Continental-scale biomass redistribution by migratory birds in response to seasonal variation in productivity

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Conflict of interest disclosure

All authors have no conflict of interest to declare.

Biosketch

Our research team works on statistical analysis and ecological applications of citizen science data and other large ecological datasets. We create analytical approaches for eBird data that are designed to enable robust ecological inference on species' distribution, status and trends. We combine hypothesis-driven questions and newly developed methodological approaches that encompass the full annual cycle of birds at very large spatial extents. We use this macroecological perspective to address questions on the role of environmental cues and habitat change on avian distributions and seasonal migration, and the proximate and ultimate drivers of population changes.

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Short running title: Bird migration and primary productivity

Abstract

Aim: Animal migration is often explained as the result of resource tracking in seasonally dynamic environments. Therefore, resource availability should influence the distributions of migratory animals as well as their seasonal abundance. We examined the relationship between primary productivity and the spatio-temporal distributions of migratory birds to assess the role of energy availability in avian migration.

Location: North America.

Time period: Full annual cycle, 2011–2016.

Major taxa studied: Nocturnally migrating landbirds.

Methods: We used observations of nocturnally migrating landbirds from the eBird community-science program to estimate weekly spatial distributions of total biomass, abundance, and species richness. We related these patterns to primary productivity and seasonal productivity surplus estimated using a remotely-sensed measure of vegetation greenness.

Results: All three avian metrics showed positive spatial associations with primary productivity, and this was more pronounced with seasonal productivity surplus. Surprisingly, biomass showed weaker association than did abundance and richness, despite being a better indicator of energetic requirements. The strength of associations varied across seasons, being the weakest during migration. During spring migration, avian biomass increased ahead of vegetation green-up in temperate regions, a pattern also previously described for herbivorous waterfowl. In the southeastern USA, spring green-up was instead associated with a net decrease in biomass, and winter biomass greatly exceeded that of summer, highlighting the region as a winter refuge for short-distance migrants.

Main conclusions: While instantaneous energy availability is important in shaping the distribution of migratory birds, the stronger association of productivity with abundance and richness than with biomass suggests the role of additional drivers unrelated to energetic requirements that are nonetheless correlated with productivity. Given recent reports of widespread North American avifaunal declines, including many common species that winter in the southeastern USA, understanding how anthropogenic activities are impacting winter bird populations in the region should be a research priority.

Keywords: Abundance, biomass, eBird, North America, productivity, seasonal bird migration, species-energy relationship, species richness, vegetation greenness

1. Introduction

Seasonal variation in resource availability is hypothesized to play a central role in driving avian migration (Dingle, 2014; Somveille *et al.*, 2015). Migratory bird populations are thought to track seasonal bursts in primary productivity in the spring to support their migratory journey and subsequent breeding activities.

Individual tracking studies have revealed phenological synchronization between spring migration and vegetation green-up (Kölzsch *et al.*, 2015; Thorup *et al.*, 2017; Lameris *et al.*, 2018; Briedis *et al.*, 2020), with spring arrivals timed to facilitate a nesting schedule where peak resource availability coincides with the critical chick growth phase (van der Graaf *et al.*, 2006). Population-level studies have also revealed synchronization between vegetation greenness and bird occurrence during spring and autumn migration across a range of dietary guilds, with the strongest evidence found among herbivores and granivores (La Sorte & Graham, 2021). Additionally, vegetation phenology is also thought to play a prominent role in the looped annual migration paths of some migratory landbird species (La Sorte *et al.*, 2014). Even outside the main migratory periods, resource availability has been identified as a potential driver of avian movement between sites during the winter (Koleček *et al.*, 2018; Knight *et al.*, 2019).

These species-level associations between occurrence and primary productivity are expected to lead to emergent patterns at the community level, such as a higher number of species and individuals occurring during the breeding season in regions with higher plant productivity. Indeed, many community-level studies have found strong positive relationships between productivity and species richness, henceforth called the species-energy relationship (Evans *et al.*, 2005). Yet, the presumed relationships between productivity, and the net avifaunal abundance and biomass remain relatively unexplored, despite their potential roles in elucidating the species-energy relationship. For example, the "more individuals hypothesis" (Wright, 1983; Srivastava & Lawton, 1998) postulates that energy availability limits the total number of individuals that can be supported in a community, which in turn influences species richness, since larger population sizes reduce the risk of stochastic extinctions. One key prediction of this hypothesis is that the abundance-energy relationship should be *stronger* than the species-energy relationship (Currie *et al.*, 2004; Storch, 2012; Storch *et al.*, 2018). Comparing the strength of these two relationships would therefore allow us to evaluate this prediction. Moreover, if energy were indeed the limiting resource shaping the distribution of individuals across space, then since individual energetic needs generally increase with body size (Daan *et al.*, 1990; Nagy *et al.*, 1999), total avian biomass should reflect energy requirements of a community better than total abundance (especially if body mass has been transformed to account for allometric relationships), and hence show an even stronger relationship with productivity.

Another consideration is that migratory birds compete not only with other migratory species for resources, but also with species that are year-round residents. It has been hypothesized that the distribution of breeding migratory birds are shaped not by absolute resource levels, but rather by the seasonal resource surplus that is not fully utilized by resident species (Hurlbert & Haskell, 2003). Since resident populations are themselves limited by the period of lowest resource availability, the seasonal productivity difference (the productivity level above the site minimum) is likely to be a better estimate of resource available to migrants than productivity alone. We would then expect an even stronger association between biomass and this seasonal productivity difference.

Another motivation for considering net abundance and biomass is to understand how different geographical regions are being utilized by migratory birds across the annual cycle at the community level (Bauer & Hoye, 2014). Breeding and wintering ranges are typically described for individual species, but identifying analogous regions at the community level is complicated by interspecific differences in migration strategies and abundance patterns. By assessing macroecological patterns of abundance and biomass year-round, we expect areas used solely as breeding grounds to show a positive temporal correlation between productivity and abundance or biomass, whereas areas used as wintering grounds may host higher numbers of birds during winter when productivity is locally at a minimum (La Sorte & Graham, 2021). Hence, a systematic evaluation of the abundance-productivity and biomass-productivity

relationships across the annual cycle would highlight the role of different regions in the ecology of avian communities.

Despite the interest in understanding macroecological relationships between biomass and primary productivity, most empirical studies have focused on the relationship between spatial patterns of species richness and vegetation greenness or other measures of productivity (Currie, 1991; Blackburn & Gaston, 1996; Hurlbert & Haskell, 2003; Evans *et al.*, 2006; Rahbek *et al.*, 2007), and only during part of the annual cycle (usually the breeding season) over limited spatial extents. The scarcity of large-scale studies on abundance-productivity and biomass-productivity relationships for migratory birds is due in part to data constraints. For example, species richness is typically estimated using range maps, which tend to be readily available. Range maps, however, provide coarse estimates of extent of occurrence and lack information on patterns of abundance or biomass within the range (Hurlbert & White, 2005; Hurlbert & Jetz, 2007; Jetz *et al.*, 2008; Gaston & Fuller, 2009). Satellite or telemetry tracking datasets provides information on patterns of occurrence within the range, but these data sources are necessarily constrained to a few individuals from a limited number of often large-bodied species, making it hard to examine population- and community-level patterns of abundance and biomass. Similarly, available abundance datasets have traditionally been relatively sparse with limited spatial and/or temporal coverage, since surveys of total abundance across many species and large spatial extents across the full annual cycle require enormous effort. Large-scale volunteer-based datasets such as eBird (Sullivan *et al.*, 2014) can satisfy these data requirement due to their extensive spatio-temporal coverage.

In this study, we explore the relationships between primary productivity and the species richness, abundance, and biomass of nocturnally migrating landbird species across the annual cycle within North America. We estimated the three avian ecological metrics using observations from the eBird community-science program (Sullivan et al. 2014), and primary productivity using a remotely-sensed measure of vegetation greenness, the Enhanced Vegetation Index (EVI; Huete *et al.*, 1994). We assessed the relationships using spatial correlations between distribution patterns calculated weekly across the annual cycle, and temporal correlations between time series calculated at each location across the study area. Assuming energy availability as the main limitation structuring the distribution of the nocturnal migrants, we hypothesize that the spatial correlations with the seasonal EVI difference should become progressively weaker from biomass to abundance to species richness, while still being stronger than the counterparts based on EVI alone. Finally, we use the patterns of temporal correlations to identify regions used for wintering and breeding at the community level.

2. Methods

a. Estimating the total biomass, abundance, and species richness of nocturnally migrating landbirds

i. Avian count data

We acquired avian count data from the 2016 eBird Reference Dataset (Fink *et al.*, 2017) for 176 nocturnally migrating landbird species (Dokter *et al.*, 2018; Rosenberg *et al.*, 2019). We chose to focus on this group of species because of their generally homogenous detection rates. Reports of diurnal migrants during migration will include many records of over-flying flocks whose locations do not reflect resource use at the checklist location, whereas nocturnal migrants reported during the day are usually on the ground utilizing local resources. Also, diurnal migrants often migrate in large flocks during the day (Beauchamp, 2011), and hence tend to have higher detectability per individual than nocturnal migrants that would make comparisons counts of detected nocturnal and diurnal migrants inappropriate.

We restricted eBird data to "complete checklists", where the observers reported counts of all bird species seen or heard, so that species with no observations could be interpreted as being undetected rather than being omitted by observer preference (Johnston *et al.*, 2021). We selected checklists from the period 2006/11/22–2016/12/31 (see Supp. Section S1b for an explanation of the choice of start date), within the region bounded by 20°–72° N latitude, and 52°–170° W longitude. We outline additional restrictions in Supp. Section S1a. In the end, a total of 8.1 million checklists were available for analysis, almost all of which (98%) were diurnal observations. These checklists were used to estimate avian biomass and abundance across the study area and period, using methods described in the next three subsections.

ii. Predictor and response variables for biomass and abundance interpolation models

Since eBird checklists are unevenly distributed across space and time, we developed models to interpolate avian biomass and abundance estimated from the checklists to any location and date within the study area and period. Species distributions are often structured by the environment, so models that include environmental predictors typically perform better than purely spatiotemporal interpolation (Elith & Leathwick, 2009). Additionally, including predictors that describe variation in the observation process can be used to control for checklist-level variation in detectability, thereby improving model performance (Hochachka *et al.*, 2012; Johnston *et al.*, 2021).

We considered four classes of predictors similar to those described by Fink *et al.* (2020a). The first class is of five effort predictors describing variation in the observation process: number of observers, observation duration, distance travelled during observation, observation protocol, and checklist calibration index (CCI; Kelling *et al.*, 2015; Johnston *et al.*, 2018). Observation protocol indicated whether the checklist corresponded to a stationary or travelling count (other protocols were removed), while CCI was a derived index designed to account for heterogeneity in the observation process among observers and checklists. The second class of predictors were three temporal predictors: start time of the checklist, day of year, and year of observation. The third class of predictors were topographical predictors estimated at each checklist location: elevation, eastness and northness, all at a 1 × 1 km spatial resolution. Eastness and northness combine both slope and aspect to describe the orientation of the surface in three dimensions (Amatulli *et al.*, 2018). Lastly, the fourth class contained 76 descriptors of landcover and watercover, again estimated at each checklist location. These 76 predictors consisted of four landscape metrics used to describe the composition and configuration of each of the 19 cover classes within a 2.8 × 2.8 km neighborhood around the location. The four landscape metrics were the proportion of each cover class, the largest continuous patch, patch density, and edge density within each neighborhood, and were calculated using FRAGSTATS (McGarigal *et al.*, 2012; VanDerWal *et al.*, 2014), based on data (Friedl *et al.*, 2010) from Moderate Resolution Imaging Spectroradiometer data (MODIS; Justice *et al.*, 1998). Landcover classes were from the University of Maryland (UMD) classifications (Hansen *et al.*, 2000). Water cover classes were derived from the MODIS data. We also included longitude and latitude as predictors to account for unexplained spatial variation, bringing the total number of predictors to 89.

As response variables for the interpolation models, for each checklist, we estimated the total biomass detected by the observer(s) by summing the body mass across all individuals reported on the checklist, using sex-averaged body mass estimate for each species from Dunning (2007). Likewise, we estimated total detected abundance using the total number of individual birds reported. We also estimated a third response variable, which we call the total *transformed* biomass, where each body mass is raised to the power of 2/3 before summing, to account for the allometric relationship between metabolic rates and body size. We choose a scaling exponent of 2/3 for two reasons. First, empirical studies on birds often found values closer to 2/3 (Daan *et al.*, 1990; Nagy *et al.*, 1999) than the 3/4 in

Kleiber's law (Kleiber, 1961). Second, by analyzing both transformed and untransformed biomass, we would have explored both limits (2/3 and 1) of the likely range of values from theoretical considerations (Glazier, 2005; Kooijman, 2010). Finally, we log-transformed these estimates of (transformed) biomass and abundance to improve their distributional properties for the models.

iii. Fitting the avian abundance and biomass interpolation models

We modelled the relationship between the predictors and the biomass (or abundance) response using Spatio-temporal Exploratory Models (STEM; Fink *et al.*, 2010, 2020a). In this modeling framework, the geographic region and study period are divided into overlapping spatio-temporal blocks called stixels. A base model is separately fitted to the data within each stixel. The model estimate at any spatio-temporal point of interest is obtained by averaging across the predictions of all base models within whose stixels the point had fallen; we call the number of models used in the prediction the ensemble size. The advantage of using STEM over single model approaches is discussed in Fink *et al.* (2010, 2020a). Henceforth, we refer to the ensemble of base models as the biomass (or abundance) interpolation model.

For our implementation, we used stixels with minimal spatial dimensions 750 $\times$ 750 km and fixed temporal dimension of 21 days based on day number only (i.e. data from all years were present, and inter-annual differences were accounted for during model fitting; see Supp. Section S1b). We used a random forest base model (Breiman, 2001), implemented using the *ranger* package (Wright & Ziegler, 2017) in R (R Core Team, 2018). We further limited the study area to regions with sufficient data to meet the model requirements (Supp. Section S1c). Additional model details can be found in Supp. Sections S1d–g, including the use of adaptive spatial sizing of stixels to increase the study area into regions of low data density (Fink *et al.*, 2013), spatio-temporal subsampling to address the issue of uneven checklist distributions (Robinson *et al.*, 2018; Fink *et al.*, 2020a; Johnston *et al.*, 2021), and data balancing to account for the interannual increase in eBird checklist volume (Fink *et al.*, 2020a).

We evaluated how model performance varied across the annual cycle using a holdout test set, by calculating the percentage variance explained for all test data within a 7-day moving window (in steps of 3 days). This test set was split from the training set used for model-fitting at the outset, in a train:test ratio of 80:20, using a procedure that minimized any potential autocorrelations between the two sets (Supp. Section S1h). We also adopted a spatial subsampling procedure of the test data to avoid having checklists from highly-sampled locations dominate the calculations (Supp. Section S1i). The percentage of variance explained within each window varied between 35–53% (mean = 44%) for the biomass model, and 39–67% (mean 53%) for the abundance model, with relatively small differences among years (interannual std. dev. within each window between 1–4% var. explained; Supp. Figure S1).

iv. Generating weekly avian biomass and abundance maps

We used the fitted biomass interpolation model to generate weekly distribution maps of total detected biomass, separately for each year from 2011 to 2016. To do so, the fitted model was used to predict the detected biomass at each location across a 8.4 $\times$ 8.4 km mapping grid covering the study region, day (spaced 7 days apart) and year, based on topographical and land cover values at the grid location, and assuming a standard sampling effort: a single observer with a high CCI of 4, performing a travelling count starting at 07:00 local time, for a duration of 1 hr and distance of 1 km. The mapping grid is the same as the ones used in eBird Status and Trends data products (eBird S&T; Fink *et al.*, 2020b). The values of the effort variables were chosen to reduce the underestimation caused by nondetection and hence bring the predicted values closer to the unknown true values: for instance, observers with high CCI tended to detect

species at a higher rate (Johnston *et al.*, 2018). While even longer durations or distances might also increase detection, they tended to be less common among checklists, so predictions at these values may be less accurate. Similar weekly maps were generated for total detected abundance. Since the estimates were based on standardized sampling efforts, they are expected to correlate well with the true biomass and abundance values despite variation in effort.

v. Generating weekly species richness maps

We generated weekly maps of species richness by using species-level estimates of (non)occurrence from the 2018 eBird S&T to determine the number of nocturnally migrating species present at each mapping grid location. In the eBird S&T estimates, the sampling protocols have been optimized separately for each species to maximize detection, so we expect these estimates to reflect the true occurrence patterns better than if a single sampling protocol had been applied across all species. This approach also avoids issues involving equalization (Roswell *et al.*, 2021) that a STEM model for species richness (analogous to the ones for biomass and abundance) would have to address. On the other hand, this also meant that eBird S&T abundance estimates are not comparable between species, which was why we did not use them earlier on for total biomass or abundance. In addition, we wanted multiple years of biomass and abundance estimates to account for year-to-year variations in the subsequent analyses, whereas eBird S&T estimates were only available for selected years and also not designed for multi-year analyses. (Year-to-year variations in richness outside the migratory period were less likely since that would require local extinctions, so the inability to perform multi-year analyses was less of a concern.)

b. Primary productivity

We estimated primary productivity using the Enhanced Vegetation Index (EVI; Huete *et al.*, 1994) derived from MODIS data. EVI measures canopy greenness, a composite property of canopy structure, leaf area and canopy chlorophyll content while minimizing soil and atmosphere influences (Myneni *et al.*, 1995). EVI is less prone to saturation than the Normalized Difference Vegetation Index (NDVI) in high biomass regions (e.g. Huete *et al.*, 2006), and EVI has been found to correlate well with gross primary production directly measured from eddy covariance towers (Rahman *et al.*, 2005). We used EVI estimates generated by La Sorte & Graham (2021) using 16-day 1-km Level-3 MODIS products MOD13A2 V.006 and MYD13A294 V.006, which combined gave estimates every 8 days. The data were aggregated to a spatial resolution of 10×10 km, and then interpolated to obtain daily estimates using generalized additive models based on cyclic penalized cubic regression splines (Wood, 2017). From the resulting surface of estimates, weekly EVI values at each mapping grid location were obtained by bilinear interpolation, using the *raster* package in R (Hijmans, 2021).

c. Associations between primary productivity and biomass, abundance, and species richness.

We examined the association of primary productivity with (transformed) biomass, abundance, and species richness using two approaches. First, for each week's estimates we calculated the correlation coefficient between EVI and each of the three ecological metrics by treating the values at each grid location as paired data points (hereafter "spatial correlation coefficients"). Changing correlations among weeks would reveal seasonal changes in the spatial associations. Second, at each mapping grid location, we calculated the temporal cross-correlation coefficient between EVI and each separate ecological metric, using the time series of the two variables from that location. We did this to reveal any regional differences in the local temporal associations. We used the Kendall rank correlation coefficient in both analyses

(Kendall, 1938), based on the fast algorithm implemented in the *pcaPP* package in R (Filzmoser *et al.*, 2018). These correlation coefficients were intended as descriptive indices describing the degree of similarity between two *fitted distributions*, and not as statistics for inference; therefore, their values should not be compared against those from studies designed for inference (e.g. Currie *et al.*, 2004). We chose Kendall correlation over other measures of distributional (dis)similarity such as earth mover's distance, because we wanted a rank-based measure to allow for monotonic but nonlinear relationship between EVI and the ecological metrics. We found no qualitative differences when we used Spearman correlation coefficients instead.

As seasonal resource surplus may play a more important role in shaping the distribution of breeding migratory birds than the absolute resource level, we repeated the above analysis of spatial correlations, but this time using seasonal EVI difference in place of EVI. The seasonal EVI difference is defined as the difference between EVI and its site seasonal minimum (see Supp. Section S2). During the winter period, most locations had EVI values close to the site minima (Supp. Figure S2), leading to low EVI difference throughout most of the study area. As a result, spatial correlations with seasonal EVI difference during this period could be misleading (see Supp. Section S2), so we only calculated the correlations for each week in a half-year period spanning May to September. We did not repeat the analysis of temporal associations, since the offset by the site minima would have no effect on the results.

To better understand regional differences in the local temporal associations between EVI and ecological metric (second approach), we looked at the summary times series of each variable from two regions: the Northeast, which showed highly positive temporal correlation, and the Southeast, which showed highly negative correlation. Each region was defined using a combination of Bird Conservation Regions (BCR; Sauer *et al.*, 2003), with the Northeast comprising BCRs 12 and 14, and the Southeast comprising BCRs 25–27, 31 and 37. For each region and week, we summarized each variable using the median and inter-quantile range across all locations within that region.

Finally, the analysis of temporal associations highlighted regions in the study area where the correlation coefficients were positive, and regions where they were negative. To determine whether these regional patterns were associated with climatic factors, we fitted a random forest model with the temporal correlation coefficients at each mapping grid location as the response, and 19 bioclimatic variables (WorldClim version 2.1; Fick & Hijmans, 2017) as predictors. Permutation importance was then evaluated for each bioclimatic variable. However, since many of these bioclimatic predictors were highly correlated, permutation-based importance metrics may be misleading (Hooker & Mentch, 2019), so we also used a forward stepwise selection approach where during each step, the variable that resulted in the largest decrease in out-of-bag mean squared error was added to the existing list of variables. The sequence in which the variables were added hence indicated their importance, in terms of how much additional predictive information each variable provided beyond that of variables earlier in the sequence; the goal was to facilitate a parsimonious bioclimatic description of the temporal association patterns.

3. Results

a. Weekly distributions of total avian biomass, abundance, and species richness, and their spatial correlations with primary productivity

The weekly distribution maps for biomass, abundance and species richness captured seasonal migration, with a northward shift of nocturnally migrating landbirds species during spring migration and a southward shift during autumn migration (Figures 1a, b and c). EVI distributions followed a similar pattern of northwards vegetation green-up in the spring and southwards vegetation senescence in

autumn (Figure 1d). Nonetheless, there were noticeable differences in the spatial patterns among these quantities, especially outside winter. During summer, both avian (transformed) biomass and abundance were mostly concentrated along a mid-latitude band between 35° – 45° N latitude of central and eastern North America (July 6 in Figure 1a, b and Supp. Figure 3a), whereas species richness was mostly concentrated in the Northeast (Figure 1c). In contrast, EVI displayed a mostly longitudinal pattern, without any pronounced latitudinal concentration in the east (Figure 1d). However, after subtracting by the minimum site EVI, the seasonal EVI difference showed closer agreement with the biomass and abundance latitudinal patterns (Supp. Figure S3b). During spring migration, biomass, abundance and richness were all distributed more northerly than both EVI and the seasonal EVI difference (May 25 in Figure 1 and Supp. Figure S3).

Weekly evaluations of the spatial correlation coefficient between (transformed) biomass and EVI across the study area revealed seasonal variation in the strength of spatial association across the annual cycle (Figure 1e and Supp. Figure S3c). The correlation was strongest between March and April (early spring migration), and weakest between September and October (the middle of autumn migration). Between mid-March and late May, biomass increased well ahead of EVI in the Northern Great Plains, whereas in the Southeast, biomass decreased even when EVI remained relatively high (Figures 1a, d). These changes increased the mismatch between biomass and EVI, hence causing the decrease in correlation seen over that period (Supp. Figure S4). The subsequent increase in correlation until early July could be attributed to EVI "catching up" with the biomass levels in the north and hence reducing the mismatch.

Similar patterns of seasonal variations were also observed in the associations between EVI and total abundance and species richness, although with quantitative differences in the strength of associations (Figure 1e and Supp. Figure S3c). EVI was more strongly correlated with richness than biomass or abundance throughout most of the annual cycle. Correlation with abundance was stronger than biomass during summer, whereas the reverse was true during fall migration.

The spatial correlations showed qualitatively similar dynamics when EVI was replaced by the seasonal EVI difference, with a peak mid-summer and sharp decreases in correlation during the migratory periods (Figure 1f and Supp. Figure S3d). The correlations were also generally higher than the EVI counterparts during the breeding season. Among the three metrics, seasonal EVI difference showed marginally higher correlation with abundance than with richness or (transformed) biomass.

b. Temporal association between avian biomass and primary productivity

Figure 2a shows the full-year temporal association between EVI and biomass, with the color at each location representing the value of the Kendall coefficient calculated at the location. The sign of the association was generally determined by the climatic zone, with positive association in the temperate zone to the north, and negative association in the subtropical zone to the south. We observed the same qualitative patterns using Pearson and Spearman correlation coefficients (Supp. Figures S6a, b). Patterns of temporal association were also similar for abundance (Supp. Fig S7).

In the Northeast, both biomass and EVI were highest in spring and summer, and lowest in winter (Figure 2b), hence the positive association in this region. Note however, that the changes in biomass and EVI were not synchronous. In particular, we found that biomass increased most rapidly in April and peaked in mid-May, nearly a month ahead of EVI. Similarly, observed biomass decreased earlier in autumn than EVI. In the Southeast, the pattern was reversed, and spring green-up was associated with a drop in biomass (Figure 2c). Biomass started to decrease in March, reaching its lowest levels in summer and early

autumn, before increasing again around October and peaking in winter. The opposite temporal trends between EVI and biomass hence explained the negative temporal association in the Southeast.

Forward stepwise selection (Supp. Figure S8a) revealed that the two bioclimatic variables that best predicted the spatial patterns of temporal associations between EVI and biomass were BIO11 (mean temperature of coldest quarter), followed by BIO18 (precipitation of warmest quarter), explaining 92% of the variations in the Kendall coefficients. There were strong positive seasonal associations between biomass and productivity where winters are cold (BIO11 was low), and strong negative associations in regions with mild winters and wet summers (both BIO11 and BIO18 were high), see Figure 3. Additional results from both forward stepwise selection and permutation importance can be found in Supp. Section S3 and Supp. Figures S8–S10.

4. Discussion

Our analyses have revealed broad-scale positive associations of primary productivity with the biomass, abundance, and species richness of nocturnally migrating landbirds across space and time. Under a scenario of resource tracking by migrants, in which energy availability is the main factor and proximate cue determining the spatial distribution of migratory landbirds, one would expect primary productivity to be more closely associated with biomass than abundance, because abundance does not reflect the higher energetic needs of larger birds (Daan *et al.*, 1990; Nagy *et al.*, 1999). The relationship between productivity and richness (Currie *et al.*, 2004; Storch, 2012; Storch *et al.*, 2018) is expected to be even more indirect and therefore weaker, as it depends on complex and diverse mechanisms that can weaken the relationship. For example, the "more-individuals hypothesis" (Wright, 1983; Srivastava & Lawton, 1998) suggests that high energy availability allows more individuals to be supported, which in turn reduces the risk of stochastic extinction and hence leads to higher species richness. A key prediction from this hypothesis is that the relationship with productivity should be stronger for abundance than diversity, since the second relationship is more distal.

Contrary to these expectations, instead of associations with productivity becoming progressively weaker from biomass to abundance to species richness, we found the opposite pattern (Figure 1e), with species richness more strongly correlated with productivity compared to (transformed) biomass or abundance. These findings are replicated in studies of other taxa where richness is often more strongly correlated with productivity compared to abundance (Currie *et al.*, 2004; Storch *et al.*, 2018). In contrast, the seasonal surplus in productivity did show a marginally stronger correlation with abundance than richness, although the correlation with biomass remained lowest. Since each metric showed higher correlation with the productivity surplus than with absolute productivity during the breeding season, productivity surplus is likely a better measure of energy available to migratory birds than productivity alone, by better accounting for competition and resource use by resident species and other non-avian taxa (Hurlbert & Haskell, 2003; Somveille *et al.*, 2018). Nonetheless, the fact that biomass still showed a lower correlation than abundance (despite being a more accurate indicator of energetic requirements) merits explanation. Besides energy availability, the spatial distribution of breeding birds may also be influenced by other limitations such as the availability and structural diversity of nesting habitats, which are often correlated with productivity (Dobson *et al.*, 2015) and can hence enhance the productivity-abundance association. Moreover, abundance and biomass patterns are likely to be driven more by common species, which may have idiosyncratic requirements unrelated to energy availability, such as nest sites. Finally, many nocturnally migrating bird species do not directly consume primary production; while higher primary productivity likely leads to higher resource availability across trophic levels, the association need not always be perfect (Piersma, 2020). Hence, one possible refinement of our analysis would be to

decompose avian biomass by dietary guilds and to study the spatial associations with productivity at the guild level (La Sorte & Graham, 2021).

We also found strong seasonal variation in the spatial association between productivity and the three ecological metrics (Figure 1e). Across the annual cycle, biomass was most strongly correlated with EVI during late winter: even though EVI was generally low across the continent, it remains relatively high in the Southeast, which is also the region where migrants were concentrated in winter, suggesting immediate and strong constraints by resource availability during this time of the year. The correlation decreased during spring migration as migrants overtook the wave of spring green-up, and then increased during subsequent green-up in summer, a pattern visible in both in the correlations with EVI and surplus EVI. This phenological lag in vegetation greenness relative to biomass can also be seen in Figure 2b, with biomass building up ahead of EVI in the Northeast during spring. Such a pattern of overtaking the "green wave" has been documented with migratory geese (Kölzsch *et al.*, 2015). Early arrival on breeding grounds prior to green-up is usually explained by selection for timing of breeding that aligns the resource requirements of nestlings with peak resource availability (Kölzsch *et al.*, 2015; Fokkema *et al.*, 2020). Our findings suggest that this explanation also generalizes to nocturnally migratory landbirds (Both *et al.*, 2010). Both the higher overall *absolute* productivity level and the ability of migratory birds to accumulate and carry large body reserves to fuel migration and initial breeding activities (Sandberg, 2008) would allow the migrants to (temporarily) deviate from the instantaneous *relative* energy landscape. The relationships between productivity and the three ecological metrics fell again during fall migration: much of the biomass stayed along the mid-latitude band while EVI was falling in the north due to leaf senescence, hence shifting the EVI distribution southward. This lower association also suggests that the migrants may be less constrained by instantaneous energy availability during this phase of the annual cycle (Briedis *et al.*, 2020; Horton *et al.*, 2020).

Seasonal shifts in the biomass distributions (Figure 1a) also led to unexpected patterns in the local temporal associations with EVI across the annual cycle (Figure 2a). Large populations of nocturnally migrating landbirds were found to aggregate in the subtropical regions of Southeast during winter. However, in these regions, spring greening was instead accompanied by a net decrease in total biomass (Figure 2c), due to the northward mass exodus of overwintering populations that the influx of Neotropical migrants could not compensate for. Increased productivity of the environment is therefore associated with a decrease rather than an increase in migrant biomass; hence the negative temporal association in these regions. The southeastern subtropical region thus plays the role of a winter refuge for many species of nocturnally migrating landbirds in North America, as also seen from the fewfold increase in abundance and biomass during winter (Figures 2c, S7c). Our analysis of bioclimatic variables showed that regions with negative local temporal associations were primarily characterized by mild winters and wet summers (Figure 3b). While this could be related to a higher winter productivity and hence food availability compared to the more northerly regions (Figure 1d), the mild winter conditions likely also play a role by reducing thermoregulatory costs (Cartar & Morrison, 1997).

We acknowledge a number of limitations with our approach. First, since the biomass and abundance interpolation models were fitted using observation data, the model estimates could have been affected by the detectability of the birds. In particular, the lower biomass estimates in Figures 2b and c during August and early September (compared to June and July) were likely affected by a decrease in detectability commonly observed during breeding and moult. Nonetheless, this should not affect the spatial correlations, which only depended on the relative values between different locations in the same week. Second, richness was obtained using a different approach (eBird S&T estimates) from the biomass and abundance estimates (STEM), which may affect the comparison between the strength of their spatial associations with productivity. Third, STEM included land cover predictors which may themselves affect

EVI, so there is a risk of circularity when analyzing correlations with EVI. However, this risk was minimized by the use of flexible base models together with many predictors that affect EVI in different ways, so the models were not constrained to learn EVI-related signals. Fourth, due to the tradeoff between coverage and accuracy, our study area did not include Central America nor the high latitudes where some of the nocturnal migratory species spend their wintering/breeding seasons. Finally, it is worth repeating that the correlation coefficients were meant as measures of similarity between two fitted distributions, so they should not be compared to values from studies designed for statistical inference.

Our findings highlight the role of the Southeast as winter refuge for short-distance migrants, which make up a large proportion of migratory landbird biomass in North America. Parts of coastal California and the Central Valley likely play a similar role for the western US. While many of the species wintering within the contiguous US are regarded as common, recent work on North American avifauna population trends (Rosenberg *et al.*, 2019) have shown that they are nonetheless experiencing steep declines. Many studies have focused on the importance of protecting wintering habitats for the conservation of Neotropical migratory species (e.g. Sherry & Holmes, 1996; Faaborg *et al.*, 2010), but relatively little is known about the impact of wintering refuge availability and quality on the long-term population trends of the short-distance migrants. We hope that our results can spur more work in this direction.

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678

679 ## Data accessibility statement

680 The estimates of total biomass, abundance and species richness derived from eBird data, as well as EVI
681 and bioclimatic variables extracted from publicly-available data sources, are available from Figshare at
682 https://doi.org/10.6084/m9.figshare.15085275.v1.

683

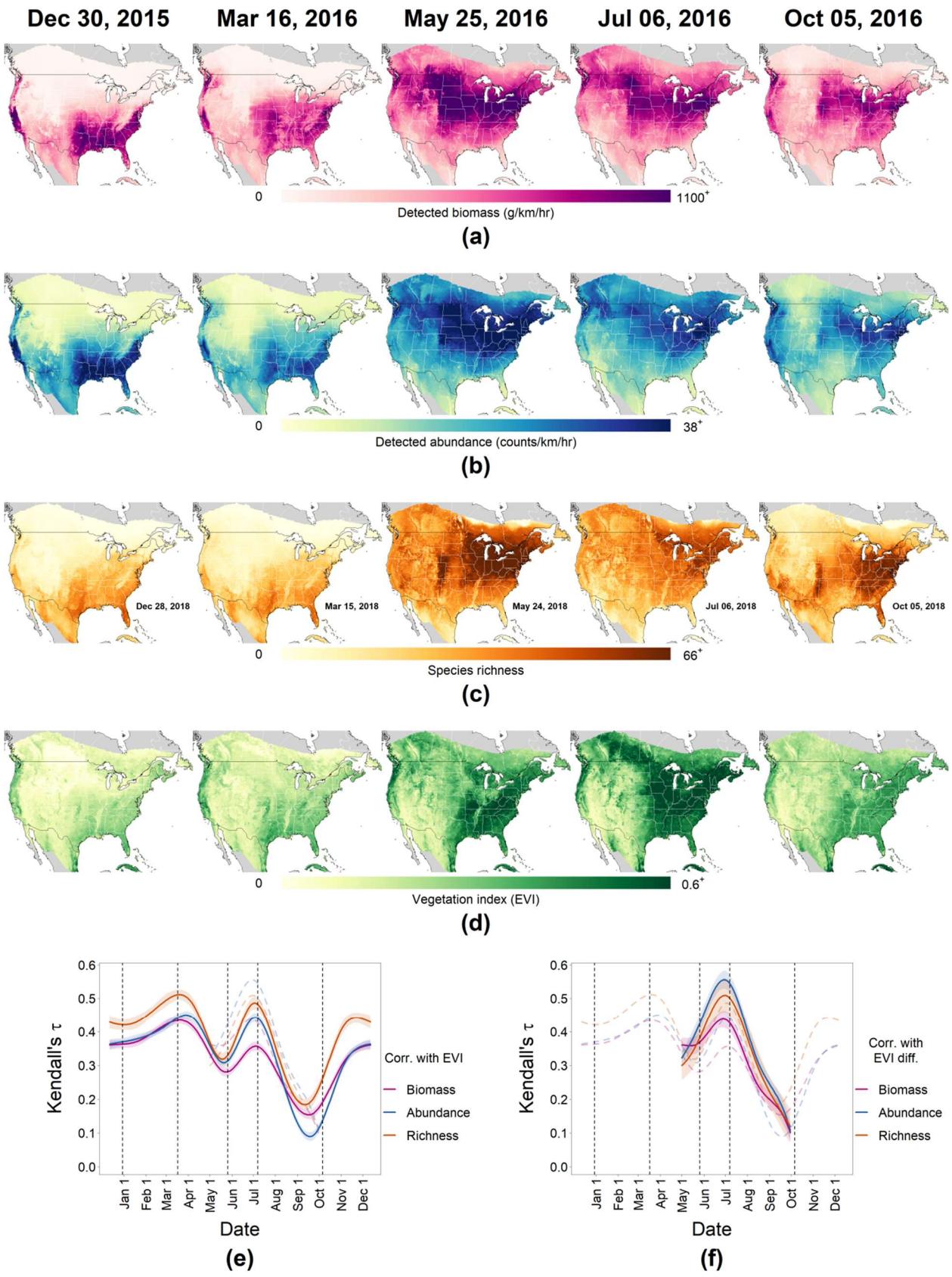
Dec 30, 2015
Mar 16, 2016
May 25, 2016
Jul 06, 2016
Oct 05, 2016
0
1100+
Detected biomass (g/km/hr)
(a)
0
38+
Detected abundance (counts/km/hr)
(b)
Dec 28, 2018
Mar 15, 2018
May 24, 2018
Jul 06, 2018
Oct 05, 2018
0
66+
Species richness
(c)
0
0.6+
Vegetation index (EVI)
(d)
Kendall's τ
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Jan 1
Feb 1
Mar 1
Apr 1
May 1
Jun 1
Jul 1
Aug 1
Sep 1
Oct 1
Nov 1
Dec 1
Date
Corr. with EVI
Biomass
Abundance
Richness
(e)
Corr. with EVI diff.
(f)

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Figure 1 | Spatial associations between primary productivity and the biomass, abundance, and species richness of nocturnally migrating landbirds. (a) Spatial distributions of total detected biomass estimated at five dates in 2016 representing different points of the annual cycle: winter (Dec 30), early spring migration (Mar 16), late spring migration (May 25), summer (July 06), and autumn migration (Oct 05). **(b)** Spatial distributions of total detected abundance at the same 2016 dates. **(c)** Species richness at the closest equivalent 2018 dates. **(d)** Primary productivity estimated using the MODIS Enhanced Vegetation Index (EVI) at the same 2016 dates. To avoid visual artifacts when comparing between maps, we used linear color scales (truncated at the 98 percentile) for all four quantities. **(e)** Spatial cross-correlation coefficients between EVI and biomass, abundance, and species richness across the study area, calculated weekly across the annual cycle. Vertical dashed lines correspond to the five dates. To reduce clutter, we only show the fitted lines and 95% confidence bands (as shaded regions) from generalized additive models (GAM); see Supp. Figure S5 for the actual correlation coefficients. **(f)** Similar to (e), except the spatial correlation is with the seasonal EVI difference, defined as EVI minus the site minima. To facilitate comparison between (e) and (f) while avoiding plot clutter, the lines in (e) have been reproduced as lighter dashed lines in (f), and vice versa. Additional maps and correlation coefficient curves can be found in Supp. Figure S3.

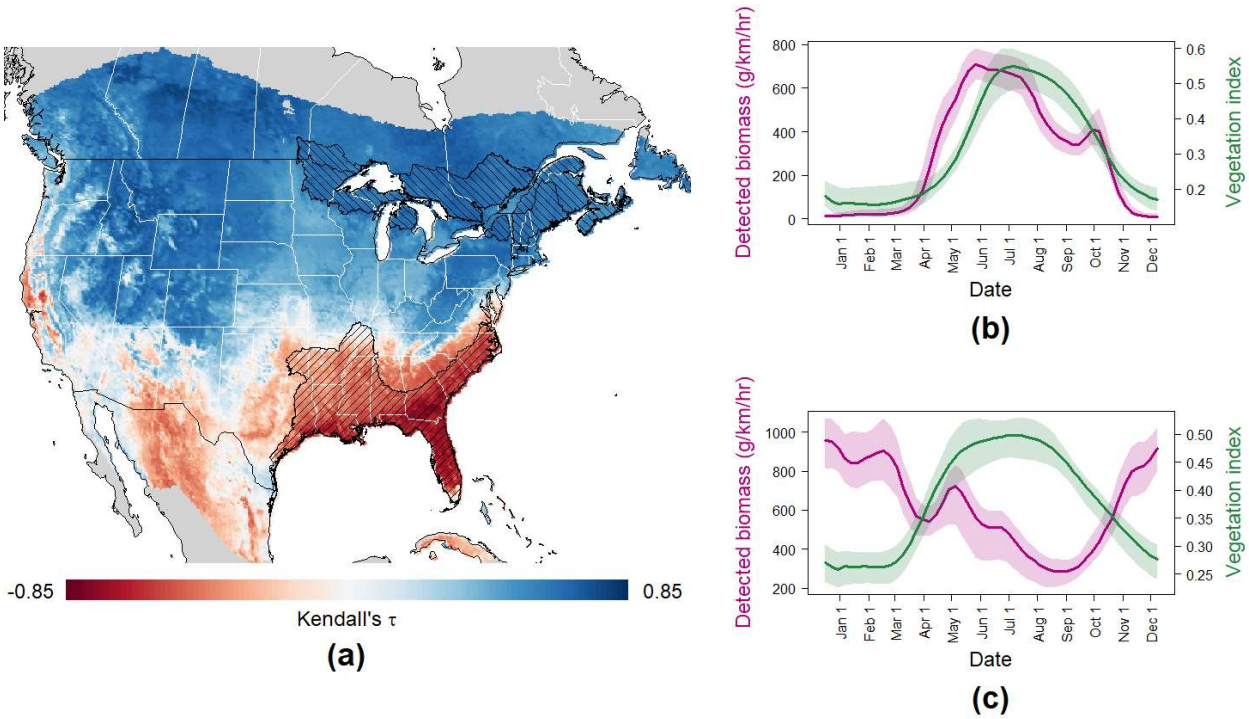
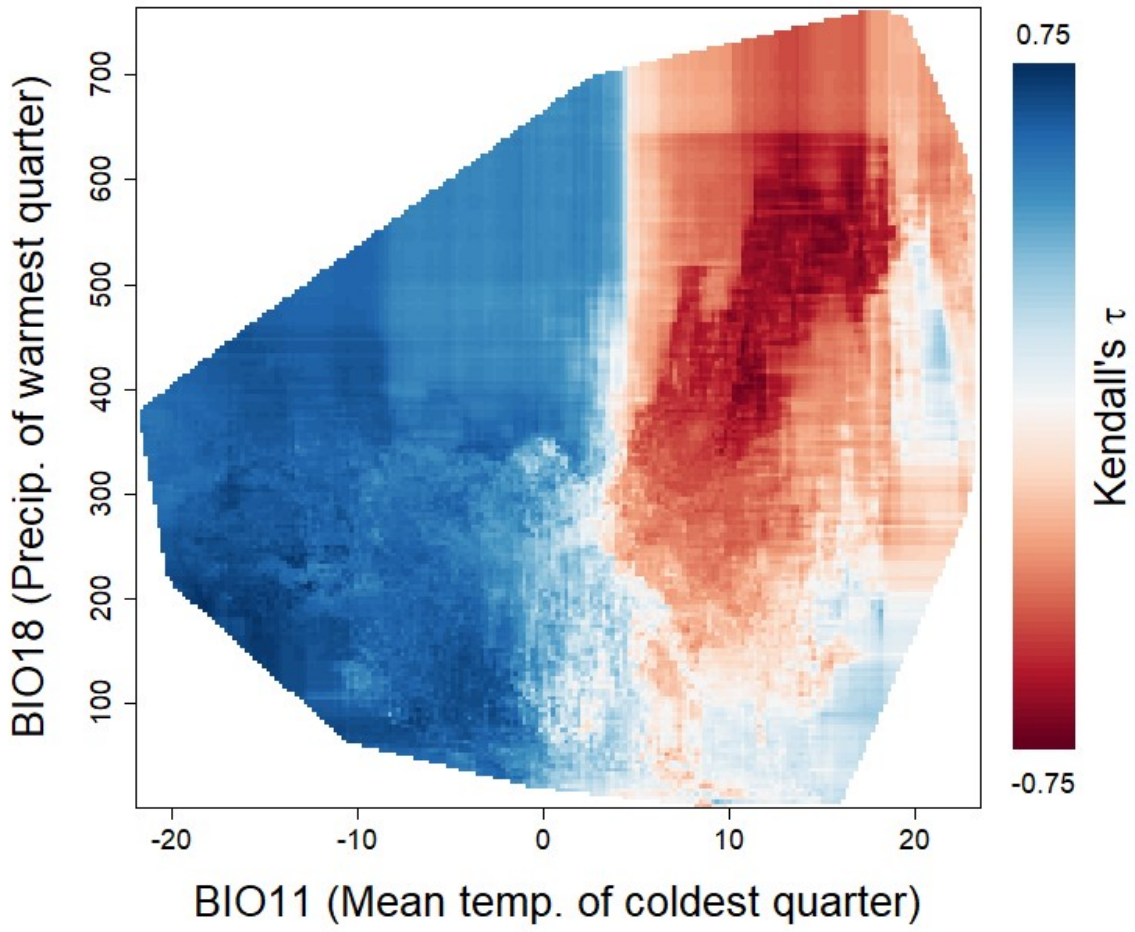


Figure 2 | Temporal association between primary productivity and avian biomass. (a) The Kendall correlation coefficient between the MODIS Enhanced Vegetation Index (EVI) and biomass across weeks at individual grid locations. Weekly median EVI and biomass across the **(b)** Northeast (blue hatched region) and **(c)** Southeast (red hatched region). The regions were defined using combinations of Bird Conservation Regions (see Methods for details). The colored bands in (b) and (c) indicate the interquartile ranges. See Supp. Figure S7 for the abundance counterpart.



745

746 **Figure 3 | Explaining the spatial patterns of temporal associations using bioclimatic variables.** This figure
747 shows the dependence of the local EVI-biomass correlations on the two bioclimatic variables with the
748 highest importance (chosen using forward stepwise selection), estimated using a two-variable random
749 forest. The two variables are mean temperature of coldest quarter (BIO11) and precipitation of warmest
750 quarter (BIO18). We restricted the plot region to the convex hull of the data distribution to avoid over-
751 extrapolation.

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