The acoustic adaptation hypothesis across terrestrial vertebrates: a meta-analysis

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ABSTRACT

Acoustic communication plays a prominent role in various ecological and evolutionary processes involving social interactions. The shape of acoustic signals is thought to be influenced not only by the interaction between a signaller and a receiver but also by the acoustic characteristics of the environment through which the signal is transmitted, which is the essence of the so-called "acoustic adaptation hypothesis" (AAH). Specifically, the AAH posits that habitat structure affects frequency and temporal parameters of acoustic signals emitted by a signaller depending on their acoustic degradation properties. To date, this hypothesis has received mixed results, with the level of support depending on the taxonomic group under study and the methodology used. We conducted a systematic literature search of empirical studies testing for an effect of vegetation structure on acoustic signalling and assessed the generality of the AAH using a meta-analytic approach based on 371 effect sizes from 75 studies and 57 taxa encompassing birds, mammals and amphibians. Overall, our results do not provide consistent evidence for the AAH, neither in within-species comparisons (suggesting no overall phenotypically plastic response of acoustic signalling to habitat structure) nor in among-species comparisons (suggesting no overall evolutionary response). However, when considering birds only, we found a weak support for the AAH in within-species comparisons, which was mainly driven by studies that measured frequency bandwidth, suggesting that this variable may exhibit a phenotypically plastic response related to habitat. For among-species comparisons in birds, we also found support for the AAH, but this effect was not significant after excluding comparative studies that did not account for phylogenetic non-independence. Collectively, our synthesis does not support a universal role of vegetation structure in the evolution of acoustic communication. We highlight the need for more empirical work on currently under-studied taxa such as amphibians, mammals, and insects. Furthermore, we outline a framework for forthcoming research on the AAH. Specifically, we advocate for a more detailed and quantitative characterization of habitats allowing to identify frequencies with the highest detection probability and to determine if frequencies with greater detection distance are preferentially used. Finally, we stress that research efforts should

focus on signals in which an increased distance of transmission is beneficial to senders and/or receivers.

Key words: acoustic communication, amphibians, bioacoustics, birds, evolution, habitat, mammals, vegetation, vocalizations

I. INTRODUCTION

(1) Acoustic signalling and the effect of multiple selective forces

Acoustic signalling is an essential facet of animal communication, spanning a wide array of species and ecosystems. These signals play a pivotal role in various contexts, including mate attraction, territory defence, predation avoidance (alerting others of a threat), rival intimidation, individual recognition, and social communication (Catchpole & Slater, 2008; Bradbury & Vehrencamp, 2011). Thus, acoustic signals are subject to multiple selective forces imposed on the signaller and receiver that shape them to finely tuned instruments of communication (Wiley & Richards, 1982; Catchpole, 1987; Catchpole & Slater, 2008). These multiple selective forces may act in concert or in opposition, which potentially complicates our understanding of the evolution of acoustic communication (i.e., the adaptive significance of the specific structure of a given signal).

One of the most studied selective forces shaping acoustic signals is the morphology of the signaller. For instance, the size of sound-producing organs is often positively associated with a signaller's body size or mass and has been shown to influence signal frequency in anurans and mammals (Fletcher, 2004; Tonini *et al.*, 2020). Similarly, in birds body size has been found to be negatively correlated with signal minimum frequency and positively with frequency bandwidth (Friis *et al.*, 2022). Thus, when individuals emit sounds, they also convey information about their size such that acoustic cues can serve as honest signals of body condition and reproductive performance, influencing mate choice (McLean, Bishop & Nakagawa, 2012; Welklin *et al.*, 2023). While the production of acoustic signals at high amplitude could attract more mates and give competitive advantages, it involves energetic costs (e.g., Gil & Gahr, 2002; Ophir, Schrader & Gillooly, 2010), to the extent that it may become challenging to produce an optimally designed sound for long-distance transmission. In addition, predators and parasites can use the acoustic signals emitted by their prey as cues to locate them (Ryan, Tuttle & Taft, 1981; Garamszegi & Avilés, 2005), potentially driving the development of signals that minimize their detectability, such as high-frequency pure tones in certain alarm calls to reduce locatability (Klump & Shalter, 1984). In vocal learners such as oscine

passerines, hummingbirds, parrots, humans, elephants, seals, and toothed whales, vocalizations are also shaped by the capability of reproducing heard sounds (Tyack, 2020). This ability might counterbalance other predicted trends in shaping acoustic signals. Likewise, interactions with other animals can shape the acoustic signals in multiple ways, for example by selecting for frequencies that exploit sensory biases to enhance engagement (Cummings & Endler, 2018).

The structure of acoustic signals can also be influenced by the acoustic characteristics of the environment (Chappuis, 1971; Slabbekoorn & Smith, 2002; Derryberry *et al.*, 2018). While propagating from signaller to receiver, signals are subject to several alterations in temporal and frequency parameters. These alterations include reverberation, the delay between the faster waves (direct) and slowest waves (indirect) causing distortion of the sound (Morton, 1975; Wiley & Richards, 1978, 1982), and attenuation, the progressive reduction in amplitude which can be attributed to three main components: (1) geometric attenuation (also known as spreading loss or spherical attenuation); (2) atmospheric attenuation; and (3) habitat attenuation (Embleton, 1996). The latter two components are often collectively referred to as degradation, resulting from scattering, refraction through obstacles, atmospheric absorption, or echoes, with greater effects typically observed for high frequencies (Aylor, 1972; Marten & Marler, 1977). In this context, natural selection is expected to have favoured the evolution of accurate and efficient transmission of acoustic signals intended for long-distance travel allowing for information transfer from signaller to receiver with respect to the constraints imposed by their environment.

(2) The Acoustic Adaptation Hypothesis

The various selective forces imposed by the environment outlined above form the theoretical background of the acoustic adaptation hypothesis (AAH), mainly grounded on the work of Morton (1975) and Hansen (1979) but coined by Rothstein & Fleischer (1987). The AAH argues that the transmission of acoustic signals is affected by the environment offering predictions regarding the optimal shape of acoustic signals to ensure accurate transmission in environments

105 characterized by high degradation, such as densely vegetated habitats (Morton, 1975; Blumenrath &
106 Dabelsteen, 2004). Animals inhabiting such hereafter called 'closed habitats' are expected to have
107 signals of longer duration because this is expected to increase the likelihood of detection and to
108 leverage the amplitude of reverberated sound waves, extending the range of signal propagation
109 (Nemeth *et al.*, 2006). To increase transmission distance in closed habitats, acoustic signals should
110 also have lower repetition rates to minimize interference with reverberated waves (Brown &
111 Handford, 2000; Naguib, 2003) and narrower frequency bandwidths to concentrate energy in
112 frequencies less susceptible to attenuation (Wiley & Richards, 1978). Additionally, animals in closed
113 habitats should be prone to emit acoustic signals at lower frequencies including minimum, mean,
114 maximum, and peak frequency (Chappuis, 1971; Morton, 1975; Marten, Quine & Marler, 1977).
115 The AAH is currently considered as a component of the broader Sensory Drive Hypothesis,
116 which predicts that signals, sensory mechanisms, and microhabitat choice evolve together based on
117 the characteristics of the habitat, ambient noise patterns, the existence of predators and parasites,
118 and various sensory and physiological factors (Endler, 1992; Cummings & Endler, 2018). Several
119 authors have also extended the AAH to a wider framework of environmental adaptation, covering
120 studies on the effect of environmental noise such as tests of the Lombard effect in the context of
121 urbanization (Job, Kohler & Gill, 2016; Zhao *et al.*, 2021). Here, we focus on the AAH in the context of
122 the effect of vegetation structure on acoustic signalling as originally tested by Morton (1975).
123 Playback transmission experiments using either natural or synthetic sounds have been
124 conducted to assess the physical foundations of the AAH (Wiley & Richards, 1978). In addition,
125 comparisons between species and populations inhabiting environments of different vegetation
126 structure have been performed to test the validity of this hypothesis. While studies testing
127 environmental filtering of sound have provided a robust foundation for the AAH (reviewed in Hardt
128 & Benedict, 2021), its influence on animal acoustic signal production remains unclear. In fact,
129 empirical support for the AAH is highly variable, with many studies supporting the hypothesis
130 (Bertelli & Tubaro, 2002; Nicholls & Goldizen, 2006) whereas many others contest its validity (Hylton

& Godard, 2001; Bosch & De la Riva, 2004; Mikula *et al.*, 2020). In addition, Hardt & Benedict (2021) uncovered that animal signals are not better transmitted in a species' habitat compared to environments they are not adapted to, raising further questions about the generality of the AAH.

In a previous meta-analysis limited to birds, Boncoraglio & Saino (2007) compiled 91 effect sizes from 26 studies of within- (including 12 species) and among-species (spanning 3 orders) comparisons to test for an overall effect of habitat structure (open versus closed) on acoustic variables. The authors found support for the AAH in terms of a lower minimum frequency, maximum frequency, peak frequency, and frequency bandwidth in more closed habitats based on a global effect size of Fisher's z = 0.160, 0.182, 0.346, and 0.230, respectively (Boncoraglio & Saino, 2007). Interval duration was the only variable that did not differ between habitats. Since its publication, this study has served as a key reference in support of the AAH in birds. However, Boncoraglio & Saino (2007) relied on a limited sample size and did not include measurements of mean frequency, total duration, or repetition rate in their analyses, despite clear predictions for these three variables within the framework of the AAH. Furthermore, this study did not explicitly control for potential sources of statistical non-independence beyond shared study identity, such as shared phylogenetic history. The lack of control for non-independence among effect sizes can result in inaccurate conclusions, often leading to spurious statistical significance (Nakagawa *et al.*, 2017), and integrating phylogenetic structure into meta-analyses is considered critical to ensure that unbiased results are obtained (Lajeunesse, 2009; Chamberlain *et al.*, 2012).

Although the AAH was initially formulated based on avian studies, there has been a growing trend in testing this hypothesis in other taxonomic groups. Aiming to examine how widespread the impact of vegetation structure on the evolution of acoustic signals actually is in vertebrates, Ey & Fischer (2009) qualitatively reviewed 55 studies on birds, anurans and mammals and concluded that the AAH did not seem to be universally valid across taxa. However, the authors claimed that in birds, minimum frequency and frequency bandwidth appeared to align with the predictions of the AAH,

whereas repetition rate, mean, peak, and maximum frequencies did not, which does not fully correspond to the results obtained by Boncoraglio & Saino (2007).

(3) Assessing the AAH across animals

Despite the large body of research aimed at testing the AAH, it remains unclear to what extent this hypothesis is valid across acoustic variables in a broad range of animal taxa, and whether contrasting findings from previous studies reflect methodological artifacts and/or actual differences among taxa. Our study aims to fill this gap by conducting a meta-analysis of empirical studies having tested the AAH in the context of airborne acoustic signalling in response to vegetation structure. In this regard, we build on the work by Boncoraglio & Saino (2007) and aim at providing a robust and comprehensive meta-analysis. More specifically, our main objective is to address two main questions: (1) Does the AAH hold across different animal taxa and acoustic parameters? and (2) does the AAH support phenotypically plastic and/or evolutionary responses to vegetations structure (inferred from within- and among-species comparisons, respectively)? For these purposes, we compiled 371 effect sizes testing the AAH in animals. We did not have a clear prediction on whether effect sizes should differ between within- and among-species comparisons. However, it seems plausible that effect sizes from among-species comparisons might be weaker, because acoustic parameters likely evolve not only in relation to the habitat itself but also due to other factors such as interspecific variation in mate preferences and/or genetic drift.

II. METHODS

This meta-analysis was pre-registered at the Open Science Framework (OSF; study details available at: https://doi.org/10.17605/OSF.IO/E7JRS). Differences between the pre-registered study design and the eventually implemented approach are mainly due to methodological improvements and are explained in Text S1.

(1) Literature search

We conducted a systematic literature search to obtain an unbiased sample of studies testing for a relationship between vegetation structure and acoustic communication in animals following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses approach (PRISMA; Moher *et al.*, 2009) in combination with the PRISMA-EcoEvo guidelines (O'Dea *et al.*, 2021). We screened the Scopus, the ISI Web of Science Core Collection (Clarivate Analytics), and the Open Access Theses and Dissertations (OATD; https://oatd.org/) databases on 16th December 2021 with the search terms defined as ((("*song" OR "vocal*") OR (("acoustic$" OR "bioacoustic$") AND "call$")) AND ("habitat$" OR "vegetation")) OR "acoustic adaptation". These searches yielded 3300, 3233, and 372 records, respectively. We also considered studies included in previous reviews on related questions (Ey & Fischer, 2009; Hardt & Benedict, 2021) and a previous meta-analysis on birds (Boncoraglio & Saino, 2007), resulting in the addition of 58 studies. Furthermore, we posted a request for unpublished data on the 'evoldir' mailing list (http://life.mcmaster.ca/evoldir.html), the ResearchGate platform (https://www.researchgate.net/), and Twitter, and directly asked colleagues who work on these topics. This resulted in one additional study (Melo *et al*., in prep). Finally, we added one unpublished study on the La Palma population of the Canary Islands Chaffinch (*Fringilla canariensis palmae*; Freitas *et al*., in prep.).

We excluded 45 studies from the OATD search because full texts were not accessible. We also excluded duplicates by following an R workflow adapted from Lagisz (2022) and by manually checking the results of the Zotero deduplication algorithm (Corporation for Digital Scholarship & Roy Rosenzweig Center for History and New Media, 2022). Then, we assigned screening efforts among authors and screened the titles and abstracts of 4558 studies. We selected potentially relevant primary studies using the *metagear* package (Lajeunesse, 2016) based on the following selection criteria:

1. The focus of the empirical study was on non-human animals (excluding domesticated species), for which acoustic signals are transmitted through the air. We did not consider

studies focusing on echolocation because it is used for orientation in space and/or to locate items rather than for communication. For syntheses on the effect of habitat structure on echolocation, see Ey & Fischer (2009). We also excluded studies on aquatic habitats due to the different acoustic properties and difficulties in defining habitat structure based on underwater vegetation.

2. At least one temporal or frequency parameter for which the AAH predicts an effect was measured for adult individuals of the same species (within-species comparisons) or multiple species (among-species comparisons) across different habitat types. Studies testing for differences among subspecies were considered as among-species comparisons. Studies that did not replicate habitat type within species or subspecies were excluded (as a conservative approach to mitigate the possibility of testing subspecies differences rather than differences due to habitat). For example, a study was excluded if testing for acoustic signal differences between a subspecies inhabiting one location of habitat type A and another subspecies in another location of habitat type B.
3. Habitat was described along a continuous gradient or based on a categorical classification of vegetation structure (from open to closed habitats). If the categorical classification of the habitat was done in more than the two categories, we pooled different habitat types into two categories: ‘open’ and ‘closed’ (e.g., grassland, open field, and meadow grouped in ‘open habitat’). We did not include studies examining differences between urban and rural habitats.
4. The study was written in English, French, German, Portuguese, or Spanish according to the languages that the authors were able to understand.
5. The study reported sufficient information to compute effect sizes (e.g., sample size, test-statistic, means with estimates of uncertainty).

During the title and abstract screening stage, we excluded 4237 studies because they did not fit at least one of the requirements listed above. Afterwards, we carried out a full-text screening of

the remaining 321 studies. During this stage we excluded 246 studies because they: (i) did not test the influence of vegetation structure on acoustic variables (N = 116), (ii) used habitat types that could not be classified as 'open' or 'closed' (N = 17), (iii) did not replicate habitat type (N = 5), (iv) focused on echolocation (N = 23), (v) focused on playback/transmission experiments (N = 15), (vi) focused on the effect on urbanization (N = 4), (vii) used acoustic variables for which the AAH does not generate predictions (N = 3), (viii) did not report sufficient data (N = 27; i.e., multivariate statistics not providing raw data, missing key data required to compute an effect size even after contacting the authors), (ix) represented reviews or non-empirical studies (N = 14), (x) were inaccessible (N = 12), (xi) were written in other languages (N = 4), or (xii) represented duplicates (N = 6; 5 of which represented theses that are already covered by other primary studies). The final dataset included 75 primary studies (see Fig. 1 for the PRISMA diagram and Table S1 for a reference list of all primary studies).

(2) Data collection

We extracted means, measures of variance (standard deviation or standard error) and sample sizes, correlation coefficients and sample sizes, or the statistical test value and degrees of freedom reported for the relationship among acoustic variables and vegetation structure from the text, tables, figures or supplementary files. We used the R package *juicr* version 0.1 (Lajeunesse, 2021) to extract summary statistics from figures. From five studies that used multivariate statistics (such as principal components analysis), we reanalysed the raw data if published together with the article or provided by the authors (N = 2), and corrected also for the phylogeny in cases in which phylogenetic data was provided (N = 1).

All comparisons included in our meta-analysis followed a descriptive approach, meaning that none of the primary studies manipulated the habitat experimentally to test for a causal effect on acoustic variables. Thus, we used the Pearson correlation coefficient (r) as an effect size to synthesize the findings of primary studies. We converted test statistics provided in the primary

studies into *r* and estimated its sampling variance (*Vr*) using formulas and guidelines reported in Lajeunesse *et al*. (2013) and using the R package *esc* version 0.5.1 (Lüdecke, 2019). To improve transparency and allow for reproducibility of data extraction, we report the method used to compute effect sizes (Table S1) following a framework provided in Ivimey-Cook *et al*. (2023). All effect sizes were assigned to a type of study: within- or among-species comparisons, to allow testing for a phenotypically plastic or an evolutionary response of acoustic signalling to vegetation structure, respectively. We interpreted the support for the AAH in within-species comparisons as suggestive of a phenotypically plastic response rather than adaptive response since we assumed no genetic divergence between the different populations tested.

(3) Moderator variables

Besides the global test for the support of the AAH across animals, we aimed at explaining heterogeneity in effect sizes among studies from a biological and methodological perspective. Specifically, we explored if support for the AAH differed among animal taxa and acoustic variables. If an acoustic variable was measured for parts and for the full signal duration, we extracted both effect sizes separately but assigned them as the same acoustic variable (e.g., song duration and note duration were both considered as duration).

In addition, we tested for four methodological moderators: habitat classification, habitat contrast, body size correction, and phylogeny correction. Firstly, we explored effects of the habitat classification (continuous versus categorical) used in primary studies, i.e., if the studies used a continuous variable or a categorical classification to describe the vegetation structure of the habitat. Secondly, we scored the magnitude of contrast between closed and open habitats (for studies using a categorical classification) that were used in the study (habitat contrast), attributing a ‘0’ when there was a moderate difference in vegetation structure (e.g., temperate broadleaf forest versus tropical rainforest), or a ‘1’ when there was a substantial difference in vegetation structure (e.g., grassland versus forest). Importantly, primary studies investigated various habitat types and used

281 different methods for classifying them. This diversity in habitat classification methods could have
282 contributed to differences in study outcomes (suggested by Hardt & Benedict, 2021). By considering
283 these two moderators, we tried to account for this potential source of heterogeneity among studies.
284 Thirdly, we recorded whether the analyses corrected for body size differences within and/or among
285 species, since this trait is known to be allometrically correlated with the morphology of the sound
286 apparatus, and therefore to affect the production of sound (Pearse *et al.*, 2018). Finally, we recorded
287 whether studies reporting among-species comparisons accounted for phylogenetic non-
288 independence.

289 **(4) Phylogeny**

290 In order to account for phylogenetic non-independence and to quantify the phylogenetic signal (also
291 termed phylogenetic heritability; de Villemereuil & Nakagawa, 2014), we reconstructed a phylogeny
292 of all sampled taxa from studies of within- (Fig. S1) and among-species comparisons (Fig. S2). We
293 used the R package *rotl* (Michonneau, Brown & Winter, 2016) to retrieve the phylogenetic
294 relationships from the Open Tree of Life (opentreeoflife.org/; Hinchliff *et al.*, 2015) and *ape* (Paradis,
295 Claude & Strimmer, 2004) to obtain the branch lengths for each taxon by applying Grafen's method
296 (Grafen, 1989).

297 In analyses of among-species comparisons, the phylogenetic position of some taxonomic
298 groups could not be assessed unequivocally so that we assigned the group in question to a higher
299 taxonomic level. Specifically, we considered Parulinae as Parulidae and Cardinalidae as
300 Passeriformes. Note that some primary studies tested the AAH across higher taxonomic ranks (such
301 as Anura, Aves and Passeriformes), while others tested it across a lower taxonomic rank, which
302 sometimes was nested within the higher ones (artificial pairs, e.g., Anura and Hylidae, Aves and
303 *Corvus*). In such cases, we retrieved pairwise estimates of divergence times for the taxonomic ranks
304 that were not nested from the TimeTree database (http://timetree.org/; Kumar *et al.*, 2017). Then,
305 for the artificial pairs, we attributed a mean estimate between the known divergence time estimates

of the nested pairs and the ones more distantly related. For example, for the pair Anura - Hylidae, we computed the divergence time as the mean between the estimate of Hylidae - *Rhinella* (a genus within Anura) and the estimate of Anura - Felidae, since Felidae is the closest outgroup of Anura in our phylogeny. Then, we computed branch lengths using the methods already specified for the within-species comparison.

(5) Data analyses

All analyses were performed in R 4.2.2 (R Core Team, 2022) through RStudio 1.4.1106 (RStudio Team, 2021), using the packages *metafor* (Viechtbauer, 2010) for the meta-regression models, *brms* (Bürkner, 2017) for models with Bayesian approach, *orchaRd* (Nakagawa *et al.*, 2023) for calculation of heterogeneity for Restricted Maximum Likelihood (REML) models, *dplyr* (Wickham *et al.*, 2022) for data manipulation, *ggplot2* (Wickham, 2016) for data visualization, and *ggtree* (Yu *et al.*, 2017) to produce our final phylogenies as shown in Figs S1 and S2. Silhouettes in figures were extracted from 'phylopic' (https.phylopic.org) using *rphylopic* (Gearty, Jones & Chamberlain, 2023).

(a) Meta-analyses

To provide a global test of the AAH across animals and to assess the impact of moderator variables, we ran both frequentist General Linear-Mixed Effects Models (GLMMs) using REML method and the correspondent Bayesian models. Bayesian models were run with 4 chains, each with 4000 iterations, a warmup of 2000 iterations, and were checked for convergence. We ran all models for datasets of within- and among-species comparisons separately. First, we obtained a weighted mean effect size (r) by fitting a model with no moderator variables but with study identifier, effect size identifier, taxon name and the phylogeny (transformed into a correlation matrix) as random effects to account for statistical nonindependence. This was done because the final dataset included multiple effect sizes from species with shared phylogenetic history, from the same species and/or from the same study. We also fitted separate models for each taxonomic class (i.e., Aves, Mammalia, Amphibia).

Second, we assessed if biological and methodological moderators impacted effect sizes. Specifically, we ran models with the same random factors as above and defined acoustic variable (minimum frequency, mean frequency, maximum frequency, frequency bandwidth, peak frequency, duration, interval duration, and repetition rate), habitat classification (categorical versus continuous), habitat contrast (0 or 1), body size correction (yes or no), or phylogenetic correction (yes or no) as fixed factors. The impact of all moderators was tested separately within Aves, which represents the taxonomic class with the highest number of effect sizes (see Results).

We assessed heterogeneity I^2 by estimating the proportion of variance among effect sizes that can be attributed to the different levels of random effects (Higgins & Thompson, 2002). Specifically, we partitioned total heterogeneity (I^2 Total) into variance arising from study identity (I^2 Study), observation (I^2 Observation), taxon (I^2 Taxon), and from phylogenetic relationship (I^2 Phylogeny; Nakagawa & Santos, 2012), which is also known as phylogenetic heritability (H^2), and equivalent to Pagel's λ (de Villemereuil & Nakagawa, 2014). For REML models with predictor variables, we calculated the pseudo-R^2 based on the proportional change in the sum of the variance components, and its 95% confidence interval based on 10000 bootstrap replicates (Viechtbauer, 2023). For models run with the Bayesian approach, we computed the proportion of variance explained by the entire model (conditional R^2) and by fixed factors only (marginal R^2; Nakagawa & Schielzeth, 2013).

(b) Publication bias

In order to assess publication bias, we ran a multilevel meta-regression as suggested by Nakagawa *et al*. (2022). In contrast to Pearson's correlation coefficient *r*, the sampling variance of Fisher's *z* statistics only depends on the sample size but not on the effect size itself. Thus, we transformed our effect size *r* into *z* and computed its sampling variance using guidelines by Borenstein *et al*. (2009). Then, we ran a GLMM with *z* defined as response variable, its standard error, moderators, and year as fixed effects and study identifier, observation identifier, taxon name and the phylogenetic

correlation matrix as random factors, which is advised when heterogeneity is high (see Results; Nakagawa *et al.*, 2022). This aimed at testing (i) whether the effect size depends on its standard error, which, similarly to the Egger's regression (Egger *et al.*, 1997), may indicate that small studies get published only (or more often) if effect sizes are large enough to provide statistically significant support for the tested hypothesis (small-study effect), and (ii) for time-lag bias (Boutron *et al.*, 2019; also known as the bandwagon effect), which suggests that supportive results get published easier in a newly emerging field but as more data are collected and scepticism about the theoretical foundations may arise, non-intuitive results increase (e.g., Jennions & Møller, 2002).

As complementary, we used Kendall's rank correlation test (Begg & Mazumdar, 1994) to quantify funnel plot asymmetry. Studies with low precision and/or high sampling error that do not support the tested hypothesis might be more prone to go unpublished. Consequently, the lack of studies meeting these criteria is expected to drive funnel plot asymmetry (Sterne *et al.*, 2011).

III. RESULTS

(1) Dataset summary

In total, we obtained 371 effect sizes from 75 studies and 57 taxa encompassing vertebrate taxa only, i.e., amphibians, birds and mammals (Fig. 2 and Table S2). Of these, 219 effect sizes were from studies reporting within-species comparisons (37 species, including 32 birds, 3 mammals, and 2 amphibians, with 189, 16, and 14 effect sizes, respectively) and 152 were from studies of among-species comparisons (20 taxa, including 14 birds, 3 mammals, and 3 amphibians, with 129, 11, and 12 effect sizes, respectively). We obtained 57 effects from analyses of minimum frequency, 12 of mean frequency, 55 of maximum frequency, 47 of frequency bandwidth, 74 of peak frequency, 71 of duration, 20 of interval duration, and 35 of repetition rate (from 39, 8, 38, 31, 46, 39, 19, and 22 studies, respectively). Regarding habitat classification, we obtained 137 effects from studies using a continuous variable to define the vegetation structure of the habitat (21 studies) and 234 with a categorical definition (54 studies), of which 163 effects came from 39 studies comparing highly

380 dissimilar habitats (habitat contrast of 1) and 71 from 16 studies comparing more similar habitats
381 (habitat contrast of 0). In total, 49 effect sizes were obtained from 15 studies correcting for body size
382 (from which 41 were retrieved from among-species comparisons) whereas 322 effect sizes from 60
383 studies did not account for body size. Finally, 73 effect sizes from 19 studies are based on analysis of
384 among-species-comparisons correcting for phylogenetic non-independence and 79 effects from 18
385 studies not correcting for it.

386 Our dataset included 22 studies (approximately 29% of our dataset) that were already
387 included in a previous meta-analysis focusing on birds by Boncoraglio & Saino (2007). Nonetheless,
388 we obtained different effect sizes for 10 (45%) of these studies. Out of a total of 78 effect sizes
389 present in Boncoraglio & Saino (2007), 7 were identical with respect to its absolute value but having
390 the opposite sign, 11 differed in more than 0.1, with 4 of them having the opposite sign, 2 effect
391 sizes could not be retrieved, and 9 differed due to a different analytical approach (most probably
392 because, contrary to Boncoraglio & Saino (2007), we did not pool data from different syllables or
393 songs). Moreover, we did not include 13 effect sizes (from 4 studies) used in the previous meta-
394 analysis because the studies did not fit our selection criteria (i.e., habitats were impossible to classify
395 as open/closed, habitat was not replicated, the study focused on urbanization, or the reported data
396 were not sufficient to compute effect sizes). We report these inconsistencies in detail in Table S3.

397 **(2) Test of the AAH for within- and among-species comparisons**

398 Overall, we did not find support for the AAH, neither for within- nor among-species comparisons
399 (Figs 3 and S3, Tables 1 and S5). None of the tested moderator variables explained a significant
400 fraction of heterogeneity in effect sizes obtained from within- or among-species comparisons (Figs
401 S4 and S5, and Tables S4 and S6).

402 When focusing only on the most studied taxonomic class, Aves, we found weak support for
403 the AAH for within- and among-species comparisons (Figs 3 and S3). Frequency bandwidth showed a
404 weak support for the AAH in within-species comparisons (Fig. S6), whereas minimum, maximum and

405 peak frequencies showed significant support in among-species comparisons (Fig. S7). Analyses of
406 other acoustic variables did not show support for the AAH. Primary studies of among-species
407 comparisons obtained significantly higher effect sizes when they did not account for phylogenetic
408 non-independence than when they did (Tables S4 and S6). When focusing on primary studies that
409 accounted for phylogenetic non-independence, we did not obtain a significantly positive global
410 effect size for birds and no acoustic variables showed a significant effect either (Fig. S8).

411 In analyses of Mammalia and Amphibia, we found no support for the AAH neither in within-
412 nor in among-species comparisons (Figs 3 and S3, Tables 1 and S5). For these analyses, the number
413 of effect sizes and species was much lower compared to Aves, which did not allow testing for the
414 impact of moderators in these taxonomic classes.

415 The effect sizes we retrieved were highly heterogeneous (REML I^2 Total > 0.80 for all models;
416 Table 1). For studies of within-species comparisons, heterogeneity arose mostly from variance
417 among observations and heterogeneity arising from other factors varied depending on the model.
418 For studies of among-species comparisons, heterogeneity stemmed primarily from among-study
419 differences for the general model and the model including only birds. For the model including only
420 studies on birds that accounted for phylogenetic non-independence (phylogeny correction),
421 heterogeneity arose mostly from variance among species. In models including only mammals or
422 amphibians, phylogeny explained the highest proportion of total heterogeneity (in both within- and
423 among-species comparisons). These patterns were confirmed by the Bayesian approach, wherein
424 the heterogeneity estimates were generally higher for among-studies and among-observations
425 differences than for the other factors, except for models with only mammals or amphibians (Table
426 S5).

427 **(3) Publication bias**

428 We detected no evidence for the small-study effect either for within- and among-species
429 comparisons, since small studies (with smaller sample size and lower precision) did not show

430 stronger effect sizes than large studies (Figs S9A and B). In fact, for studies reporting within-species
431 comparisons, we detected the opposite trend, i.e., a significant negative relationship between effect
432 size and its standard error (Fig. S9A).

433 We also detected no evidence of the time-lag bias since the year of publication did not
434 predict effect sizes of within-species comparisons (slope = 0.003, 95% CI = [-0.006, 0.012]) or among-
435 species comparisons (slope = -0.003, 95% CI = [-0.012, 0.006]). We observed a negative relationship
436 for studies not accounting for phylogenetic non-independence and a slightly positive relationship for
437 species that accounted for it, but these relationships were not statistically significant (Figs S9G and
438 H).

439 Finally, we found no evidence for funnel plot asymmetry (Figs S9C, D, E, and F) inferred from
440 Kendall's rank correlation test (Kendall's tau [within-species comparisons] = -0.059, $P = 0.212$;
441 Kendall's tau [among-species comparisons] = -0.005, $P = 0.928$).

442 IV. DISCUSSION

443 The acoustic adaptation hypothesis (AAH) posits that animals produce acoustic signals that have
444 evolved in response to the structure of their habitat, but ever since its original formulation, there
445 has been much uncertainty about the hypothesis' validity and generality within and among species.
446 We analysed a dataset of 371 effect sizes across 75 studies and 57 vertebrate taxa to demonstrate
447 that acoustic variables do not differ significantly between habitats of different vegetation structure
448 in both within- and among-species comparisons. Therefore, current empirical evidence does not
449 support the idea that the AAH is universally valid. Only comparisons within bird species provided
450 weak support for this hypothesis indicating that variation in acoustic signals in relation to vegetation
451 structure may be more complex and context-dependent than previously thought. Below we discuss
452 these findings along with the limitations of our study and future directions for research.

(1) Limited support for the AAH

Our phylogenetically informed synthesis provides no overall support for the AHH, offering quantitative evidence that acoustic signals do not show predictable responses to vegetation structure across vertebrates. This result might seem unexpected given the established principles of the physics of sound transmission (Hardt & Benedict, 2021) and questions the broader utility of the AAH for understanding the evolution of acoustic communication in natural settings.

We acknowledge that our final dataset exhibits a taxonomic bias with an overrepresentation of birds. While this reflects a limitation of our study, it also underscores the evident need for additional research examining the influence of vegetation on acoustic signals of taxa beyond birds—a call that has been made by numerous authors before (e.g., Ey & Fischer, 2009; Goutte *et al.*, 2018; Mikula *et al.*, 2020) but remains largely unaddressed. As research extends to taxa that are currently underexplored, the inclusion of reptiles, insects, and more species of anurans and mammals would likely enable the examination of other potential moderators, such as signal development (i.e., innate versus learned acoustic signals), suggested by other authors to influence results, but that could not be tested in this study (see Text S1). This would ultimately contribute to a more comprehensive understanding of acoustic adaptation and animal communication.

The substantial variation in effect size across our dataset (REML I^2 Total > 0.80 for all the models; Table 1), a common pattern of meta-analyses in ecology and evolution (with the average I^2 being as high as 92%; Senior *et al.*, 2016), remained largely unexplained. For within-species comparisons, most of the heterogeneity originated from variation among observations, while differences among studies, taxa or phylogeny had less impact. This among-observations variability may reflect the within-studies contrasting support of the AAH depending on the acoustic variables analysed, sometimes even within the same acoustic variables when measured for the entire signal and its fragments (i.e., for studies that measured acoustic variables across the entire song as well as its syllables). On the other hand, the heterogeneity of among-species comparisons arose mostly from variation among studies, which could be due to differences among study designs such as using

479 a different assessment of vegetation structure, analysing different acoustic variables, correcting or
480 not for body size or phylogenetic non-independence. Remarkably, only a fraction of primary studies
481 of among-species comparisons accounted for phylogenetic non-independence and our analyses
482 suggest that this methodological aspect has an impact on the study's outcome, particularly in birds.
483 In contrast to a qualitative review by Ey & Fischer (2009), our results suggest that studies not
484 accounting for phylogenetic non-independence obtained stronger support for the AAH than those
485 that did. This underscores the need for comparative studies to consider phylogenetic relatedness to
486 avoid misinterpreting the role of vegetation structure in shaping acoustic signals.
487 Why then does the AAH not seem to apply universally? Several factors may contribute to the
488 limited support of the AAH. First, the complexity of the habitat and the methodological difficulties
489 regarding its classification could render the AAH an oversimplified concept if applied too broadly.
490 Second, the diversity of acoustic signals across taxa and the multiplicity of selective pressures acting
491 on them may lead to complex and diverse responses that may override a potential effect of the
492 habitat.

493 **(a) Complexity of the habitat**

494 Although the AAH predicts that selection should favour acoustic signals that propagate well in an
495 environment, it has been primarily tested in terms of effects of vegetation on sound transmission.
496 This approach might be too simplistic, as many other elements may influence sound propagation in a
497 given habitat (Attenborough & Renterghem, 2021). Physical features of the landscape (hills, valleys,
498 or slopes), type of substrate, weather conditions, as well as background noise (arising from wind,
499 moving water, or other species) are only a few of the factors that can also affect how sound travels
500 (Sueur, Krause & Farina, 2019; Guibard *et al.*, 2022). For example, there is increasing evidence that
501 animals can adjust their acoustic signals to surrounding noise (Slabbekoorn & Peet, 2003; Gil *et al.*,
502 2015; Gomes *et al.*, 2022). The significant heterogeneity detected in our analyses probably reflects

503 variation among studies arising not only from methodological aspects including differences in data
504 collection, analysis, and reporting but also from the physical features of the habitat.
505 Even when focusing on vegetation only, characterizing the habitat proves to be a challenging
506 and not yet standardized task. Early work on the AAH used broad habitat categories (forest, edge,
507 and grassland; Morton, 1975) and general predictions were then formulated for open versus closed
508 habitats. These classifications of vegetation structure do not only oversimplify specific habitat
509 characteristics crucial for sound transmission but also tend to be subjective and prone to ambiguity.
510 Even the use of more quantitative continuous variables does not resolve this issue because a wide
511 array of both small-scale (measured at a microhabitat level, e.g., number of trees) and large-scale
512 (representative of macrohabitat characteristics, e.g., tree cover, canopy cover) variables have been
513 used, which challenges to generalization of findings. The differences in the assessment of vegetation
514 structure among studies may have contributed to the heterogeneity in our results as suggested by Ey
515 & Fischer (2009). However, we found that support for the AAH did not significantly differ among
516 studies using categorical versus continuous characterization of vegetation structure, or among
517 studies with varying magnitudes of contrast between closed and open habitats. This indicates that
518 including different classifications of the habitat did not change the overall results, possibly reflecting
519 the lack of power of the current classification to capture the environment structure. Additionally,
520 within the same habitat, both season and the time of day can have a significant influence on signal
521 transmission. For example, an empirical study conducted in two different forests demonstrated that
522 these factors impacted detection distance by up to a factor of five (Haupert, Sèbe & Sueur, 2022).

523 **(b) Alternative determinants of signal evolution overriding habitat effects**

524 Animal acoustic signals are shaped by a multitude of selective forces, which can give rise to
525 contrasting responses, potentially reducing the significance of habitat effects, thus challenging the
526 universality of the AAH. Whilst our results provide no global support for the AAH, we found weak
527 evidence for the AAH in birds for within-species comparisons. Avian acoustic signals might therefore

present phenotypic plasticity in response to different vegetation types but the weak support observed in our analysis suggests that habitat structure plays a minor role, if any, in shaping acoustic signals even in birds. The lack of support for the AAH in Mammalia and Amphibia aligns with the previous qualitative review (Ey & Fischer, 2009) and may reflect the limited importance of habitat in explaining global signal variation in these taxa. Nevertheless, these results demand caution due to the limited number of species tested for these animal classes.

Further complicating the application of the AAH as a universal framework are diverse constraints associated with each acoustic variable, that also depend on the taxa. Anuran calls, for instance, exhibit greater morphological constraints on frequency than on temporal parameters (Escalona Sulbarán *et al.*, 2019; Tonini *et al.*, 2020), and this has been suggested as the reason for temporal parameters being more susceptible to environmental selection than spectral ones (Mendoza-Henao *et al.*, 2023). For birds, there seems to be no consensus regarding the acoustic parameters that are more prone to be selected by environmental factors. While the previous meta-analysis found that all frequency variables differed between habitats, consistently supporting the AAH (Boncoraglio & Saino, 2007), Ey & Fischer (2009) identified minimum frequency and frequency bandwidth as the only acoustic variables presenting global support for the AAH. Recent findings propose frequency bandwidth as a more labile acoustic variable, in opposition to peak frequency, which is more constrained by a species' genetic background (Rivera *et al.*, 2023). Although our results focussing on plastic changes (i.e. within-species comparisons) align with the findings from Rivera *et al*. (2023), this is not the case for the results obtained for evolutive changes (i.e. among-species comparisons), which reveal a lack of support by all the acoustic variables when using studies that accounted for phylogeny.

Even if animals do not adjust acoustic parameters, they can exhibit other adaptive communication strategies to optimize signal transmission. In particular, they may move to a more suitable microhabitat and height for broadcasting (Kime, 2000; Seddon, 2005; Chitnis, Rajan & Krishnan, 2020) or for listening (Jensen, Larsen & Attenborough, 2008). In the presence of background noise

554 from biological, abiotic, or urban sources, animals may also adjust the broadcasting time to minimize
555 signal overlap and competition for 'signal space' with other sound-producing species (Hart *et al.*,
556 2015; Chronister, Rhinehart & Kitzes, 2023; Staniewicz *et al.*, 2023). Ultimately, the benefits of long-
557 distance transmission, such as improved communication over larger distances or enhanced mate
558 attraction, may be offset by the predatory, competitive, and parasitic costs associated with it (Ryan
559 *et al.*, 1981; Garamszegi & Avilés, 2005).

560 **(3) Changing the paradigm**

561 As Brown & Handford (1996) concluded: "*With all the possible selective forces acting on signal*
562 *design, investigators looking for specific or finely detailed differences within or among species, across*
563 *habitats, should not be surprised to find results that do not always agree with AAH predictions*". This
564 conclusion is echoed in more recent work (e.g., Ey & Fischer, 2009; Goutte *et al.*, 2018; Mikula *et al.*,
565 2020) but the AAH has remained a focal point of investigation.

566 The lack of support for the AAH in our analyses calls for a more comprehensive and
567 integrative approach to study acoustic adaptation, considering the complex interplay of ecological
568 and evolutionary factors. We propose this field to move beyond the current confines of the AAH by
569 highlighting promising avenues for future studies.

570 **(a) Standardizing habitat attenuation measurements to refine AAH predictions**

571 We believe that advances in understanding how environmental features affect acoustic signalling
572 can be achieved through a different approach to how the habitat is characterised and analysed. This
573 involves refining the description of the habitat and adopting a broader ecosystem perspective,
574 moving beyond a sole focus on vegetation structure. Ey & Fischer (2009) suggested a detailed
575 characterization of each habitat, including altitude, humidity, temperature, local animal acoustic
576 signals, and vegetation structure. However, obtaining and interpreting such an extensive amount of
577 information at the relevant scale for communication may pose practical challenges due to the
578 multitude of factors involved and difficulties in comparing studies. Instead of considering multiple

factors of the habitat separately, it may be preferable to use a single variable that integrates the direct effects of multiple factors on sound propagation.

A promising approach to characterise the acoustic properties of the environment has been emphasised recently by Haupert *et al*. (2022). By recording ambient sound and broadcasting white noise and recording it at various distances from the emitter in two forest types, they found that the coefficient of attenuation (a_0, expressed in dB/kHz/m) can describe with high accuracy the attenuation characteristic of an environment for large frequency bandwidths (for 5 kHz frequency bandwidths between 0-20 kHz in their study). This singular parameter is modelled based on acoustic physics rather than descriptive statistics and summarizes the contribution of various variables, including temperature, relative humidity, atmospheric pressure, distance, frequency, ambient sound pressure level, and vegetation, to global attenuation (Haupert *et al.*, 2022). Moreover, Haupert *et al*. (2022) used the same playback technique to describe the attenuation spectrum (the pattern of attenuation by frequency) of the two studied forests. Despite having similar a_0 values, both forests exhibited very different attenuation spectrum profiles. Within the same environment, detection distance varied by up to a factor of five depending on the frequency considered. These spectrum profiles potentially reveal frequencies with the highest detection probability and could be used as starting point to describe the habitat. Subsequently, studies could establish correlations between the attenuation profile and the species' (or population's, or even individual's) specific power spectrum of acoustic signals, in order to test whether frequencies with greater detection distance are preferentially used. Therefore, we suggest a more comprehensive examination of attenuation in each locality, employing methodologies such as those outlined by Haupert *et al*. (2022). This would facilitate global comparisons (through a single variable) and offer a more objective and standardized assessment of the acoustic properties of a given habitat.

Furthermore, we propose to rephrase the predictions of the AAH to take into account the attenuation spectrum. Specifically, animals inhabiting environments with different attenuation spectra are predicted to emit acoustic signals at frequencies (minimum, mean, maximum, and peak

605 frequency) such that detection distance is maximized. This implies that there is no universal pattern
606 for the expected change in these variables, unless habitats share similar profiles. Instead, the
607 alterations will be contingent upon the specific characteristics of the environment. This adjustment
608 also overcomes an early noticed limitation of the AAH that for maximum efficiency, long-range
609 acoustic communication in any habitat should employ the lowest possible frequencies (Wiley &
610 Richards, 1982).

611 **(b) Towards a narrower framework to test the AAH**

612 While the AAH offers valuable insights, it may not fully capture the processes underlying the
613 evolution of acoustic signalling as it does not account for alternative strategies that animals use in
614 response to multiple selective pressures acting on signal structure or their interactions. To
615 comprehensively assess the environmental influence on signal evolution, a more comprehensive
616 approach is necessary.

617 Considering the probable lack of generality of the AAH, it would be valuable to narrow down
618 the focus to signals for which an advantage in transmission over long distances is likely. Studies not
619 selecting for these signals (e.g., Mikula *et al.*, 2020) might reflect this limitation. For example, many
620 acoustic signals are part of private duets (i.e., do not need long-distance transmission) such that
621 there is no selection against easily degrading communication (Larsen, 2020). Likewise, for some
622 species song is not used for distant communication, as reported in zebra finches, where it may be
623 more pertinent to assess whether their distance call, rather than their song, is adapted for long
624 distance transmission through the local environment (Loning, Griffith & Naguib, 2022). This
625 approach requires an in-depth knowledge of the study species, which might not always be readily
626 available and can be challenging to obtain. Nevertheless, we believe that tests of the AAH are only
627 meaningful for signals that are meant for long-distance communication.

V. CONCLUSIONS

(1) Our meta-analysis challenges the general validity of the acoustic adaptation hypothesis (AAH) by showing no overall support for the correlation between vegetation structure and acoustic variables.

(2) The weak support for the AAH in within-species comparisons of birds, mostly driven by frequency bandwidth differences, suggests a phenotypically plastic response of this variable to the vegetation structure of the habitat. By contrast, the AHH is not supported by among-species comparisons of studies accounting for phylogenetic non-independence.

(3) Although many years have passed since the formulation of the AAH, major efforts are still required to confirm the predictive ability of the hypothesis. Future research should refine the characterization of the habitat through a standardized quantification of the attenuation, which will lead to habitat- and species-specific predictions. Moreover, we expect that major advances in the field will benefit from broadening the studied taxonomic range while concurrently being selective about the tested signals.

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VII. AUTHOR CONTRIBUTIONS

B.F. Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Visualization, Writing – original draft;

P.B.D. Writing – review and editing

B.M. Supervision, Writing – review and editing

C.T. Supervision, Writing – review and editing

T.J. Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Supervision, Validation, Visualization, Writing – review and editing

VIII. DATA AVAILABILITY

All data and R scripts associated with this study can be retrieved from the OSF data repository (available at xxx; it will be made available upon article acceptance).

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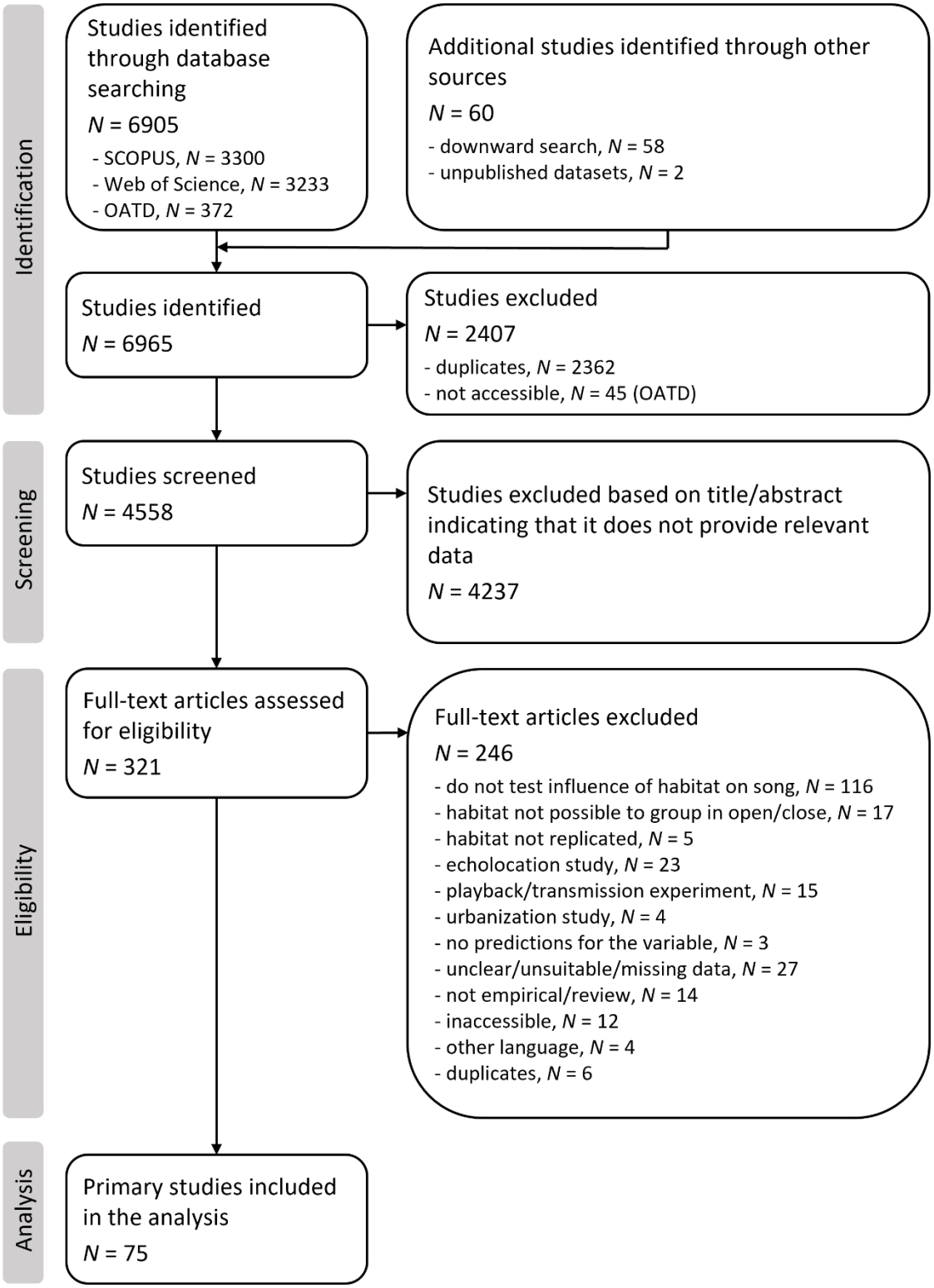


Fig. 1. Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) diagram of the protocol for screening, including and excluding studies for this meta-analysis and number of studies identified at each stage. OATD, Open Access Theses and Dissertations.

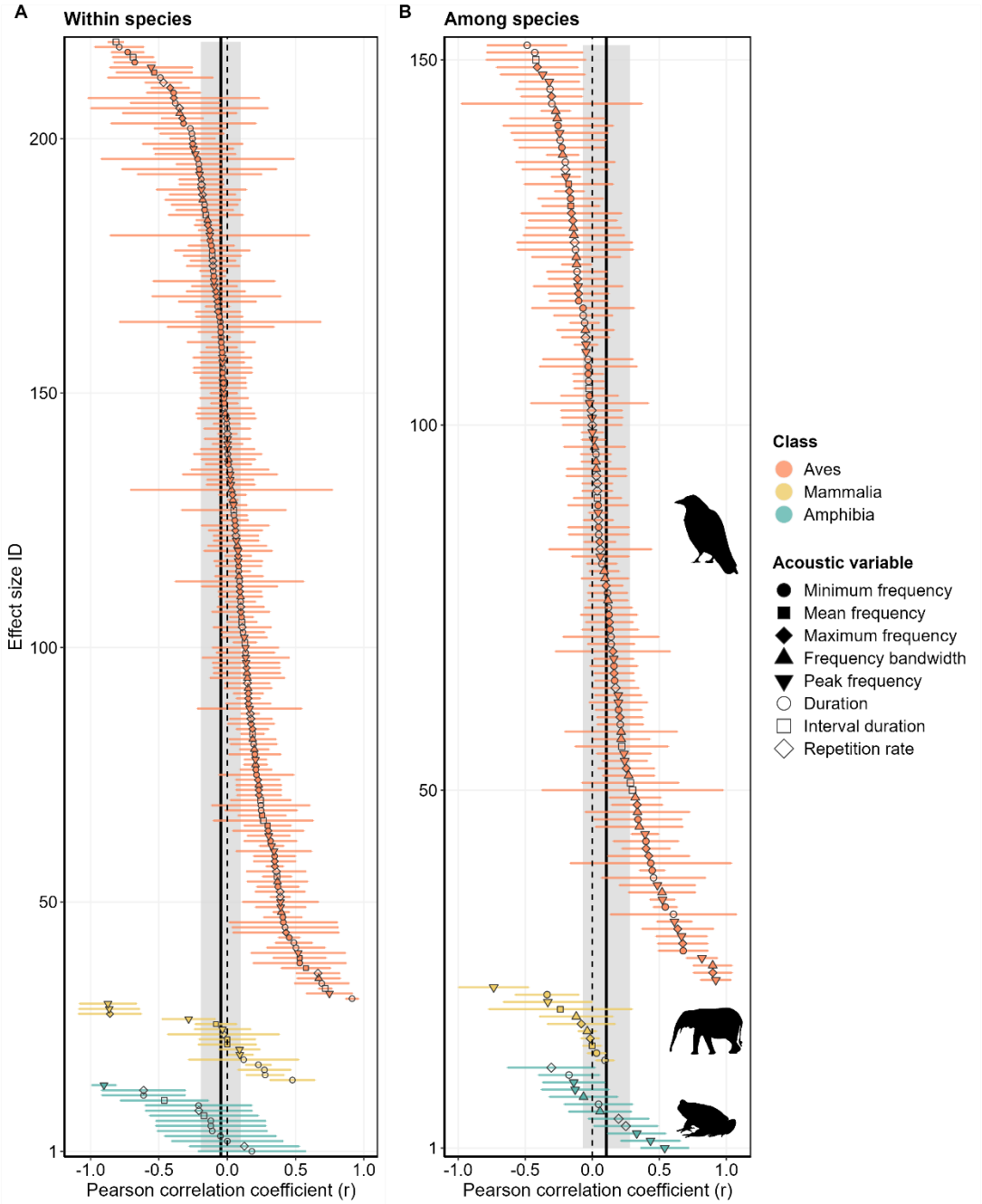
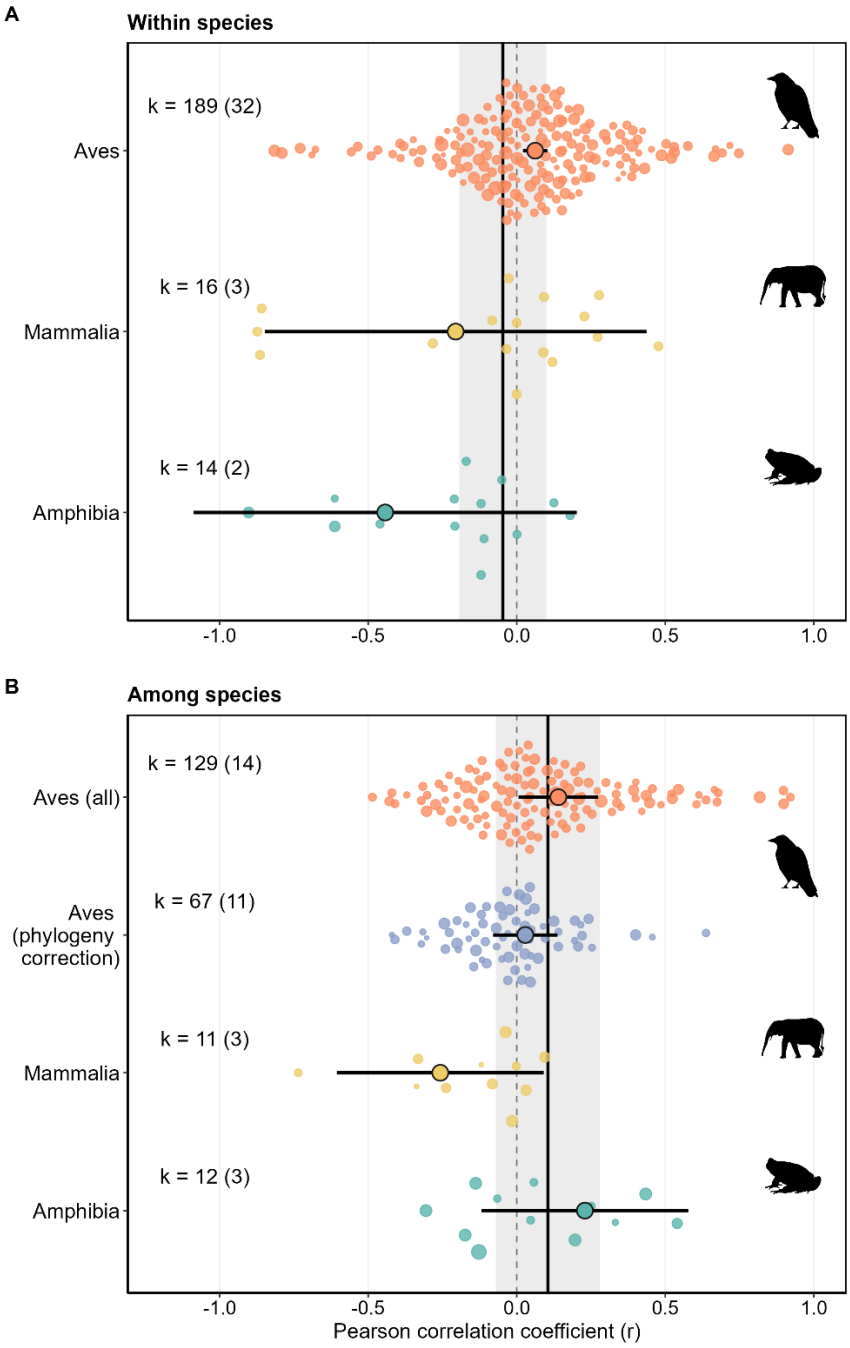


Fig. 2. Caterpillar plot for (A) within- and (B) among-species comparisons. Effect sizes are displayed by taxonomic class, ordered by mean estimate, and with horizontal bars showing 95% confidence intervals (CIs). Symbols of the point estimate illustrate the acoustic variable measured. Positive Pearson correlation coefficients (*r*) indicate support for the acoustic adaptation hypothesis. Solid vertical black lines indicate the estimated global effect size obtained from the REML model with random factors only, and the grey area denotes the 95% CIs (A: *r* = -0.047, 95% CIs: -0.193 to 0.099; B: *r* = 0.105, 95% CIs: -0.070 to 0.280).



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934 **Fig. 3.** Orchard plots for (A) within- and (B) among-species comparisons showing effect sizes

935 (Pearson correlation coefficients, *r*) and number of taxa (k = total number of effect sizes (total

936 number of taxa) and mean effect size from REML models. Solid horizontal bars are 95% confidence

937 intervals (CIs) of global effect sizes obtained for each taxon. Solid vertical black lines indicate the

938 estimated global effect size from the REML model with the random factors only, and grey bands

939 denote the 95% CIs (A: *r* = -0.047, 95% CIs: -0.193 to 0.099; B: *r* = 0.105, 95% CIs: -0.070 to 0.280).

940 Circle size reflects effect size precision (log(1/SE)).

Table 1. Global effect sizes for the acoustic adaptation hypothesis obtained from the restricted maximum likelihood approach. Results of intercept-only General Linear-Mixed Effects Models are shown for the entire dataset (global model) and for subsets with respect to animal class (Aves, Mammalia or Amphibia). For among-species comparisons of Aves, the results are shown for a subset of studies that accounted for phylogenetic non-independence (Aves (phylogeny correction)). Table shows number of effect sizes (k), number of species or taxa (N), estimates of *r* and heterogeneity I^2 (total, variance arising from phylogenetic affinities, taxon, study identity, and observation).

Type of study	Taxonomic range	k	N	*r*		z-value	*P*-value	I^2 Total	I^2 Phylogeny	I^2 Taxon	I^2 Study	I^2 Observation
Within species	Global model	219	37	-0.047	(-0.193,0.099)	-0.628	0.530	0.954	0.129	0.000	0.298	0.528
	Aves (all)	189	32	0.062	(0.021,0.103)	2.965	**0.003**	0.936	0.000	0.000	0.000	0.936
	Mammalia	16	3	-0.205	(-0.847,0.437)	-0.627	0.530	0.979	0.000	0.897	0.000	0.082
	Amphibia	14	2	-0.443	(-1.087,0.202)	-1.346	0.178	0.904	0.284	0.284	0.284	0.050
Among species	Global model	152	20	0.105	(-0.070,0.280)	1.172	0.241	0.950	0.141	0.049	0.572	0.188
	Aves (all)	129	14	0.140	(0.006,0.274)	2.049	**0.040**	0.943	0.010	0.054	0.673	0.206
	Aves (phylogeny correction)	67	11	0.029	(-0.079,0.137)	0.523	0.601	0.841	0.000	0.425	0.269	0.148
	Mammalia	11	3	-0.257	(-0.605,0.091)	-1.448	0.148	0.966	0.722	0.000	0.223	0.021
	Amphibia	12	3	0.229	(-0.119,0.577)	1.292	0.196	0.864	0.554	0.000	0.000	0.310