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SHORT REPORT

The influence of time-of-day on estimates of taxonomic versus functional diversity in avian communities

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ABSTRACT
Avian communities composed of a total of 79 species were sampled repeatedly at different times of day throughout the breeding season in Norfolk, Virginia, USA. Estimates of taxonomic diversity (species richness, Shannon index and probability of interspecific encounter) were highest in the morning, whereas estimates of functional diversity (functional richness, evenness, Rao's entropy and mean distinctiveness) did not vary significantly throughout the day. These results suggest that estimates of taxonomic diversity in avian communities are biased by time-of-day, but measures of functional diversity may be more robust to such bias.

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Ornithologists have traditionally censused birds in the morning to maximize detection, especially during the breeding season (Bibby *et al.* 2000). This practice assumes that most birds exhibit peak vocal activity, a period of maximal detection probability, at dawn or soon after sunrise (Robbins 1981, Horn 1996, Woodall 1997, Ohgushi *et al.* 2015). A biological rationale for why birds might have increased vocalizations at sunrise has been debated for decades and includes, but is not limited to, the following reasoning: (i) air conducts sound better at dawn or early morning (Brown & Handford 2003), (ii) birds that are quiet throughout the night need to re-establish territorial boundaries after a period of nocturnal inactivity (Kacelnik & Krebs 1983), (iii) song activity is related to varying light conditions (Keast 1994) and (iv) activity and detectability is related to feeding behaviours that differ throughout the day (Kacelnik 1979).

The near universal recommendation to conduct surveys during morning hours is commonly incorporated into sampling designs for local studies that are used to draw conclusions about avian community structure or diversity (Leston & Rodewald 2006, Newell *et al.* 2013, Mellink *et al.* 2017, Mayorga *et al.* 2020, Mulvaney & Cherry 2020, Morelli *et al.* 2021). Moreover, large-scale monitoring schemes (e.g. North American Breeding Bird Survey) typically use protocols that census at a time of greatest activity for the majority of taxa being sampled (Fink *et al.* 2010, Sauer & Link 2011). Such methodology is justifiable for studying those species for which the probability of highest detection overlaps with morning hours, but those efforts likely underestimate entire suites of species (Rollfinke & Yahner 1990, Palacio *et al.* 2020) such as nocturnal taxa (La Sorte *et al.* 2018), biasing results and leading to inaccurate conclusions (Eddleman *et al.* 2020, Amundson *et al.* 2014). Therefore, conventional sampling may not be suitable for studies of species that are likely to be under-reported due to their activity patterns.

The fact that probability of detection varies across taxa can be incorporated to yield rigorous estimates of species richness by using time-standardized sampling schemes (Boulinier *et al.* 1998) while species abundances can be corrected using a detection-occupancy probability framework (Williams *et al.* 2017, Link *et al.* 2018, Stanton *et al.* 2019). Although it is common practice to pair the timing of sampling with local sunrise, it is likely that such sampling under-estimates the abundance of some taxa with low activity at this time of day. This bias suggests that sampling should be frequent enough and distributed across the day as some taxa may not be detected even though they are present and such biased sampling may affect estimates of taxonomic diversity. Moreover, taxa that go undetected may exhibit particular traits (e.g. nocturnal behaviour or specific foraging

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techniques) that lead to undersampling. Species traits are considered within a functional diversity framework, which views community diversity as a variety of functional traits rather than as discrete taxa, linking natural history and ecological interactions to ecosystem functioning (Violle *et al.* 2007, Carmona *et al.* 2016). We hypothesize that some traits make taxa unevenly detectable throughout the day, which results in peaks of taxonomic diversity when functionally similar species are readily detectable, but the range and distribution of functional traits remain relatively consistent because of variety of species observed.

In the study presented here, we tested how time-of-day affected estimates of taxonomic and functional diversity. We surveyed all birds observed within a 50 m radius of 15 points assigned randomly, but over 100 m from each other, within residential areas and public parks in Norfolk, Virginia, USA, a medium-sized city with a population of 240,000 people, that borders the Chesapeake Bay (online Figure S1, Appendix S1). All points were in residential neighbourhoods of similar habitat type (i.e. suburban one- or two-story buildings surrounded by vegetation within a developed matrix of secondary roads).

To address time-of-day, we used relative local solar time as a predictor of species detectability. The day was partitioned into four equal parts based on local sunrise and sunset: morning (0–25th percentile of day length), noon (25th–50th percentile), afternoon (50th–75th percentile) and evening (75th–100th percentile) for stratified sampling (online Figure S2, Appendix S2). Thus, counts were conducted only between sunrise and sunset. The counts were conducted daily from 08 March to 22 June 2021, which overlapped with the typical breeding season of most bird species in Virginia. Each point was sampled for 5 min on 5–8 randomly assigned days during each of the four times of day spread over the 106 days of sampling (online Figure S3).

To assess taxonomic diversity, we used species richness, and both a raw and standardized-by-species-richness Shannon index (Magurran 2004). These indices have been criticized heavily by ecologists because they may be interpreted ambiguously (Hurlbert 1971), whereas raw species richness leads to a loss of information (McGill *et al.* 2007). We, thus, also used the probability of interspecific encounter (PIE; Hurlbert 1971) as a more informative metric of diversity.

Functional diversity metrics were chosen to reflect the range of observed traits (functional richness), their uniqueness within a regional pool (weighted by abundance mean functional distinctiveness), distribution of species abundances and dissimilarities in trait space (functional evenness) and the mean dissimilarity among all co-occurring species within a community (Rao's quadratic entropy). To estimate these metrics, data describing 23 functional traits related to resource consumption, intensity of effect on ecosystems and biotic interactions (online Appendix S3) compiled from the literature (Ehrlich *et al.* 1988, Wilman *et al.* 2014, Billerman *et al.* 2020, Sheard *et al.* 2020) were used to build trait hyperspace (Table S1). To reduce trait space dimensionality and account for collinearity among traits (Mouillot *et al.* 2021), we constructed a centroid of mean values of each trait for all observed species and calculated deviations of species' trait values from this centroid. Trait deviations were z-rescaled and used to construct principal components, six of which accounted for 46% of total trait variation and represented reproductive biology, nest traits, nesting requirements, degree of sociality, dispersal and foraging ecology (online Appendix S4). Values of these six principal components for species in each observation were used to estimate functional richness as convex hull volume (Villéger *et al.* 2008) using the R package *Momocs*, which constrained our analyses to observations of four or more species for which a convex hull could be constructed. Functional evenness (Villéger *et al.* 2008) and Rao's quadratic entropy (Pavoine *et al.* 2005) were estimated based on pairwise Euclidean distances between species in a z-scaled 6-dimensional trait space (online Appendix S5). Finally, weighted-by-abundance functional distinctiveness was based upon species distinctiveness within a pool of all observed species, calculated as the root mean square of probabilities of observation of a random normally distributed value less than or equal to the z-score of trait distinctiveness.

We tested the hypothesis that solar time-of-day was a predictor of observed community diversity. Each diversity metric was modelled using mixed effect generalized additive models (GAMs) with a random term accounting for observation location and a cubic regression spline term based on the elapsed time (in days) of the study to account for possible phenological shifts in community composition as the season progressed. We included solar time-of-day in the models as an intercept term, linear term or non-linear terms (second-, third-order polynomials). The models were built using the R package *mgcv* (Wood 2017). We compared these models using a small-sample-corrected Akaike's Information Criterion (AICc) to rank model support.

Overall, 422 point counts were conducted uniformly throughout the day (Figure S2), and a total of 79 species were detected. In 367 of 422 cases, there were four or more species observed, to allow an estimate of all measures of diversity. All measures did not meet assumptions of a Gaussian distribution, based on a Shapiro–Wilk test (Figure S5; Table S2). All metrics were correlated (Kendall's test, $P > 0.01$) with some or all of the other metrics (Figure S6).

Flexible non-linear models were most supported relative to linear and intercept models for two of four metrics of taxonomic diversity (namely, species richness and Shannon index) when compared among candidate models (intercept, linear, second- and third-order polynomials) for each measure (Table S3). Linear models were best supported for standardized Shannon index and PIE (Table S3) among candidate models. On the other hand, functional diversity estimates were distributed relatively evenly throughout the day (Figure 1), leading to intercept models garnering the most support within the AIC framework for all four metrics of functional diversity.

Taxonomic diversity measures were strongly associated with species richness and some measures of functional richness (Figure S6), consistent with numerous other studies that imply some redundancy among measures of diversity (Petchey & Gaston 2002, Magurran 2004, Keylock 2005, Jost 2006, Gallardo *et al.* 2011, da Silva Camilo *et al.* 2018). A correlation among measures of diversity suggests a dependence on species richness, especially when the latter is low (Magurran 2004, Wilsey 2005, Flynn *et al.* 2009, Devictor *et al.* 2010, Mouchet *et al.* 2010, Cadotte *et al.* 2011, de Arruda Almeida *et al.* 2018), which might explain why different estimators of taxonomic diversity showed similar patterns throughout the day.

Time-of-day was not as good at predicting functional relative to taxonomic diversity (Figure 1). The difference between functional and taxonomic diversity predicted by solar time is likely attributed to lower functional distinctiveness of species observed in the morning (e.g. passerine taxa that are functionally similar to each other) and higher functional distinctiveness of those taxa observed later in the day (e.g. raptors), patterns of which could compensate for the effects of lower species richness on functional diversity. Therefore, observations of a large number of functionally similar taxa in certain periods of the day likely lead to higher observed taxonomic diversity, although the range and distribution of traits exhibited by those species did not differ considerably from observations of less speciose communities comprising more functionally distinctive species.

While the work presented here attempted to demonstrate how time-of-day matters when estimating diversity of avian communities, we have also shown that it depends on which metric is being used to assess diversity. Metrics of taxonomic diversity

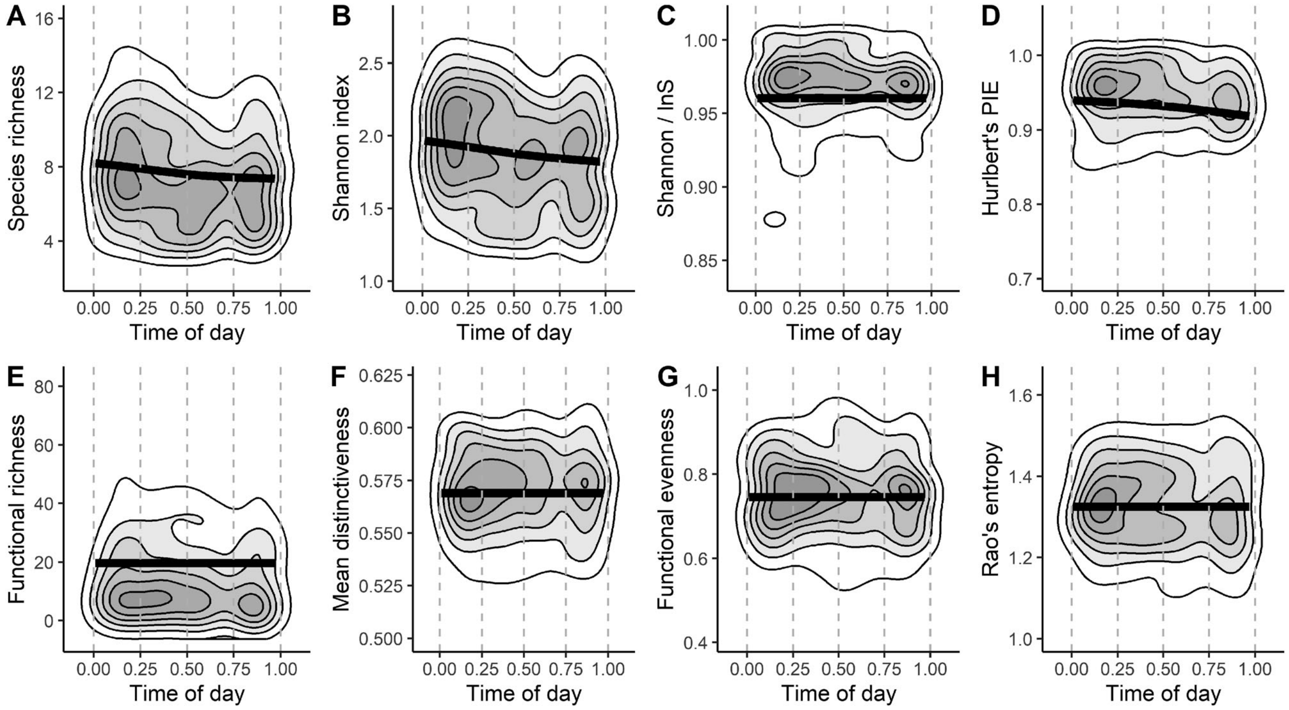

Figure 1. Variation of observed (A) species richness, (B) Shannon index, (C) standardized Shannon index, (D) Hurlbert's probability of interspecific encounter, (E) functional richness, (F) weighted-by-abundance functional distinctiveness, (G) functional evenness and (H) Rao's quadratic entropy as a function of local solar time. Black line denotes fitted generalized additive models with a cubic regression spline smoothing function and contours represent density of data points.

are more sensitive to time-of-day and thus comparisons among avian communities should be avoided when surveys are conducted at different times of day, even at the same location. Metrics of functional diversity, however, appear to be more robust because morning hours are expected to lead to low detection of functionally distinctive bird species, such as raptors or owls. Thus, even though there may be a lower detection probability later in the day for a range of less distinctive taxa, such as passerines, this effect is likely compensated by observation of other functionally distinctive taxa. Therefore, when estimating functional diversity in avian communities, sampling at different times of day may be allowed if necessary. We recognize the limitations of our study and that our findings could be an idiosyncratic artefact of the species pool at a particular location at a particular time of year. We are not aware of any available datasets, however, with a sampling design similar to ours that could be used to test our conclusions. Further studies where, presumably, detection probabilities differ among locations are needed to test the robustness of our conclusions.

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