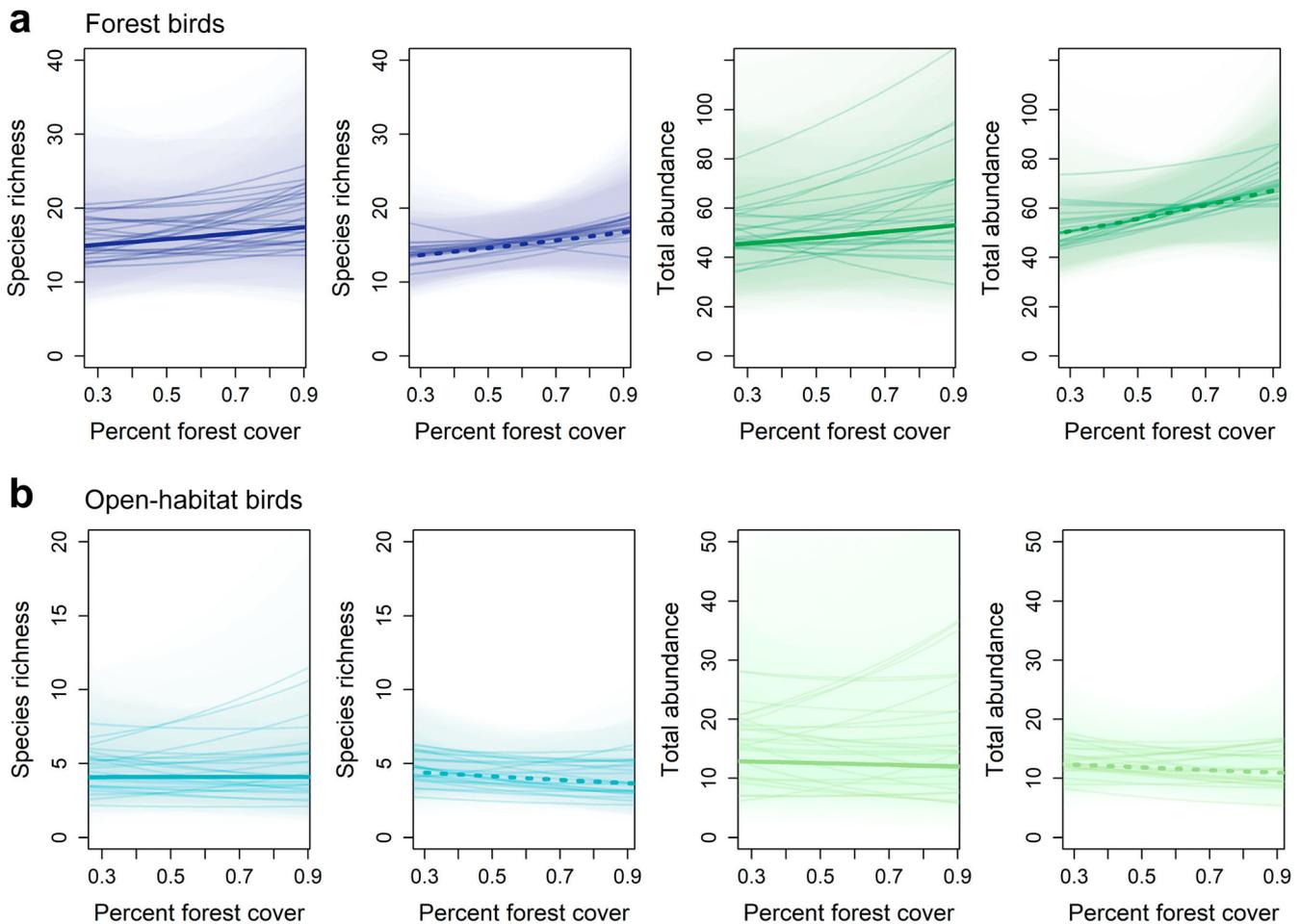


FIGURE 4 Bird–forest cover associations over time and space for forest birds (a) and open-habitat birds (b). Shaded areas show 95% CIs around regression lines (thin lines) for each temporal site (left-hand plot of each pair) and for each set of matched spatial sites (right-hand plot of each pair). Thick regression lines reflect the average slope across all 25 comparisons in time (thick solid line) and space (thick dashed line).

changes in climate (e.g., phenological mismatches in spring migration with optimal food supply [Both et al., 2006] and reproductive timing [Møller et al., 2008]; weather events [Drake et al., 2014; Wilson, Smith, et al., 2018; Hill et al., 2019]). These cases could help direct research and conservation efforts on the mechanisms limiting populations.

A second possible mechanism is that unmeasured lag effects might further decouple the relationship in time between birds and forest cover. Observed annual bird richness and abundance may be more strongly related to past forest cover at a site than to the forest cover present in that year. For instance, a site’s past landscape has been shown to be a powerful predictor of present-day species assemblages in birds and other taxa (Ernault et al., 2006), in some cases with a time lag of up to 25 years (Brooks et al., 1999; Wiens & Rotenberry, 1985). In our study, lag effects may be particularly relevant to effects of forest cover measured over time. At the temporal sites, bird assemblages are likely in the process of detecting and

appropriately responding to the large forest change that occurred rapidly over 20 years. This may not be true for each of the sites used to construct the spatial component of each comparison, which did not experience any notable net forest cover change (ranging only from -0.60% to 0.05%) over the same 20 years. Thus, at the spatial sites in 2019, lag effects are more likely to have already played out because birds had more time to appropriately adjust to any significant changes in landscape composition. If so, then measured species richness and abundance across space may be a better reflection of the birds that can occur in those landscapes over the long term. Under this speculation, space-for-time substitution may in fact be working effectively by isolating the “true” long-term effect of forest cover change on bird assemblages from the other ecological temporal processes that interact in complex ways, each with their own lag times.

A third possible explanation for the high variability in the correspondence in bird–forest relationships between

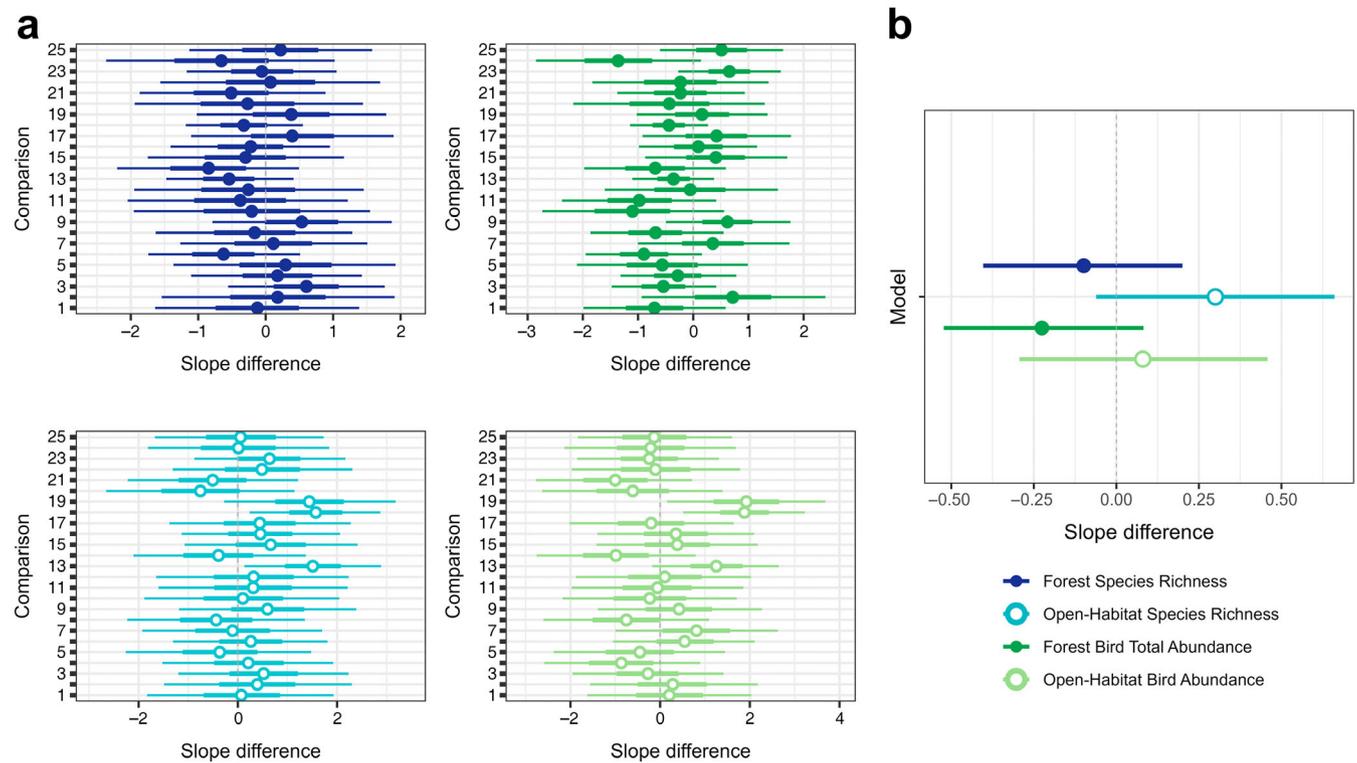


FIGURE 5 (a) Computed differences ($\Delta\beta_c$) between temporal and spatial slopes ($\beta_{c,time} - \beta_{c,space}$), each measuring the relationship between forest- or open-habitat bird responses and percent forest cover in a landscape over time (2000–2019) or over landscapes in space (2019). Error bars show 95% CIs around average values. (b) Mean differences between mean of 25 temporal slopes and mean of 25 spatial slopes (calculated as $\Delta\bar{\beta} = \bar{\beta}_{time} - \bar{\beta}_{space}$) measuring the relationship between forest- or open-habitat bird responses and percent forest cover in a landscape over time or across many landscapes in space.

space and time is that the nonforest variables influencing bird richness and abundance in space are different from those influencing bird richness and abundance in time. In particular, the different landscapes that go into calculating a spatial slope will vary in terms of the other land-cover types (i.e., the matrix) present in them, which will affect the strength of the bird–forest relationship. In contrast, at the temporal site, bird richness and abundance may be less influenced by changes in other land-cover types than in the more temporally variable factors discussed previously, such as weather, nonbreeding habitat, and disease.

We also acknowledge that some of the uncertainty in the space-for-time predictions we observed could be related to the small number of landscapes in each comparison. Landscape-scale studies often sample relatively small numbers of landscapes due to logistical trade-offs between within-landscape sample replication and the total number of landscapes that can be surveyed (Brennan et al., 2002). However, our study indicated that large numbers of landscapes will be needed for building the spatial model for studies that use a space-for-time substitution to make inferences about change through time. Large-scale species data collection efforts (e.g., through

community science) and widely available remotely sensed land-cover data, combined with open data policies, are making such many-landscape analyses increasingly possible.

Our results are somewhat consistent with the findings of other studies that found associations between birds and environmental variables to be less variable in space than in time. A study by Flather and Sauer (1996) estimated regional-scale spatial associations between Neotropical migratory bird relative abundance and 18 landscape attributes and analyzed temporal bird–landscape attribute associations from 1966 to 1993, for the same attributes. They found that birds were associated to 13 of the 18 landscape attributes in space, but to only three of the landscape attributes over time. For forest habitat in particular, they found that bird abundance increased with forest cover over space but decreased with forest cover over time. Our results are also similar to those of Bonthoux et al. (2013), who, in a study of birds in agricultural landscapes in France from 1982 to 2007, found that bird species and communities had a stronger association to landscape composition over space than they did over time.

We issue two caveats in the data and the design that might have influenced our results. First, the GFC data set has limited ability to track and quantify forest-cover gain over time. We could only calculate forest-cover gain in 2012, unlike loss, which was calculated every year. This difference may have resulted in some error relative to the true forest-cover amount at our sites. However, we note that this error does not explain our finding that bird responses to forest cover in space were less variable than they were over time. This is because the forest data for the spatial slopes were from 2019 and so contained all of the cumulative error in the forest-cover estimates. Second, several of the spatial sites were included in more than one space–time comparison due to their geographical overlap in the southeastern United States. This may have resulted in greater homogeneity in the spatial component of each of the 25 comparisons and may explain why forest bird–forest cover associations over space were less variable across the comparisons than they were over time. This limitation of nonindependence in space may contribute to the higher variation of forest-cover effects on birds in time than in space: Because spatial slopes sometimes shared a similar data pool, it would make sense for those slopes to be similar to each other. However, while there was a correlation between the number of shared sites between pairs of spatial components and the absolute difference in spatial slopes (Appendix S2: Figure S7), the correlation was extremely weak. Thus, the spatial site overlap between comparisons likely plays a minor role in explaining the results in Figures 3–5, and some or all of the mechanisms proposed above are the main reasons for the high variability, and in some cases the weaker space–time substitutions, that we observed across space–time comparisons.

Our results suggest that changes in bird richness and abundance across space in response to forest cover can provide a general picture of how a similar change in forest cover over time would ultimately affect these same bird responses. Future work on the space-for-time substitution hypothesis should continue to untangle when and where it works best. For instance, continued investigations of how substitutable space is for time in other ecological systems and/or based on observed associations between different landscape attributes and community metrics (such as species turnover) would help further our understanding of the applicability and limitations of the space-for-time substitution.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and codes (Attinello, 2023) are available in Zenodo at <https://doi.org/10.5281/zenodo.8291352>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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