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CORRESPONDENCE

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Exposure to noise pollution across North American passerines supports the noise filter hypothesis

Abstract

The noise filter hypothesis predicts that species using higher sound frequencies should be more tolerant of noise pollution, because anthropogenic noise is more intense at low frequencies. Klingbeil et al. (Klingbeil, La Sorte, Lepczyk, Fink, & Flather, [2020]. Geographical associations with anthropogenic noise pollution for North American breeding birds. *Global Ecology and Biogeography*, 29, 148–158) analysed continental-scale data on anthropogenic noise across the USA and found that passerine species inhabiting more noise-polluted areas do not have higher peak song frequency but have more complex songs. However, this metric of song complexity is of ambiguous interpretation, because it can indicate either diverse syllables or a larger frequency bandwidth. In the latter case, the finding would support the noise filter hypothesis, because larger frequency bandwidths mean that more sound energy spreads to frequencies that are less masked by anthropogenic noise. We reanalysed questions asked by Klingbeil et al. using a more thorough dataset of acoustic song measurements and showed that it is large frequency bandwidths, rather than diverse syllables, that predict the exposure of species to noise pollution. Given that larger bandwidths often encompass higher maximum frequencies, which are less masked by anthropogenic noise, our result suggests that tolerance to noise pollution might depend mostly on having the high-frequency parts of song little masked by noise, thus preventing acoustic communication from going entirely unnoticed at long distances.

1 | INTRODUCTION

Anthropogenic noise can mask animal acoustic signals and have detrimental effects on individual fitness and on populations (reviewed by Shannon et al. [2016]). Given that noise pollution is more intense at low sound frequencies (e.g., noise power spectra in the studies by Curry, Des Brisay, Rosa, and Koper [2018], Damsky and Gall [2017], Hu and Cardoso [2010]), the noise filter hypothesis predicts that species using lower sound frequencies are more sensitive to noise, whereas species using higher sound frequencies are more tolerant of noise pollution (Francis, Ortega, & Cruz, 2011). Some large-scale comparative work across species supports the noise filter hypothesis, but there are few studies, and most pertain to urban environments (reviewed by Cardoso, Hu, and Francis [2018]).

A new study by Klingbeil, La Sorte, Lepczyk, Fink, and Flather (2020) used spatial models of anthropogenic noise pollution across the continental USA and citizen-science data on bird sightings in the breeding season (eBird; Sullivan et al., 2014) to compute the mean exposure of several avian species to noise pollution. Klingbeil et al. (2020) reported that the peak sound frequency of song did not predict how much each species is associated with noise pollution and that species with more complex song were more exposed to noise pollution.

Two issues prevent these new results to from being clearly related to the noise filter hypothesis. First, the cross-species association between exposure to noise and song complexity is of ambiguous interpretation and might, in fact, support the noise filter hypothesis. The metric of song complexity used to generate this result was the standard deviation of peak sound frequency, computed across parcels of song detected by a machine-learning algorithm (from Pearse et al., 2018). As discussed by Mikula, Petrusková, and Albrecht (2018), this metric does not appear to capture the conventional meaning of song complexity, related to the diversity of syllables in the song. A larger standard deviation of sound frequency might indicate use of a wider frequency bandwidth rather than greater diversity of sounds. If that is the case, the association with exposure to noise found by Klingbeil et al. (2020) would support the noise filter hypothesis because, all else being equal, species using larger frequency bandwidths should be less masked by low-frequency anthropogenic noise. Second, detecting a relationship between song frequency and tolerance to noisy environments might require controlling for confounding factors. For example, an association between song frequency and regular occurrence in cities could be shown only when controlling for additional species traits (Cardoso, 2014), most importantly body size (Cardoso et al., 2018).

To clarify these issues, we reanalysed the data of Klingbeil et al. (2020) on the strengths of association with noise pollution across North American avian species. Rather than using song peak frequency and its standard deviation from Pearse et al. (2018; covering

64 of the species in the study by Klingbeil et al., 2020), we used data from Cardoso (2010; covering 82 of the species in the study by Klingbeil et al., 2020), which include measurements of song peak frequency, frequency bandwidth and several aspects of song complexity. These data allow multivariate tests of whether it is syllable diversity or wide frequency bandwidth that predicts exposure to noise pollution and, thus, allow disambiguation of whether or not the results of Klingbeil et al. (2020) support the noise filter hypothesis.

2 | METHODS

We used data on mean noise pollution and body mass (log$_{10}$-transformed) for each species from the Supporting Information (Table S1.1) of Klingbeil et al. (2020), and data on song peak frequency, frequency bandwidth, mean song duration, mean duration of syllables and between-syllable intervals, the proportion of repeated syllables in the song, and typical vegetation density of habitats (1 = open, 2 and 3 = semi-closed with low or high vegetation, respectively, and 4 = forested) from the Supporting Information (Table S1) of Cardoso (2010). We refer to the original articles for detailed methods. There are 82 species common to these two datasets (Supporting Information Appendix S1, Table S1.1).

Following Klingbeil et al. (2020), we based phylogenetic analyses on 100 random trees from www.Birdtree.org (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012), constructed on the backbone tree of Hackett et al. (2008). We ran phylogenetic generalized least squares (PGLS) regressions (Pagel, 1999) using the pgls function in the R package caper (v.1.0.1; Orme et al., 2018) and estimating λ to adjust the phylogenetic correction in the models (Freckleton, Harvey, & Pagel, 2002). We report Akaike information criterion (AIC)-weighted model-averaged results (Garamszegi & Mundry, 2014) across the 100 trees.

To test whether frequency bandwidth predicts exposure of the different species to noise, while accounting for song complexity, we first computed syllable diversity as the number of syllables per song (i.e., mean song duration/mean syllable plus interval durations) multiplied by the proportion of non-repeated syllables (i.e., one minus the proportion of repeated syllables). We then ran a PGLS multiple regression model of noise pollution on song frequency bandwidth and on the above metric of syllable diversity. Log$_{10}$ body mass, vegetation density of habitats and song peak frequency were also included as predictors, to account for confounding effects of body size and habitat type and to confirm whether peak song frequency predicts exposure to noise pollution. To aid in interpretation of the results, we also report the phylogenetic signal (λ) for each individual trait and, as post hoc analyses, univariate PGLS regressions of noise pollution on each predictor.

TABLE 1 Phylogenetic generalized least squares regressions of exposure to noise pollution on predictor traits across 82 North American passerine species

Predictor	Multiple PGLS regression	Univariate PGLS regressions
Frequency bandwidth λ = .82	β_{st} = .32 (***p* = .002**)	.41 (***p* < .001**)
Syllable diversity λ = .03	−.07 (*p* = .45)	.04 (*p* = .73)
Peak song frequency λ = .63	.08 (*p* = .47)	.08 (*p* = .46)
Log$_{10}$ body mass λ = 1	.18 (*p* = .10)	.28 (***p* = .01**)
Vegetation density λ = .38	−.31 (***p* = .003**)	−.45 (***p* < .001**)
Model λ	.003	< .001 in all cases

Abbreviations: PGLS, phylogenetic generalized least squares; β_{st}, standardized regression coefficient or, in the case of the multiple PGLS model, partial standardized regression coefficient; λ, a measure of phylogenetic signal of traits or of trait relationships in PGLS models. *p*-values < .05 are indicated in bold.

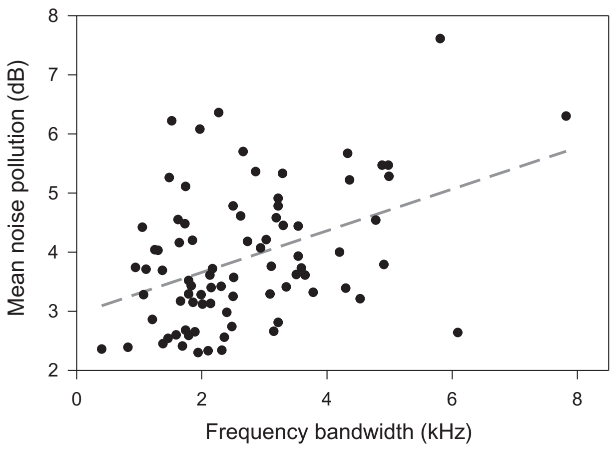

FIGURE 1 Association between mean anthropogenic noise pollution and song frequency bandwidth across 82 North American passerine species (black dots). The regression line is for illustration only, because analyses control for phylogeny and covariates (see Table 1)

3 | RESULTS

The degree of exposure to noise pollution had very low phylogenetic signal (λ < .01) across the 82 species analysed here, which explains why the phylogenetic signal was also low in all PGLS models. Phylogenetic signal in the other traits ranged from very high (body mass) to very low (syllable diversity; Table 1).

The PGLS multiple regression model showed that singing with wider frequency bandwidth, rather than singing with diverse syllables, predicts species exposure to noise pollution (effect of frequency bandwidth: partial standardized regression coefficient [partial β_{st}], = .32, *p* = .002; Figure 1; effect of syllable diversity: partial β_{st} = −.07, *p* = .45). For the remaining predictors in this model, peak sound frequency of song (partial β_{st}, = .08, *p* = .47) and body size (partial β_{st}, = .18, *p* = .10) did not predict exposure to noise pollution, and denser vegetation of habitats was associated with less exposure to noise pollution (partial β_{st} = −.31, *p* = .003; first column in Table 1). Figure 1 shows two species in the upper right corner that have very high values of frequency bandwidth and exposure to noise (*Quiscalus mexicanus* and *Sturnus vulgaris*), which could contribute unduly to the association between those two traits, but removing them did not change results appreciably (Supporting Information Appendix S1, Table S1.2).

Results from univariate PGLS regressions of exposure to noise pollution on each predictor (second column in Table 1) agreed with those from the earlier multivariate model, with the exception of body size. There was a significant association of body size with exposure to noise in the univariate analysis, which appears artefactual because it disappears when controlling for the stronger effects of frequency bandwidth and vegetation density (Table 1).

4 | DISCUSSION

The analyses shown here clarify that using a larger frequency bandwidth, rather than having diverse syllables in songs, predicts exposure to noise pollution across North American passerine species, whereas inhabiting more vegetated habitats is associated with less exposure to anthropogenic noise pollution. These results are robust to controlling for body size and peak frequency of songs. The strength of the association between frequency bandwidth and exposure to noise was commensurate with that of the negative association between vegetation density and noise pollution.

Using a large frequency bandwidth should make parts of the song less masked by noise pollution, because the amplitude of anthropogenic noise gradually decreases towards higher frequencies (e.g., noise power spectra in the studies by Curry et al. [2018], Damsky and Gall [2017], Hu and Cardoso [2010]). Therefore, all else being equal (e.g., identical peak frequency of songs), species using a larger frequency bandwidth spread more sound energy to higher frequencies that are less masked by noise pollution and where acoustic signals can be detected farther. Note that, at the within-species level, augmenting frequency bandwidth should not be an efficient way of overcoming low-frequency noise because it spreads sound energy both to higher frequencies that are less masked, but also to lower frequencies that are more masked. In fact, birds living with anthropogenic noise are often reported to have narrower frequency bandwidths than conspecifics in non-noisy environments, owing to the use of higher minimum frequencies (e.g., Hu & Cardoso, 2010; Job, Kohler, & Gill, 2016; Redondo, Barrantes, & Sandoval, 2013; Slabbekoorn & Boer-Visser, 2006; Walters, Guralnick, Kleist, & Robinson, 2019; Wood & Yezerinac, 2006). At the between-species level, however, where there are larger differences in frequency ranges, the higher maximum frequencies associated with larger frequency bandwidths could be beneficial for long-range communication.

Klingbeil et al. (2020) reported that species with a higher standard deviation of sound frequency (computed from automatically detected parcels of song; Pearse et al., 2018) are more exposed to noise pollution, and interpreted this as indicating that song complexity facilitates tolerance to noise-polluted environments. Although Pearse et al. (2018) proposed that the standard deviation of frequency could be a metric of song complexity, this has been criticized because the standard deviation of frequency is not correlated with syllable or song repertoire sizes across species (Mikula et al., 2018). Instead, the standard deviation of frequency can be large in simple songs, with few syllables spreading over different frequencies. Complexity is an ill-defined term in the birdsong literature (Benedict & Najar, 2019), but discussions of song complexity, including those by Pearse et al. (2018) and Klingbeil et al. (2020), generally centre on the idea of using diverse sounds. As discussed by Klingbeil et al. (2020), it is unclear by what mechanism song complexity would facilitate tolerance to anthropogenic noise. A large frequency bandwidth, in contrast, is predicted to make parts of the song less masked by anthropogenic noise, and thus help in tolerating noise pollution.

The analyses presented here also confirmed the original result of Klingbeil et al. (2020) that mean exposure to noise pollution is not predicted by the peak song frequency of each species, even accounting for putative confounding effects of body size (which strongly influences sound frequency; Wallschläger, 1980), vegetation density of habitats (which reduces exposure to noise) and other factors. Unlike this continental-scale comparison, most evidence for noise filtering based on song frequency comes from studies at local scales, comparing population densities in quieter and noisier sites, and finding that species with higher frequency songs are generally more resilient to decreasing density in noisy sites (review and meta-analysis by Francis [2015]). Klingbeil et al. (2020) discuss reasons why comparisons at large geographical scales might have more difficulty in testing the noise filter hypothesis, such as limitations controlling for landscape correlates of noise pollution. Nonetheless, the continental-scale analyses by Klingbeil et al. (2020) and here did find one pattern supporting the noise filter hypothesis: species using larger frequency bandwidths are more exposed to noise pollution. Together, these results suggests that, rather than having the entirety of song little masked by noise pollution (i.e., having a higher minimum song frequency) or the most important frequencies of song little masked (i.e., having a higher peak song frequency), tolerance to noise pollution might depend mostly on having some parts of the song little masked (i.e., having higher maximum song frequency, which happens in species with large frequency bandwidths). The latter, having the higher frequencies of song little masked by anthropogenic noise, might suffice to prevent the songs from going entirely unnoticed at long distances.

Work on the noise filter hypothesis has focused on either the minimum or the peak frequencies of vocalizations. Although the minimum frequency of vocalizations are most masked by anthropogenic noise and, within species, most often found to change in urban or noisy environments (e.g., Hu & Cardoso, 2010; Job et al., 2016; Redondo et al., 2013; Slabbekoorn & Boer-Visser, 2006; Walters et al., 2019; Wood & Yezerinac, 2006; but see also Mendes, Colino-Rabanal, & Peris, 2017), species differences in minimum frequency do not appear to be the best acoustic predictor of noise tolerance. For example, bird species occurring in cities were found to have, on average, higher peak frequencies but not higher minimum frequencies than closely related species not described as regularly inhabiting urban habitats (Hu & Cardoso, 2009). The effects of using a large frequency bandwidth, particularly if encompassing higher maximum frequencies, has not been given attention in research on noise tolerance. The results provided by Klingbeil et al. (2020) and here suggest, for the first time, that this might be a key trait of animal vocalizations determining species tolerance to noise pollution.

KEYWORDS

anthropogenic noise, birdsong, habitat types, noise filter hypothesis, song complexity, song frequency bandwidth

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DATA AVAILABILITY STATEMENT

This study used data in the Supporting Information (Table S1.1) of Klingbeil et al. (2020) and the Supporting Information (Table S1) of Cardoso (2010).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.