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Geographical associations with anthropogenic noise pollution for North American breeding birds

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Abstract

Aim: Anthropogenic noise pollution (ANP) is a globally invasive phenomenon impacting natural systems, but most research has occurred at local scales with few species. We investigated continental-scale breeding season associations with ANP for 322 bird species to test whether small-scale predictions related to breeding habitat, migratory behaviour, body mass and vocal traits are consistent at broad spatial extents for an extensive group of species.

Location: Conterminous USA.

Time period: 2004–2011.

Major taxa studied: North American breeding birds.

Methods: We calculated, for each species, the association between the breeding season and ANP, using spatially explicit estimates of ANP from the National Park Service and weekly estimates of probabilities of occurrence based on observations from the eBird citizen-science database. We evaluated how the association of the breeding season for each species with ANP was related to expectations based on size, migratory behaviour and breeding habitat. For a subset of species, we used vocal trait data for song duration, pitch and complexity to evaluate hypotheses from the birdsong literature related to habitat complexity and sensitivity to ANP.

Results: Species that breed predominantly in anthropogenic environments were associated with twice the level of ANP (~7.4 dB) as species breeding in forested habitats (~3.2 dB). However, we did not find evidence to suggest that birds with higher-pitched songs are more likely to be found in areas with higher levels of ANP. Residents and migratory species did not differ in associations with ANP, but songs were less complex among forest-breeding species than non-forest-breeding species and increased in complexity with increasing ANP.

Main conclusions: Anthropogenic noise pollution is an important factor associated with breeding distributions of bird species in North America. Vocal traits could be useful to understand factors that affect sensitivity to ANP and to predict the potential impact of ANP, although future studies should aim to understand how and why patterns differ across spatial scales.

KEYWORDS

avian, birdsong, body mass, distributions, eBird, life history, noise pollution, North America, vocalization

1 | INTRODUCTION

Human activities have altered the majority of Earth's natural land cover (Ellis, 2011). There remains an urgent need to understand how these activities have affected biodiversity and what traits make species more or less vulnerable to population declines. Anthropogenic noise pollution (ANP) is now ubiquitous and accompanies nearly all human-induced environmental changes, from urbanization and transportation networks to industrial agriculture and resource extraction. Anthropogenic noise pollution has the potential to alter habitat quality and degrade natural acoustic conditions, raising concerns about the impact of ANP on the behaviour and distributions of species (Barber, Crooks, & Fristrup, 2010; Bayne, Habib, & Boutin, 2008; Buxton et al., 2017; Francis, Ortega, & Cruz, 2009; Shannon et al., 2016).

Birds have played a leading role in ANP research (Shannon et al., 2016). In particular, the reliance of birds on vocal communication for mating and territory defense (Slabbekoorn & Ripmeester, 2008; Warrington, Curry, Antze, & Koper, 2018), predator avoidance (Damsky & Gall, 2017) and migratory flight (Farnsworth, 2005; Hamilton, 1962) makes them especially sensitive to ANP (Francis, 2015; Shannon et al., 2016). Much of our understanding about how birds are affected by ANP is from short-term behavioural work that has investigated whether birds alter acoustic signals in response to various types of ANP (e.g., Brumm & Naguib, 2009; Gross, Pasinelli, & Kunc, 2010; Roca et al., 2016) or studies at local scales that have investigated whether birds persist in areas exposed to chronic or high levels of ANP (Bayne et al., 2008; Francis et al., 2009; Francis, Paritsis, Ortega, & Cruz, 2011, Francis, Kleist, Ortega, & Alexander, 2012). Based on these studies, we can conclude that many of the investigated bird species avoid, decline or alter their behaviour in high-ANP environments (Shannon et al., 2016). Nevertheless, the intensity of ANP is increasing globally, and the macroecological consequences for community structure and ecosystem function remain largely unknown. Currently, > 88% of the conterminous USA (CONUS) experiences elevated ANP levels (Figure 1; Mennitt, Fristrup, Sherrill, & Nelson, 2013; Mennitt, Sherrill, & Fristrup, 2014), necessitating an understanding of how ANP might influence the geographical distribution of birds.

We evaluated continental-scale breeding season occurrence associations with ANP for 322 bird species in the CONUS based on observations from the eBird citizen-science database (Sullivan et al., 2014). To identify whether life-history characteristics or vocal traits can help us to predict sensitivity to ANP, we evaluated relationships as a function of breeding habitat affinity, migratory behaviour, body mass and vocal traits. We selected vocal traits that quantify the pitch of the loudest note (peak frequency), song complexity (*SD* of frequency; number of syllable types) and song duration. These are common metrics that facilitate direct comparison among species (Francis, 2015; Morton, 1975; Pearse et al., 2018), enabling us to make informed predictions on how variation in vocal traits might be related to life history and ANP. For example, dense vegetation found in forests limits the transmission of high-frequency sounds more than low-frequency sounds, whereas ANP is dominated by low-frequency sounds (Barber et al., 2010; Morton, 1975; Ryan & Brenowitz, 1985; Slabbekoorn & Peet, 2003). Additionally, previous research has identified a negative relationship between bird size and song pitch (Cardoso, 2010; Francis, Ortega, & Cruz, 2011; Pearse et al., 2018; Ryan & Brenowitz, 1985). Song complexity has also been found to differ as a function of habitat complexity (Boncoraglio & Saino, 2007; Pearse et al., 2018; Tobias et al., 2010; Weir & Wheatcroft, 2011), although there is evidence for multiple relationships. Lastly, theory suggests that redundancy or the duration of songs should improve communication in noisy environments, and bird species with longer or more repetitive vocalizations might be less sensitive to ANP (Bradbury & Vehrencamp, 2011; Francis, 2015).

Based on these considerations, we developed several predictions on how the breeding distribution of bird species in the CONUS is likely to be associated with ANP. Independent of ANP, we expect bird species that breed in more complex habitats where sound transmission of high frequencies is less effective (e.g., forests) to be larger and have lower-pitched songs, and we expect bird species that breed in less complex habitats where sound transmission of high frequencies is more effective (e.g., grassland) to be smaller and have higher-pitched songs. Within the context of ANP, we expect bird species with lower-pitched songs to be less common in areas with elevated ANP, and species with higher-pitched songs to maintain associations with areas of elevated ANP. Following from the idea that simple and repetitive vocalizations are likely to be more successful in noisy environments, we expect song duration to be positively associated with ANP, whereas song complexity would probably have a negative association with ANP. Lastly, given recent evidence that migratory species are more likely to have specialized breeding habitat associations than residents (Martin & Fahrig, 2018), we expect residents to be associated with a greater range of ANP, and thus a higher average level of ANP than migratory species.

Local studies confirm that birds alter their distributions in response to the presence of ANP (McClure, Ware, Carlisle, Kaltenecker, & Barber, 2013), and traits can be used to identify sensitivity to ANP for some species (Francis, 2015). At broad spatial extents, extensive overlap between ANP and protected areas that support a wide range of endangered species has already been identified (Buxton et al., 2017). Evidence supporting predictions from local studies at broad spatial extents with an extensive group of species would enable a better consideration of ANP as a global change process, expanding

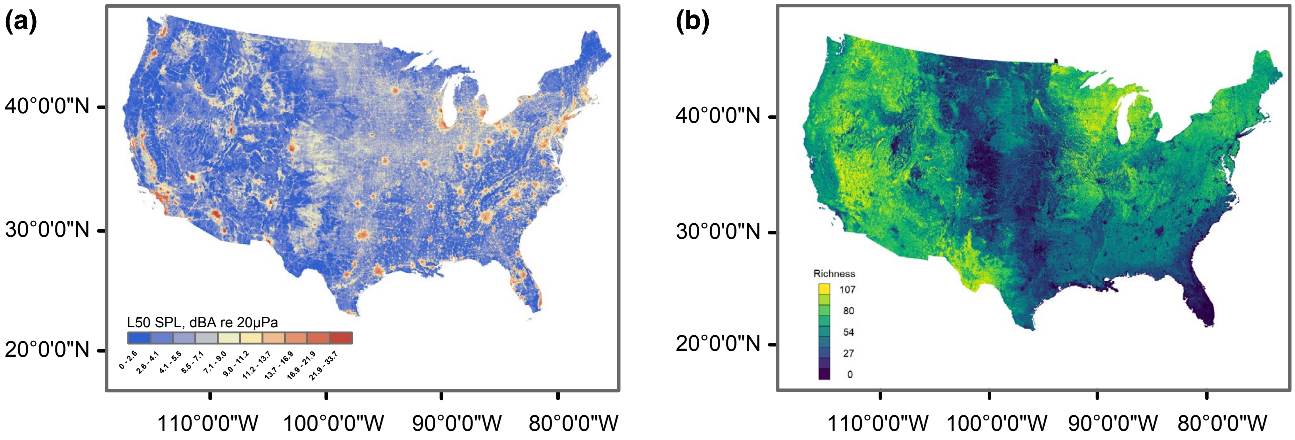

FIGURE 1 (a) Anthropogenic noise pollution predicted by a geospatial sound model and depicted as A-weighted L_{50} sound pressure levels (SPL) within the conterminous USA. A-weighting is applied to instrument-measured sound levels in an effort to account for the relative loudness perceived by the human ear and LA_{50} represents the A-weighted sound pressure level that is exceeded half of the time during a typical summer daytime hour during the period from 2000 to 2014 (after Mennitt et al., 2013, 2014). (b) Species richness of breeding birds within the conterminous USA derived from weekly estimates of probability of occurrence for 322 species (see Supporting Information Appendix S1, Table S.1) summarized over the period from the beginning of June to the beginning of August. See Methods for additional details [Colour figure can be viewed at wileyonlinelibrary.com]

the context of our understanding of the broad-scale implications of global change for species and ecosystems, providing a pathway for inclusion into regional conservation planning.

2 | METHODS

2.1 | Anthropogenic noise pollution

We generated spatially explicit estimates of ANP from georeferenced maps of sound levels across the CONUS developed as part of the National Park Service Natural Sounds and Night Skies and Inventory and Monitoring Divisions (Mennitt et al., 2013, 2014). Maps were derived from geospatial sound models at a spatial resolution of 270 m. Random forests (Breiman, 2001) were used to analyse the relationship between > 1.5 million hours of sound measurements from 492 geographically unique sites distributed across the CONUS and variables that are known to influence acoustic propagation, such as topography, climate, land cover, hydrology, anthropogenic activity and time (Mennitt & Fristrup, 2016). Given that temporal and seasonal variation in the acoustic environment exists, sound models projected the median A-weighted sound pressure levels re 20 μPa (L_{A50}) for an average summer day, which overlaps with the breeding season of many North American bird species. The L_{A50} represents the A-weighted sound pressure level that is exceeded half of the time during a typical summer daytime hour during the period from 2000 to 2014. The L_{A50} statistic is less sensitive to infrequent loud events than other common sound pressure level statistics (e.g., L_{A10} or L_{Aeq}), emphasizing persistent long-term trends. From the L_{A50} statistic, a model of natural sound pressure level was estimated by systematically minimizing contributions from all anthropogenic model inputs, leaving only biotic and abiotic sources of sound (Mennitt et al., 2013, 2014). Our estimate of ANP is the difference between the predicted existing and natural sound pressure levels (i.e., the amount that anthropogenic noise increases sound above natural levels) and is expressed in decibels (dB). Georeferenced maps of existing, natural and anthropogenic sound pressure levels are available from the National Park Service (https://irma.nps.gov/DataStore/Reference/Profile/2217356).

2.2 | Probability of occurrence for terrestrial bird species

We used spatio-temporal exploratory models (STEM; Fink et al., 2010) to estimate the weekly probability of occurrence of 443 bird species using observations from the eBird citizen-science database (Sullivan et al., 2014) compiled during the period 2004–2011. For the STEM analysis, eBird data were limited to stationary and travelling counts (≤ 8.1 km) with local start times between 05:00 and 20:00 hr and counts that were < 3 hr in duration. STEM uses landscape (land cover, elevation), temporal (year, day of year, time of day), location (latitude and longitude) and effort information (duration, distance, number of observers) to generate estimates of probability of occurrence. STEM uses an ensemble of randomized overlapping local models applied across a restricted geographical and temporal extent (Fink et al., 2010) to discern associations between observed patterns of bird occurrence (eBird data) and local land-cover characteristics (Fry et al., 2011). For each species, a separate STEM model was fitted, and probabilities of occurrence of species, corrected for variation in detection rates, were estimated, with one daily estimate calculated per week for all 52 weeks of a calendar year. These estimates represent the probability of observing a species by a single typical eBird participant who searches from 07:00 to 08:00 hr while travelling 1 km. See Fink et al. (2010) for additional details on the STEM procedure.

We reduced the 443 species to 322 for analysis (see Supporting Information, Appendix S1, Table S1.1) by eliminating species that do not breed in the CONUS or those that have only a small fraction of their breeding range in the CONUS. Additionally, we eliminated hummingbirds, aquatic and coastal species because they may interact with sound in a different manner from other terrestrial species, in addition to species not included in a recent global phylogeny of birds (i.e., Jetz, Thomas, Joy, Hartmann, & Mooers, 2012; Jetz et al., 2014). The weekly estimates of the probability of occurrence for each of the 322 species were rendered at 993,688 points at a spatial resolution of *c*. 3 km × 3 km within the CONUS using a geographically stratified random design (SRD). Using the method of La Sorte et al. (2014), we considered SRD points with very low probabilities of occurrence to be unoccupied. This was done for each species, for each week, by calculating the occupancy threshold as the 80th percentile of the non-zero occurrence probabilities. If the 80% quantile was < .0175, our minimum probability threshold, the threshold was set to .0175.

2.3 | Analysis

We summarized weekly associations with ANP for each of the 322 species by first extracting the ANP values for each of the 993,688 SRD points based on the 270 m ANP grid cell that the points intersected. We then calculated the weighted average ANP for each species and week using the probability of occurrence of the species at the SRD points as a weighting factor. We then calculated, for each species, the association of breeding season with ANP, by averaging across a 9-week period from the beginning of June to the beginning of August (weeks 23–31) centred on the North American breeding season. We estimated species richness within the CONUS during the breeding season for the 322 species by summing across the SRD points where the probabilities of occurrence greater than zero for each species were converted to one.

We used a set of phylogenetic comparative analyses to determine how species' breeding season associations with ANP were related to mean body mass (Dunning, 2007), and whether it differed among species based on migratory behaviour (Neotropical migrant, temperate migrant and resident) or breeding habitat affinity (see Supporting Information Appendix S1, Table S1.1). Information on migratory behaviour and breeding habitat affinity were acquired from the Birds of North America (https://birdsna.org/; Rodewald, 2015). We classified breeding habitat affinity into five categories: (a) forest = forest/woodland; (b) open = grassland/desert/scrub; (c) mixed = shrub/forest edge/secondary forest/ecotones; (d) human = urban/introduced species; and (e) generalist = forest/open/mixed/human. We evaluated whether differences in association with ANP were present among species based on migratory and habitat classifications with separate one-way phylogenetic ANOVA using the *phylANOVA* function in *phytools* v.0.6-99, followed by phylogenetic post hoc *t* tests (with Holm sequential Bonferroni correction for multiple groups) based on 10,000 simulations (Revell, 2012) in R v.3.6.0 (R Core Team, 2019). We used phylogenetic generalized least squares regressions with the *pgls* function in the *caper* R package v.1.0.1 (Orme et al., 2018) to assess relationships between $\log_{10}$-transformed body mass with ANP, using the maximum likelihood estimate of Pagel's λ (Pagel, 1999) to correct for phylogenetic non-independence during model fitting. To account for uncertainty in the phylogeny, each analysis was run over a random sample of 100 phylogenetic trees taken from the posterior distribution of the "Hackett All Species" global phylogeny of birds (birdtree.org; Jetz et al., 2012, 2014). We report the mean and *SE* for values of all model coefficients across these phylogenies.

We acquired vocal trait information for a total of 105 unique species. We used estimates of song duration, peak frequency and the *SD* of frequency from Pearse et al. (2018) for 64 passerine species (28 forest and 36 non-forest) and estimates of the number of syllable types from Weir and Wheatcroft (2011) for 57 passerine species (30 forest and 27 non-forest). We used vocal trait data to evaluate differences in song duration, song pitch (peak frequency) and song complexity (*SD* of frequency; number of syllable types) based on body mass and ANP using phylogenetic generalized least squares regression, accounting for uncertainty in the phylogeny as described above. Owing to small sample sizes, we compared differences in song duration, pitch and complexity between forest-breeding bird species and all other species using phylogenetic ANOVA. Song duration is the length (in seconds) of the average male song available from the Xeno-Canto database of birdsongs (http://www.xeno-canto.org/) classified as "A" quality, with confirmed visualization of the bird and no other bird species occurring in the recording (for full details on song download, quality and measurement, see Pearse et al., 2018). We summarized peak frequency, the frequency at which the amplitude was the highest, to characterize song pitch because it is less sensitive to background noise than mean frequency (Pearse et al., 2018). To estimate song complexity, we used the *SD* of the frequency and the number of distinct types of syllables per song for each species. The *SD* of the frequency has recently been proposed as a measure of song complexity, with the idea that it will be larger for songs with more unique notes or elements, providing a basic measure that is readily comparable among species (Pearse et al., 2018). The number of syllable types per song is an established and biologically relevant estimate of song complexity (Catchpole & Slater, 2008), where songs with many syllable types are considered complex, whereas those with few syllable types are considered simple (Mikula, Petrusková, & Albrecht, 2018; Weir & Wheatcroft, 2011). We averaged each metric across all songs for a species from raw data provided by the authors, excluding any records that were >1 min in duration, for consistency with previous approaches. We used nonparametric correlations to determine whether the vocal traits were able to identify independent aspects of birdsong among species.

3 | RESULTS

Anthropogenic noise pollution within the CONUS was greatest within urban centres (range = 0–33.7 dB; Figure 1a). Breeding season species richness for the 322 bird species was lowest within the upper Great Plains and the Florida Peninsula and highest in the

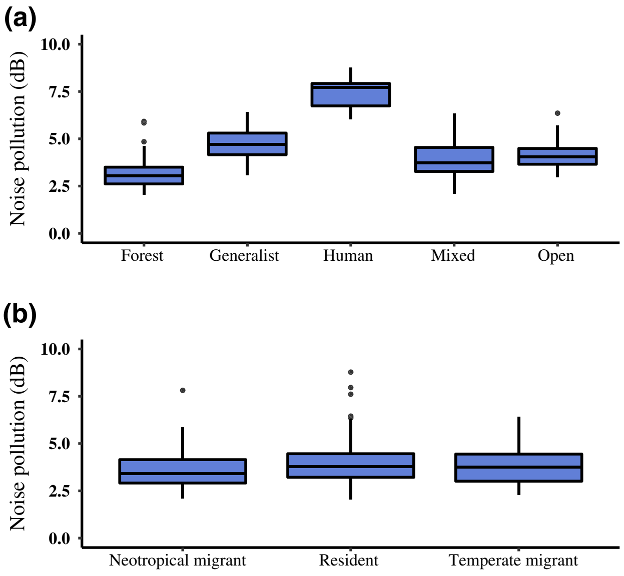

FIGURE 2 Association with anthropogenic noise pollution for 322 bird species (see Supporting Information Appendix S1, Table S.1) within the conterminous USA during the breeding season (see Figure 1) based on: (a) their breeding habitat affinity and (b) migratory behaviour [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Phylogenetic ANOVA examining associations with anthropogenic noise pollution in the conterminous USA for 322 bird species organized by breeding habitat affinity (see Supporting Information Appendix S1, Table S1.1)

Comparison	Mean difference ± 95% CI	*t*	*p*-Value
Generalist–forest	1.59 ± 0.42	11.62	**< .001 ± .00**
Human–forest	4.3 ± 1.65	13.16	**< .001 ± .00**
Mixed–forest	0.75 ± 0.46	5.76	**< .001 ± .00**
Open–forest	0.98 ± 0.25	8.96	**< .001 ± .00**
Human–generalist	2.71 ± 1.62	7.95	**< .001 ± .00**
Mixed–generalist	−0.83 ± 0.56	−5.11	**< .001 ± .00**
Open–generalist	−0.61 ± 0.43	−4.14	**.001 ± .00**
Mixed–human	−3.54 ± 1.62	−10.48	**< .001 ± .00**
Open–human	−3.32 ± 1.65	−10.03	**< .001 ± .00**
Open–mixed	0.23 ± 0.46	1.60	.169 ± .00

Note.: *p*-Values estimated with phylogenetic posthoc *t*-tests (with Holm sequential Bonferroni correction for multiple groups) with 10,000 simulations in *phytools* (Revell, 2012) represent the mean ± *SE* of comparisons from 100 trees drawn at random from the posterior distribution of the time-calibrated phylogeny assuming the Hackett backbone topology (Jetz et al., 2012, 2014). Significant relationships ($p \leq .05$) are shown in bold.

Upper Midwest and the Southwest (Figure 1b). Significant differences in association with ANP were identified among habitat groups (phylANOVA, $F = 75.96 \pm 0.00$, $p < .001 \pm .00$; Figure 2), but not migratory strategy (phylANOVA, $F = 4.34 \pm 0.00$, $p = .498 \pm .00$; Figure 2). Post hoc comparisons indicated that only birds associated with open and mixed habitats were associated with similar amounts of ANP, whereas birds associated with all other habitat types differed in exposure to ANP (Table 1). Forest species were associated with the lowest levels of ANP [3.15 ± 0.12; mean ± 95% confidence interval (CI)], whereas species found primarily in anthropogenic habitats were associated with ANP levels that were twice as high (7.44 ± 0.80; mean ± 95% CI; Supporting Information Appendix S1, Table S1.1). We found no significant relationship between body mass and ANP for the 322 bird species considered ($R^2 = .016$, $p = .78$; see Supporting Information Appendix S1, Table S1.2), although Pagel's λ ($\lambda = .68$) indicated moderate to high phylogenetic signal in the residuals.

For the subset of 64 passerines with estimates of song duration, peak frequency and *SD* of frequency, correlations among these three vocal traits were low (maximum Spearman's $\rho < .108$, $p = .395$), suggesting that these metrics describe independent aspects of birdsong. Correlations between the two estimates of song complexity (*SD* of frequency; number of syllable types) were moderately positive (Spearman's $\rho = .443$, $p = .086$), but based on only 16 species shared between datasets. Significant nonlinear associations between peak frequency and body mass were observed ($R^2 = .465 \pm .00$, $p < .001 \pm .00$), indicating that smaller birds had higher-pitched songs (Figure 4; see Supporting Information Appendix S1, Table S1.2). The *SD* of frequency had a positive relationship with ANP ($R^2 = .097 \pm .00$, $p = .045 \pm .00$; Figure 3; see Supporting Information Appendix S1, Table S1.2), and songs were less complex among forest-breeding than non-forest-breeding species (phylANOVA $F = 12.57 \pm .00$, $p = .013 \pm .00$). Forest-breeding and non-forest-breeding species did not differ significantly in peak frequency (phylANOVA $F = 1.12 \pm .00$, $p = .514 \pm .00$), duration (phylANOVA $F = .60 \pm .00$, $p = .605 \pm .00$) or number of syllable types (phylANOVA $F = 9.54 \pm .00$, $p = .077 \pm .00$; Figure 4; see Supporting Information Appendix S1, Table S1.3).

4 | DISCUSSION

Our findings provide a continental perspective on how bird species that breed in North America are currently associated with ANP during the breeding season. Forest bird species are thought to be more susceptible to effects of ANP because they sing at a lower pitch than species that inhabit open spaces (Boncoraglio & Saino, 2007; Morton, 1975). We observed that species that breed predominantly in anthropogenic environments are associated with twice the level of ANP as species breeding in forested habitats. However, similar to recent work comparing urban-tolerant and non-urban species (Francis et al., 2011), we found no difference in peak song frequency between forest and non-forest species. One possible explanation is that the differences between forest and non-forested acoustic environments are becoming less distinct as fragmentation increases edge habitats, and sound associated with anthropogenic activities expands into less disturbed areas. Species with open, mixed and generalist breeding habitat affinities were associated with intermediate

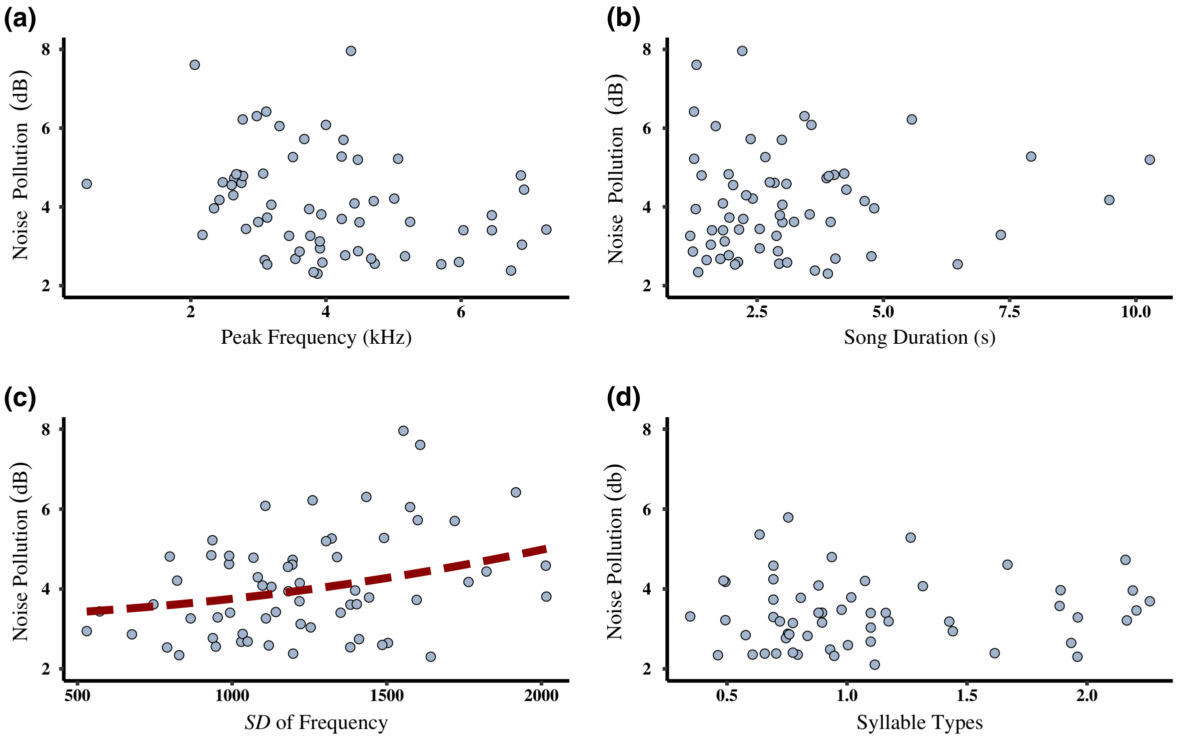

FIGURE 3 Associations between anthropogenic noise pollution and the (a) peak frequency, (b) song duration, (c) *SD* of frequency and (d) number of syllable types of songs for 64 (a–c) and 57 (d) passerine bird species (see Supporting Information Appendix S1, Table S1.1). The fitted line is from phylogenetic generalized least squares regression, in which a significant ($p \leq .05$) relationship was identified (Supporting Information Appendix S1, Table S1.2) [Colour figure can be viewed at wileyonlinelibrary.com]

levels of ANP and, although they differed significantly from both forest and human-dominated environments, levels of ANP were more similar to forested than human environments.

Our results suggest that although species that breed in urban areas continue to experience ANP levels far exceeding natural levels (e.g., ≤ 33.7 dB), these species are no longer subject to completely novel environments because the vast majority of North American bird species are subject to some level of ANP during the breeding season. Much research has documented how urban-adapted species may have greater behavioural, physiological and ecological flexibility than non-urban species (Bonier, Martin, & Wingfield, 2007), enabling them to use higher minimum frequencies in places with higher background noise levels to avoid the concealing effects of urban noise (Gross et al., 2010; Nemeth & Brumm, 2009; Slabbekoorn & Peet, 2003). However, the degree to which this reflects behavioural flexibility or developmental plasticity is unclear (Swaddle et al., 2015). Given the ubiquity of ANP, it is conceivable that selection for higher-frequency songs could begin to manifest as microevolutionary changes in populations (Swaddle et al., 2015) across all habitats, rather than simply being considered an urban phenomenon. This is one of many possible explanations to consider when evaluating why we did not find evidence to support the popular hypothesis that suggests higher-pitched birds are more likely to be found in areas with higher levels of ANP, despite identifying that peak song frequency is negatively related to body size, similar to previous findings (Cardoso, 2010; Francis et al., 2011; Pearse et al., 2018; Ryan & Brenowitz, 1985).

Although many studies evaluating the response of bird species to ANP have focused on elements of pitch or loudness (Francis, 2015; Shannon et al., 2016), understanding how song complexity relates to ANP is also important because it can play a central role in mating success and may function as a sign of mate quality in some species, possibly affecting fitness (Catchpole & Slater, 2008; Mountjoy & Lemon, 1996; Searcy & Nowicki, 2005). Body size is likely to impose physiological constraints on song complexity (Cardoso, 2010; Pearse et al., 2018), but evidence also suggests that environmental constraints (i.e., acoustic adaptation hypothesis; Morton, 1975) may play a considerable role in structuring current communities (Tobias et al., 2010). Our findings indicate that one measure of song complexity was greater in non-forested than forested habitats, and generally increased with increasing ANP but was not significantly related to body size. In contrast, a second measure of song complexity did not differ significantly between forest and non-forest habitats and was unrelated to ANP or body size. Despite these differences, both our complexity metrics describe similar aspects of song complexity (i.e., within-song traits rather than repertoire size), had similar numbers of species used in analyses, defined habitat complexity equivalently (forest versus non-forest) and were moderately associated for the subset of species for which we had estimates of both metrics. It is thought that relationships between song complexity and the environment remain poorly understood because of differences in temporal and spatial scales of analysis and differences in how habitat complexity and song complexity are measured. Consequently,

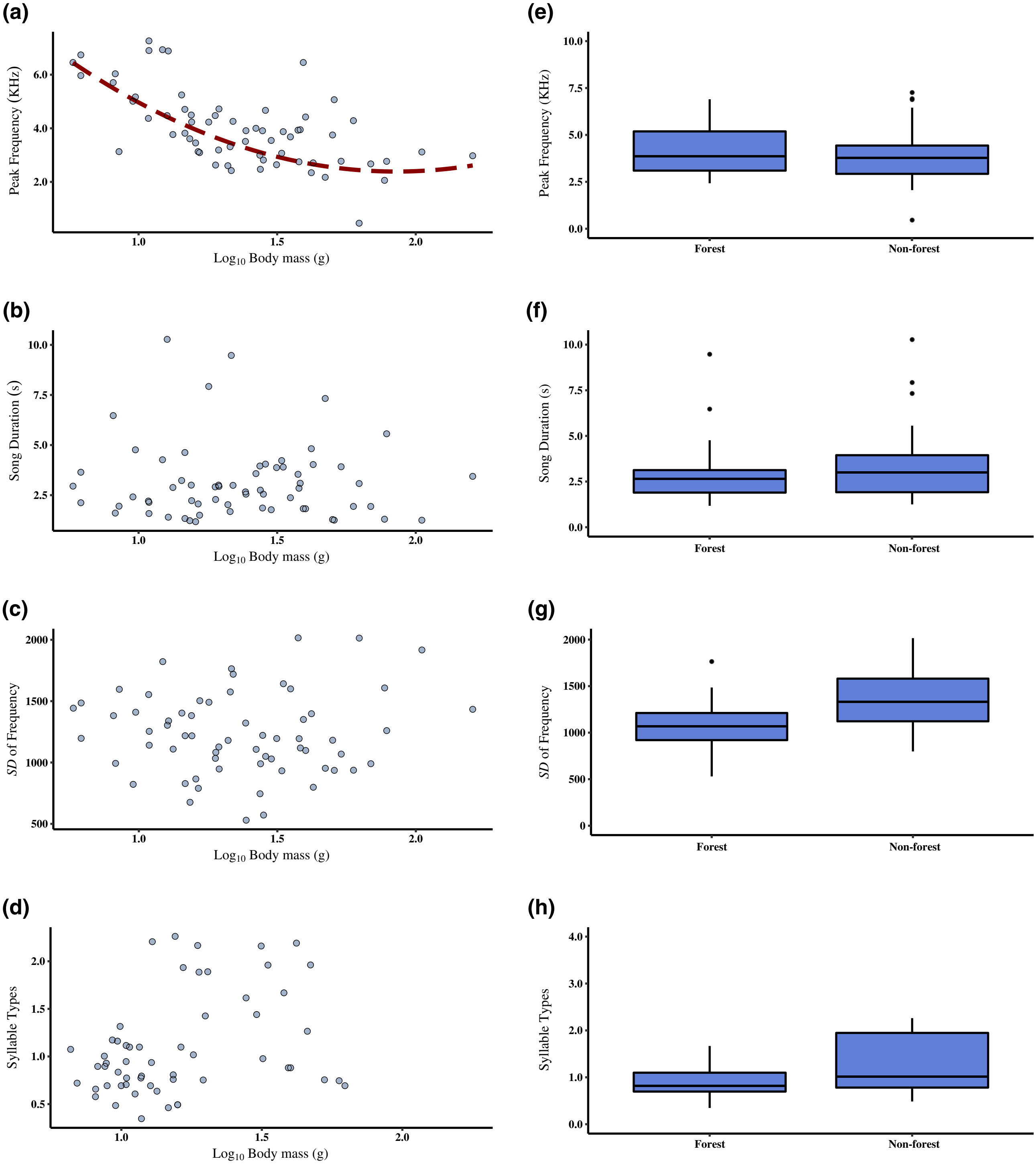

FIGURE 4 Associations between log$_{10}$-transformed body mass and (a) peak frequency, (b) song duration, (c) *SD* of frequency and (d) number of syllable types of songs for 64 (a–c) and 57 (d) passerine bird species (see Supporting Information Appendix S1, Table S1.1). The fitted line is from phylogenetic generalized least squares regression, in which a significant ($p \leq .05$) relationship was identified (Supporting Information Appendix S1, Table S1.2). Difference in (e) peak frequency, (f) song duration, (g) *SD* of frequency and (h) number of syllable types of songs between birds with forest and non-forest breeding habitat affinities (Supporting Information Appendix S1, Table S1.3) [Colour figure can be viewed at wileyonlinelibrary.com]

research has shown that songs increase (Pearse et al., 2018; Tobias et al., 2010) or decrease (Irwin, 2000; Weir & Wheatcroft, 2011) in complexity with increasing habitat complexity, explaining why a meta-analysis of evidence for the acoustic adaptation hypothesis suggests that habitat structure is only a weak predictor of the acoustic properties of bird songs (Boncoraglio & Saino, 2007). Our results suggest that increased attention to the identity of the species evaluated and the metric used to characterize song complexity might lead to a better understanding of the relationships between song complexity and the environment. Alternatively, it has been proposed that song complexity might increase in response to competition for acoustic signal space (Brumm & Naguib, 2009; Pearse et al., 2018). A finding that song complexity increased with increasing ANP could be interpreted as support for competition as a driving factor. Competition for acoustic signal space has historically been viewed through the lens of interspecific competition (e.g., Cardoso & Price, 2010), rather than competition with ANP. Nevertheless, ANP can be a strong selective force on bird songs that can affect minimum frequencies and regional dialects (Luther & Baptista, 2010; Podos & Warren, 2007; Slabbekoorn & Peet, 2003). Given the steady increase in ANP levels over the past few decades, the short generation time of many passerines and the existence of regional dialects that can change over time, differences in song complexity among habitats could be a reflection of changes in the acoustic environments driven by an increase in ANP.

Of the vocal traits we evaluated, song duration was the least informative for understanding the response of species to ANP. Song duration did not differ between forest and non-forest breeding habitats and was unrelated to ANP and body mass. The absence of any strong relationships was somewhat unsurprising, because previous studies have also failed to identify significant relationships (Cardoso, 2010; Francis et al., 2011). In general, we might expect short songs to be less effective in noisy environments because they are more likely to be masked by frequent unpredictable loud noises. However, in areas subject to energy extraction, where chronic noise is likely to maintain a consistent volume, duration is less likely to be important than other characteristics, such as frequency or loudness. Additionally, long songs can be either highly repetitive or contain many unique elements, thus the amount of information susceptible to interference by ANP is likely to differ, complicating interpretations of observed associations.

Migratory bird species face considerable threats worldwide, and long-distance migrants are declining faster than residents and short-distance migrants (Bairlein, 2016). Recent evidence suggests that migratory bird species in North America are associated with more specialized breeding habitat requirements than both partial migrants and resident species (Martin & Fahrig, 2018). A possible explanation is that residents in temperate regions have adapted to seasonal fluctuations in resource availability by becoming habitat generalists, whereas migrants have retained more specialized habitat associations by avoiding seasonal resource declines through migration (Cox, 1985; Holt & Fryxell, 2011). Although this may be true from a perspective of resource availability, residents and migratory species did not differ in association with ANP during the breeding season. Many migratory bird species occur in high numbers in urban areas during spring and, especially, autumn migration (La Sorte, Fink, Buler, Farnsworth, & Cabrera-Cruz, 2017; La Sorte et al., 2014; Zuckerberg, Fink, Sorte, Hochachka, & Kelling, 2016), possibly because of the disorienting effects of light pollution emanating from urban areas during nocturnal migration (La Sorte et al., 2017). Nevertheless, additional work is needed to determine whether sensitivity to ANP is related to behavioural or ecological aspects associated with migration or whether migrants and residents that associate with particular regions of North America are more susceptible to effects of ANP.

Our findings indicate that ANP is an important factor associated with the breeding distributions of bird species in North America, but difficulties remain in predicting the long-term consequences of exposure to ANP and understanding the factors that affect ANP sensitivity. Our results highlight the importance of phylogenetic history in shaping present-day associations of birds and birdsong with ANP and the importance of controlling for phylogenetic non-independence when performing comparative analyses of species. Phylogenetic signal was moderate to high in the residuals of most of our comparisons and in ANP across the phylogeny of 322 species (see Supporting Information Appendix S1, Table S1.2, Figure S1.1). Macroecological studies, such as ours, provide crucial information but suffer from similar shortcomings to other large-scale analyses. For example, our findings fail to capture instances when organisms show little to no response to ANP in terms of broad-scale habitat occupancy, but may experience strong negative impacts in terms of pairing success, number of offspring, physiological stress or other measures of fitness (Francis & Barber, 2013). Likewise, many factors associated with increasing ANP (e.g., habitat fragmentation, susceptibility to predators and light pollution) are likely to influence the distribution and occupancy of species, making it difficult to identify independent effects of ANP at this scale. Moreover, although we were able to identify traits that could be used to understand vulnerability to ANP, our study was limited to assessing relationships between ANP and vocal traits for only 30% of the species for which we had other life-history data. In addition, measurements of vocal traits were summarized from songs recorded in any habitat rather than confined to the dominant breeding habitat of species, limiting the degree to which habitat-specific relationships can be supported.

The growth of citizen-science initiatives, such as eBird (www.ebird.org), where users upload the identity and location of bird observations, and Xeno-Canto (www.xeno-canto.org), where users upload and identify bird vocalizations, have the potential to improve the quality and breadth of existing data and offer insights into questions at previously unexplored spatial scales across many species concurrently, but the semi-structured nature of the data presents its own unique set of challenges for analysis and interpretation. For example, our estimates of the probability of occurrence for 322 bird species across North America are subject to challenges such as the preferential recording of some species over others, variation in search effort that can affect the detectability of species, spatial bias in the search locations selected by participants and variation in observer skill (Bird et al., 2014). As a semi-structured citizen-science project (Kelling et al., 2019), eBird collects essential metadata describing the observation process in addition to recording species observations. This additional information (e.g., the duration searching for birds, search start time, distance travelled while searching) enables analysts to account and control for many of the biases inherent in citizen-science data during analysis (Fink et al., 2010; Johnston et al., 2019; Kelling et al., 2019). The ability to control for these biases with eBird data allows analysts to take advantage of the unique spatial and temporal coverage of these data for individual species and across communities of birds.

Problems associated with ANP will only grow as the Earth is increasingly dominated by human-altered landscapes (Ellis, 2011), especially given that sources of ANP are growing faster than human population size (Barber et al., 2010). Substantial progress has been made over the last few decades, but much remains to be learned about how species are being affected by ANP, how these effects act in combination with other global change processes, and the cumulative effects on ecosystem structure and function. Despite these limitations, evidence is mounting that ANP needs to be integrated into research efforts and management plans if we are to gain an accurate understanding of the broad-scale implications of global change for natural systems.

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DATA ACCESSIBILITY

Georeferenced maps of existing, natural and anthropogenic sound pressure levels are available from the National Park Service (https://irma.nps.gov/DataStore/Reference/Profile/2217356). eBird observational data were freely accessible via DataONE (dataone.org), the Global Biodiversity Information Facility (gbif.org), the Avian Knowledge Network (avianknowledge.net) and VertNet (vertnet.org). A species list of the 322 bird species considered in the study and their life-history traits, body mass, average association with ANP and song characteristics: peak frequency, *SD* of frequency, number of syllable types and song duration, are available in the Supporting Information (Appendix S1).

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SUPPORTING INFORMATION

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

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