Cuckoos: The holy grail of avian biodiversity conservation?

Birgen Haest

Institute of Avian Research 'Vogelwarte Helgoland', Wilhelmshaven 26386, Germany

A B S T R A C T

The ongoing rapid loss of biodiversity is urging conservationist to develop biodiversity monitoring methods that are both effective and inexpensive. The identification of areas that are rich in biodiversity is an essential prerequisite to guide further conservation actions. Next to several data-intensive and more complex modelling approaches to identify biodiversity 'hotspots', there are also many conservation scientists and practitioners that are looking for approaches based on surrogate species or taxa. In certain cases, single-species surrogates have been proposed to represent a certain aspect of a broader set of species, but their effectiveness is a highly debated issue. A number of recent studies have suggested the common cuckoo (*Cuculus canorus*) to be an extremely effective, yet inexpensive, single-species surrogate to map and monitor avian biodiversity across continents and at different spatial scales. If this would indeed be the case, the implications towards conservation planning would be tremendous, which raises the question: Has the holy grail of avian biodiversity conservation been found? In this paper, the methodology and significance of the results of these studies are questioned and, hence, the use of the common cuckoo as a single-species surrogate for avian biodiversity. The studies all heavily rely on the AUC value to assess model accuracy of estimating common cuckoo occurrence using species richness (and not vice versa). Using simulations of different scenarios of relative species commonness and evenness, I show that the underlying statistical dependency between species richness and occurrence of a species results in highly inflated and volatile AUC values for the majority of the 300 simulated species, depending on their commonness and the overall species evenness. As such, I hope to be able to discourage conservation scientists and practitioners from investing time, effort, and money in using the common cuckoo as a single-species surrogate for avian biodiversity conservation.

1. Introduction

Conservation organizations and practitioners are typically faced with limited funding and knowledge, and identifying priorities to be able to support the most species at the least cost, hence, becomes of utmost importance (Mac Nally and Fleishman, 2002; Myers et al., 2000; Rodrigues and Brooks, 2007). Knowledge on where areas rich in biodiversity are located is an essential prerequisite to be able to set these priorities (Pearman and Weber, 2007). Although there are many definitions of biodiversity (Jacobs et al., 2013), in practice it often centers on species richness, i.e., the number of species present, in an area (Caro, 2010; Chao and Chiu, 2016).

Methods for species richness estimation have been a research topic for several decades (Fleishman et al., 2018). Despite the familiarity of species richness, it is surprisingly difficult to measure accurately (Gotelli and Colwell, 2011). Several more recent methods to estimate species richness, such as stacked and joint species distribution models, try to take advantage of increased computing power, but many of these still need to be tested for transferability and repeatability (Fleishman

et al., 2018). Because of the limitations in funding and knowledge, conservation organizations, practitioners, and scientists, have also been looking for shortcuts in the form of surrogate species or taxa (Roberge and Angelstam, 2004). Surrogate species are individual species that are used to represent a broader set of species in order to simplify conservation and management planning and communication (Wiens et al., 2008). The effectiveness of various surrogate groups and approaches for biodiversity conservation in general, however, remains a highly debated issue (Cabeza et al., 2008; Kosicki and Hromada, 2018; Wiens et al., 2008). The search for taxonomic surrogates of species richness has yielded mixed results, with studies reporting from no over tentative to great promise for the approach (Jyväsjärvi et al., 2018).

Recently, a number of studies have suggested the common cuckoo (*Cuculus canorus*) to be an excellent single-species surrogate for avian species richness, from the local and regional (Møller et al., 2017; Morelli et al., 2017b, 2015; Tryjanowski and Morelli, 2015), to the national and (inter-)continental scale (Morelli et al., 2017a, 2015). The common cuckoo is a charismatic species that is easy to monitor, widespread both geographically and across the main types of

landscapes, and also adequate for citizen science approaches as it easy to detect from its familiar song (Morelli et al., 2017b; Tryjanowski and Morelli, 2015). The first study on the common cuckoo as a surrogate for species richness (Tryjanowski and Morelli, 2015), suggested that the common cuckoo was a better predictor of avian species richness than a group of "top predators", consisting of Buzzard (*Buteo buteo*), Goshawk (*Accipiter gentilis*), Sparrowhawk (*Accipiter nisus*), and Kestrel (*Falco tinnunculus*), in an agricultural area in Poland at a local level with a study site covering 141 km^2. Morelli et al. (2015) subsequently proposed that the utility of the common cuckoo as a surrogate species could be extended to larger scales (e.g. France at a national scale) across Europe, and to additional indices of taxonomic bird diversity, such as Shannon-Weaver bird diversity, host species richness, and host species richness rank. They also suggested that cuckoo occurrence outperforms two landscape heterogeneity indices, i.e., land-use diversity and weighted edge density. Morelli et al. (2017b) then suggested that the common cuckoo, apart from being an excellent surrogate of taxonomic avian diversity, is also a good surrogate for other avian biodiversity components, such as functional richness and functional evenness. Møller et al. (2017) used, amongst other things, the link between cuckoo occurrence and bird species richness to propose that the folklore about the link between the longevity of farmers and the syllables of cuckoos is indeed likely to be true. Morelli et al. (2017a) put forward that the multi-scale expediency of the common cuckoo as a surrogate for avian species richness can be extended to an even wider geographic range by demonstrating links between cuckoo occurrence and bird species richness in ten European and two Asian countries. They conclude that the common cuckoo is a suitable intercontinental bio-indicator for bird richness hotspots, including under climate change scenarios and in areas where other cuckoo species co-occur. These studies altogether suggest that the common cuckoo is an extremely effective but also inexpensive tool to map and monitor avian biodiversity across continents at different spatial scales. As such, this could have tremendous implications in terms of avian conservation efforts and success, which raises the question: Has the holy grail of avian biodiversity conservation been found?

In this paper, the methodology and the validity of the results that have led to the suggestion of the common cuckoo as a surrogate species for avian species richness are questioned. All of the publications have in common that they use bird species richness as an independent variable to predict cuckoo occurrence, and not vice versa. Moreover, they all heavily rely on the Area Under the Curve (AUC) from Receiver Operating Characteristic (ROC) analysis to demonstrate the accuracy of these predictions of cuckoo occurrence. I use the data from Morelli et al. (2017a) to first show the large uncertainty in the estimates of the AUC of their model. I then use simulations to estimate the AUC value distributions of 300 simulated species, from very common to rare, for the model of Morelli et al. (2017a) as a function of different plausible relative species commonness distributions and species evenness, based on data from Tryjanowski and Morelli (2015). This allowed to more appropriately assess the significance of the AUC values obtained by Morelli et al. (2017a). I hypothesized that the underlying statistical dependency between species richness and occurrence of a species as a function of the relative commonness and evenness may result in highly inflated AUC values.

2. Material and methods

2.1. Data

Data on bird species richness (i.e., the number of species) and cuckoo occurrence (detected/not detected) at each sample site in ten European and two Asian countries, including the type of survey and dominant environment, have been published as supplementary material by Morelli et al. (2017a). Details on the number of sites per country and other summary statistics can be found in Morelli et al. (2017a) and are

not reproduced here. I first used this dataset to repeat the analysis of Morelli et al. (2017a), but now appropriately assess the uncertainty in the reported AUC values (see Section 2.2). I also used this dataset as a baseline for the simulations to estimate the distributions of expected AUC values for all species from different plausible relative species commonness and evenness distributions.

Unfortunately, the dataset from Morelli et al. (2017a) does not include data on relative frequency of occurrence for each species in the samples, i.e. species commonness and evenness data. As such, to obtain representative reference values for a typical relative species commonness distribution, I fit an exponential function to the relative species commonness data from Tryjanowski and Morelli (2015) using nonlinear least squares. The intercept a and slope b for the function $y = e^{a + bx}$ with x = 1 to 157 (i.e., the number of species in Tryjanowski and Morelli (2015) and y = the occurrence frequency of each species, were 4.22 and −0.05, respectively. The R script (R Core Team, 2018) to estimate the coefficients of the exponential function can be accessed at Haest (2018). I used these estimated coefficients as a baseline for the relative species commonness distributions in the simulations of the AUC value distributions under different species evenness scenarios (see Section 2.3).

2.2. AUC uncertainty estimation

Important distinctions exist between inferential (or explanatory) and predictive model assessment. In inferential modelling the emphasis of model performance lies in assessing explanatory power, i.e. measuring the strength of relationships for example through R^2-type statistics or predictor statistical significance. In predictive modelling, the emphasis of model assessment lies in predictive power, referring to the performance of the model on new or unseen data (Shmueli, 2010). AUC is a measure to assess predictive accuracy (Elith et al., 2006), and AUC estimation, just as other predictive performance measures, should be performed on data that has not been used to train the model to avoid overestimation of model accuracy (Congalton and Green, 2009). Several methods exist to approach splitting a dataset into training and test (and possibly also validation) data. The most important difference, however, lies in whether a single split of some given proportion is used, or the split is repeated several times through some sort of resampling. Using a resampling method allows the estimation of confidence intervals around the accuracy measure, and as such provides information on model uncertainty (Lyons et al., 2018).

The studies that have proposed the common cuckoo as a surrogate species of avian species richness all calculated AUC values on the model that uses the full dataset. I repeated the modelling of common cuckoo occurrence using avian species richness as in Morelli et al. (2017a), but instead of using the full dataset to calculate only one AUC value (per country), I more appropriately used resampling to estimate the uncertainty in the AUC estimations. I repeated a 5-fold cross-validation a 1000 times, resulting in 5000 AUC estimates based on different subsets of the full dataset. In each 5-fold cross-validation, the dataset is randomly split into 5 groups, of which 4 are then used as training data for the cuckoo occurrence model and 1 to calculate AUC, iterated 5 times so each group functions as the test set once. The R script to perform this uncertainty analysis can be accessed at Haest (2018).

2.3. Simulations of AUC value distributions as a function of relative species commonness and evenness

I hypothesized that AUC values for models that estimate occurrence of a species using species richness may be highly inflated due to the intrinsic underlying increased probability of occurrence of any species when species richness increases. To test this hypothesis, I estimated the distributions of AUC values for all species under different scenarios of relative species evenness, i.e. species commonness distributions with different exponential slopes, given the species richness data from
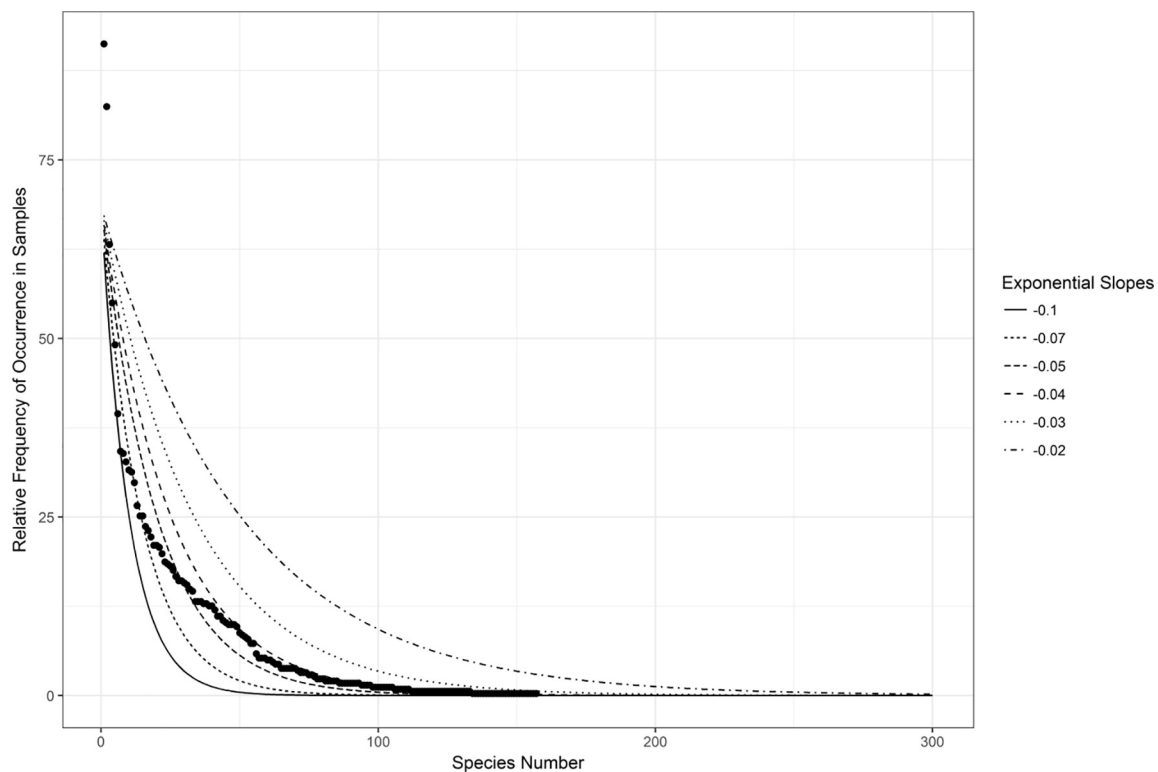
Fig. 1. Functions of species commonness in samples, i.e. relative frequency of occurrence, used as a baseline to sample species from in the simulations of the AUC null distributions.

Morelli et al. (2017a).

The exponential function that was fit to the relative species commonness distribution data of Tryjanowski and Morelli (2015) had an intercept and slope of 68 ($e^{4.22}$) and -0.05, respectively (see Section 2.1). To represent plausible overall relative species commonness distributions with varying species evenness in our simulations, I used the values -0.1, -0.07, -0.05, -0.04, -0.03, and -0.02 for the slope of the exponential function, keeping the intercept constant at 68. A plot of the exponential functions that were used to represent the relative species frequency of occurrence in the samples is provided in Fig. 1, together with the data of Tryjanowski and Morelli (2015). A total of 300 simulated species were used.

To estimate the AUC value distributions as a function of species commonness and evenness, given the species richness values of Morelli et al. (2017a), I repeated their cuckoo occurrence modelling a thousand times for each of the exponential functions that represent species commonness and evenness. Prior to model evaluation in each repetition, I first simulated species occurrence for all species by drawing from all possible species until the species richness at each sample was reached. At each draw, the relative probability of drawing a species was based on the exponential functions that represent relative species commonness and evenness. For the exponential function with a -0.05 slope, for example, the relative probability of drawing 'species 1', 'species 5', and 'species 100' was 65%, 53%, and 0.46%, respectively. After all species occurrences at each sample were simulated in a repetition, I applied the model used in Morelli et al. (2017a), i.e. a Generalized Linear Mixed Model (binomial link) with species richness as a predictor variable, country and 'dominant environment' as random effects, and species occurrence as the response variable, for all of the simulated species. For each of the countries, I then calculated the AUC value for that repetition. Repeating these simulations a thousand times for each of the exponential functions resulted in AUC value distributions for each country and each of the simulated species under different species evenness conditions, hence providing insights in the behavior of AUC values as a function of species commonness and evenness.

Based on the percentile of the thousand repetitions in which the AUC values reported by Morelli et al. (2017a) fall for each combination of country, species evenness (i.e. exponential slope), and species commonness (i.e. "species number"), I then also calculated the probabilities of obtaining these AUC reported values as a function of country, species evenness and commonness.

Predictive performance should always be assessed on an independent test or validation set to avoid accuracy overestimation (Congalton and Green (2009), but see Lyons et al. (2018) for practical recommendations). The previously discussed cuckoo papers (see Section 1), however, all calculated AUC on the model that includes all of the sample data. To permit comparison between the simulated AUC values and the ones in Morelli et al. (2017a), I also calculated AUC values on the models with all of the sample data. The R scripts to simulate the distributions of the AUC values and probabilities as a function of species commonness and evenness are provided in Haest (2018).

3. Results

3.1. AUC uncertainty estimation

Based on a thousand repetitions of a 5-fold cross-validation, I found large uncertainties in the AUC values for the common cuckoo occurrence predictive model reported by Morelli et al. (2017a) (Fig. 2). Depending on the country, the 90% confidence interval (i.e. the difference between the 95th and 5th quantile) spanned a range of 0.05 (China) to 0.41 (Switzerland) AUC values. The average range over all countries of the 90% confidence interval was 0.24 AUC values.

3.2. Simulated AUC value distributions as a function of relative species commonness and evenness

Our simulations of the AUC value distributions for species occurrence prediction using species richness clearly indicate how as a
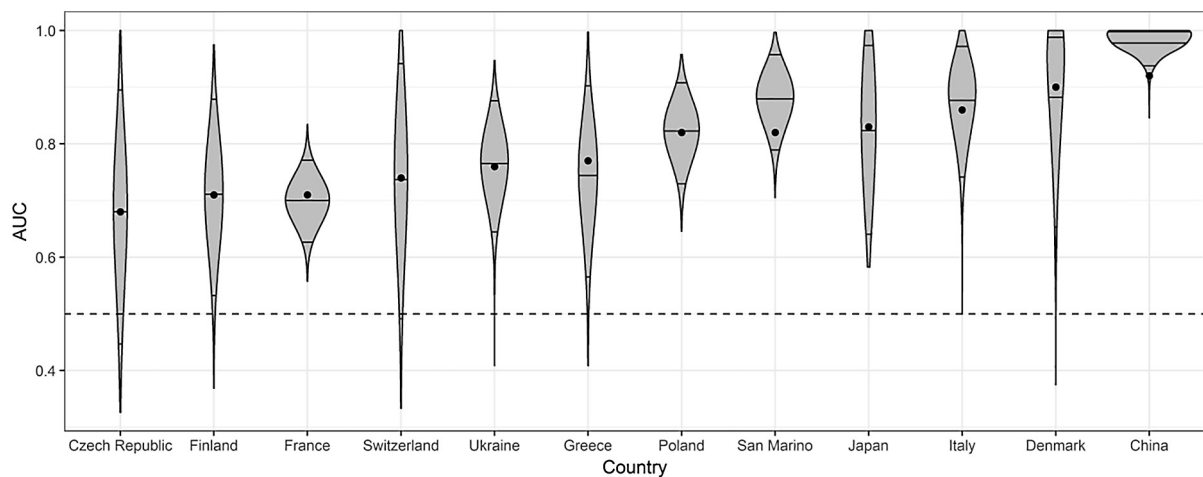
Fig. 2. Violin plot illustrating the uncertainty in the AUC estimates of species occurrence prediction by Morelli et al. (2017a). Horizontal lines on violins indicate the median and the 90% confidence interval. Dots in the violins represent the values that were indicated for the AUC in Morelli et al. (2017a).

function of the country, relative species commonness, and species evenness, the expected AUC values strongly vary (Fig. 3). The expected AUC values vary from very high median values with small confidence intervals (e.g. 0.99–1 for the most common "Species 1" in France with an exponential slope of −0.1) to low median values with large confidence intervals (e.g. 0.45–0.95 for "Species 150" in Switzerland with an exponential rate of −0.02). In the majority of the simulations, large overlaps exist between the 90% confidence intervals of the AUC values for the cuckoo occurrence model of Morelli et al. (2017a) (calculated in Section 3.1) and the 90% confidence intervals of the AUC values for the simulated species (Fig. 3). Similarly, in most cases, the median AUC values obtained for the cuckoo occurrence model of Morelli et al. (2017a) clearly fall below the 95% upper confidence limit of many species, depending on species rarity and evenness. In certain cases, the AUC value distributions of simulated species fall even (almost) entirely above the 95% upper confidence limit of Morelli et al. (2017a), e.g. the more common species in France and Czech Republic. Not surprisingly then, the large majority of the probabilities of obtaining AUC values similar to those of Morelli et al. (2017a) as a function of country, species commonness and evenness for the prediction of species occurrence using species richness, were also higher than 0.05 (Fig. 4).

These results altogether mean that, independent of the observed species evenness in the samples, AUC values that are higher than those reported in Morelli et al. (2017a) are likely to be found using their model for most of the species in the overall species set.

4. Discussion

4.1. The common cuckoo is not a surrogate for avian biodiversity

Our results provide compelling evidence on how AUC values for a model that predicts occurrence of a single species using species richness as an independent predictor, can be extremely positively biased. The amount of bias is dependent on both how common a species is and the overall species evenness in the samples (Fig. 3). This means that, if one relies on the previously repeatedly suggested qualitative interpretation of AUC values (i.e. 0.9–1.0: excellent; 0.8–0.9: good; 0.7–0.8: fair; 0.6–0.7: poor; and 0.5–0.6: fail) for a model that predicts a species' occurrence based on species richness, and accepts this to also be indicative for the validity of the reverse relation, many species can be indicated, albeit faulty, as good single-species surrogates of species richness. The high probabilities of obtaining AUC values similar to those of Morelli et al. (2017a) (Fig. 4) in most of the simulated scenarios, combined with the fact that the other publications that suggest the common cuckoo as an excellent surrogate for species richness all

heavily rely on the same methodology, strongly question that the common cuckoo can indeed be used as single-species surrogate for avian biodiversity over a multitude of spatial scales. As such, it is not advisable that conservation practitioners and decision makers base their biodiversity conservation decisions on spatial distributions of the common cuckoo, and changes thereof.

4.2. AUC misinterpretations

An academic urban legend (Rekdal, 2014) seems to exist around the qualitative interpretation of AUC values as 0.9–1.0: excellent, 0.8–0.9: good, 0.7–0.8: fair, 0.6–0.7: poor, and 0.5–0.6: fail (e.g. Araújo et al. (2005) and Morelli et al. (2017a), but there are many more). Swets (1988) is continuously referenced as a source, but he did not propose such an interpretation of AUC values. In a footnote of the publication, he does suggest: 0.5–0.7: rather low; 0.7–0.9: useful for some purposes; and > 0.9: rather high accuracies. This seems to be a much more carefully worded and nuanced interpretation of the AUC value that suggests the reader to tread carefully. In contrast, the currently derived interpretation lacks these nuances, which leads to overly positive and misleading interpretations by providing the sense that when the AUC > 0.7 your model is already doing ok. Further usage of this qualitative AUC scale for the interpretation of model performance using AUC values should therefore be strongly discouraged.

There are many distinct differences between predictive and inferential (or explanatory) modelling. One important distinction lies in how the model performance is evaluated. In inferential modelling the emphasis of model performance assessment lies in assessing explanatory power, e.g. with R^2-type statistics or statistical significance of independent variables, using all of the available data. In predictive modelling, model assessment is mainly directed at predictive power, i.e. the performance of the model on new or unseen data. In environmental science, statistical models have been mainly used for inference (Shmueli, 2010), which might explain the confusion on model assessment of predictive modelling within this field. For predictive models to be meaningful, it is essential that environmental scientists, including conservationists, familiarize themselves with this difference in model performance assessment, as only then accuracy assessment statistics such as AUC can be applied appropriately. Doing so also brings along valuable insights into model uncertainties (see Section 3.1), enabling more appropriate interpretations of the model performance.

Using AUC for accuracy assessment of predictive species occurrence models has been criticized before (Allouche et al., 2006; Lobo et al., 2008). In the context of species' distribution modelling (SDM) using environmental predictors, Raes and Ter Steege (2007) provide excellent
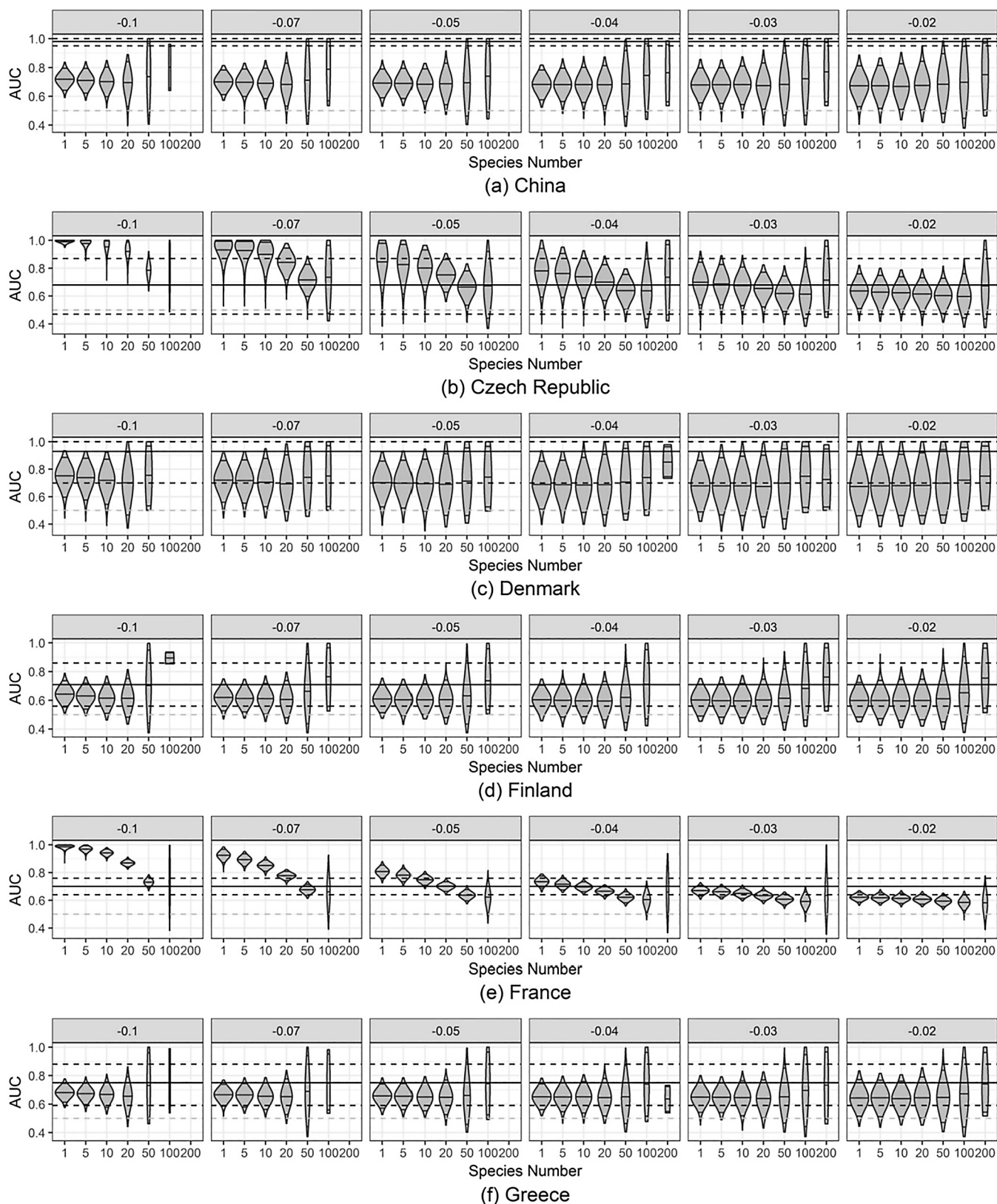
Fig. 3. Per country violin plots of the simulated AUC null distributions as a function of species commonness (i.e. relative frequency of species occurrence) and species evenness. Species Numbers in the X-axis represent species with decreasing relative frequencies of occurrence (Species 1: most common species, Species 200: rarest species). Plot columns represent the different slopes of the exponential function to simulate different species evenness (−0.1: lowest species evenness to −0.02 highest species evenness; see Fig. 1). Horizontal lines within the violin plots represent the 5th, 50th, and 95th quantile (i.e. median and 90% confidence interval). Horizontal full and dashed lines across the plots represent the 5th, 50th, and 95th (i.e. median and 90% confidence interval) AUC values of the cuckoo occurrence models calculated using the data from Morelli et al. (2017a) for the respective country (see Sections 2.2 and 3.1).
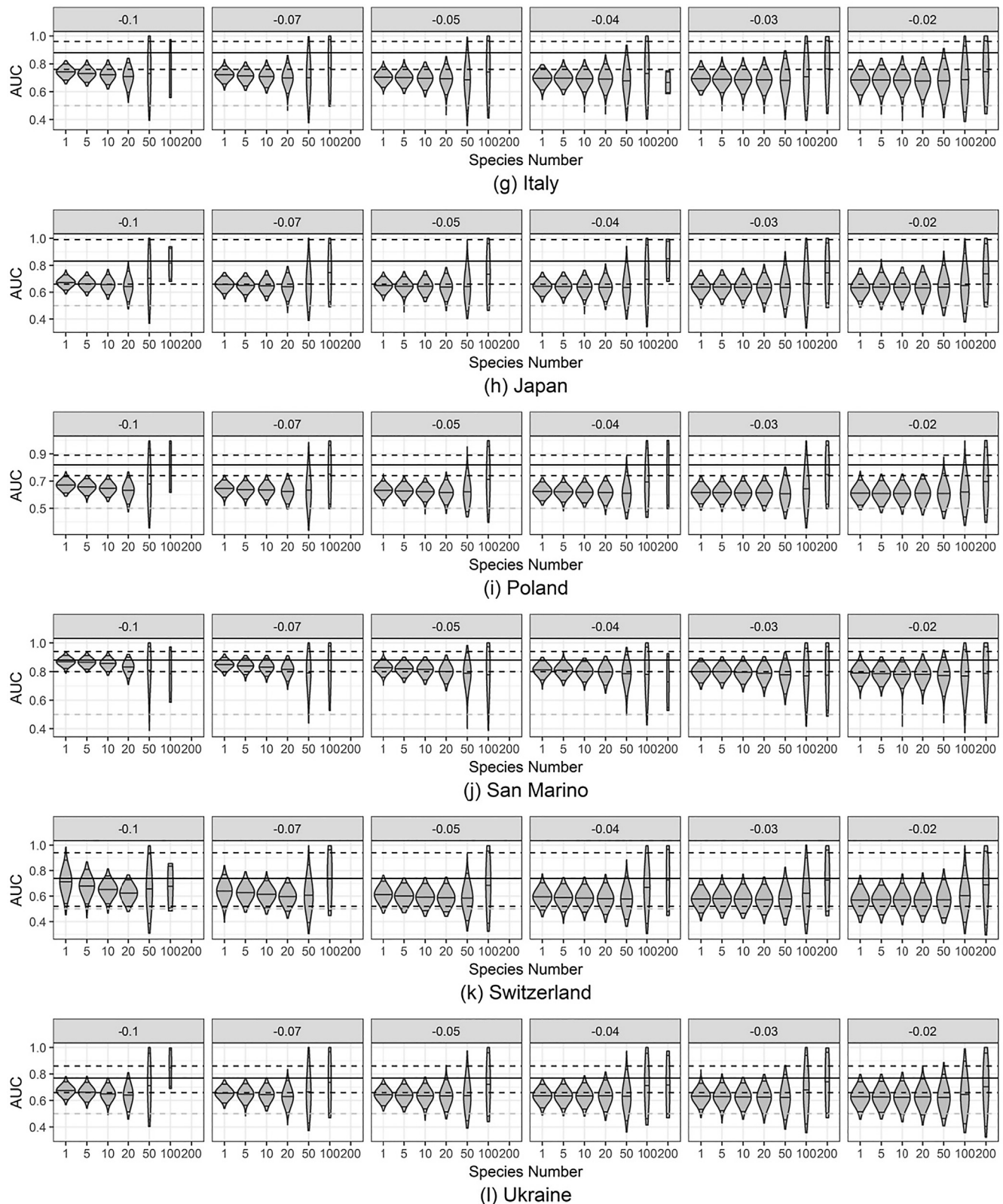
(g) Italy

(h) Japan

(i) Poland

(j) San Marino

(k) Switzerland

(l) Ukraine

Fig. 3. (*continued*)

recommendations on how to assess whether the predictions differ substantially from what would be expected by chance alone. This paper contributes to these previous suggestions to be careful in interpreting AUC values by showing how underlying statistical, yet ecologically meaningless, dependencies between the response and predictor variable can result in inflated AUC values.

4.3. Predicting the presence of a species using species richness is not the same as predicting bird richness using the presence of a species

All of the studies that suggest the common cuckoo to be an excellent surrogate for avian species richness mainly relied on predicting common cuckoo occurrence using avian species richness, instead of vice
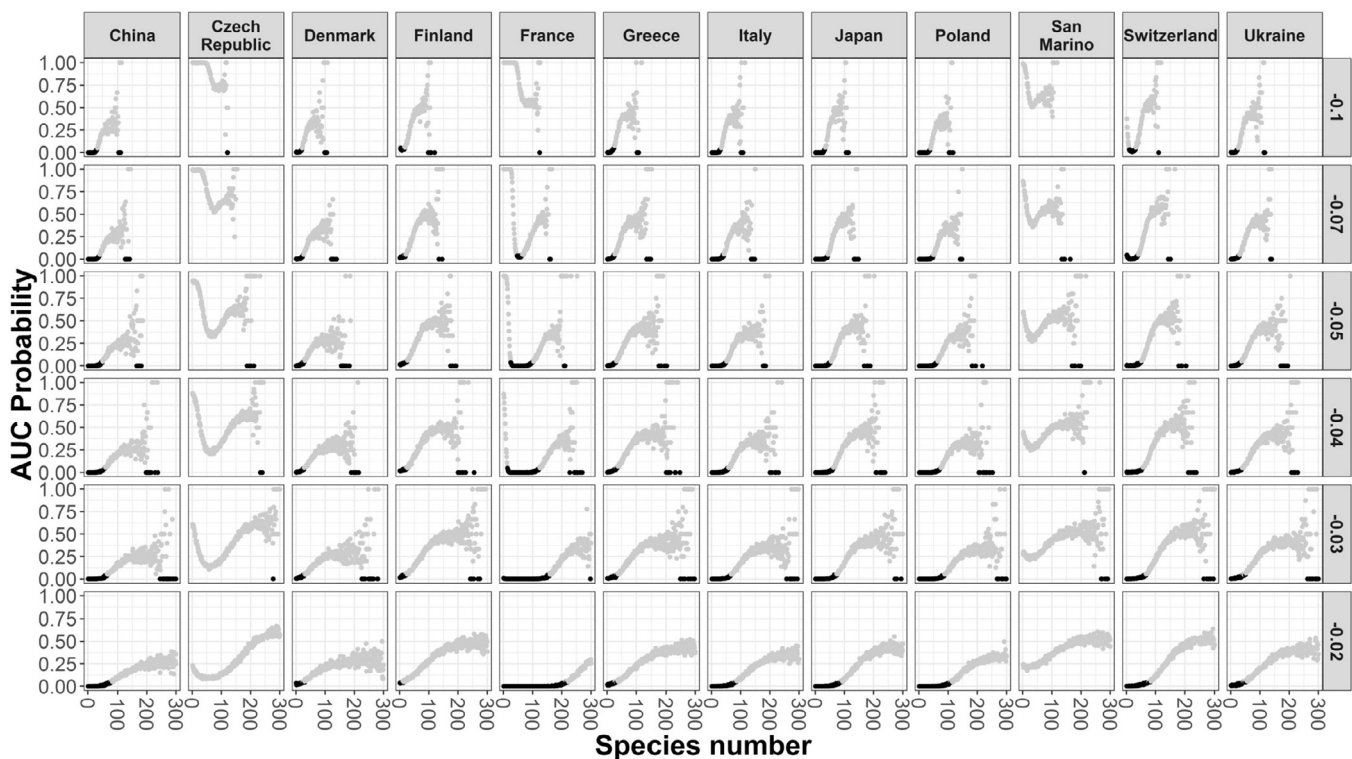
Fig. 4. Probabilities of obtaining AUC values similar to those of Morelli et al. (2017a) as a function of country, species commonness and evenness for the prediction of species occurrence using species richness. Plot Rows represent the different slopes of the exponential function to simulate different species evenness (−0.1: lowest species evenness to −0.02 highest species evenness; see Fig. 1). Black dots indicate where the AUC values of Morelli et al. (2017a) are significant at the 0.05 level, i.e. the AUC probability is below 0.05. Grey dots indicate where the AUC values are not significant at the 0.05 level.

versa (but see Morelli et al. (2015)). While species occurrence is indeed likely to be 'significant' in the reverse model when species richness is 'significant' in the original model to predict species occurrence, the interpretation changes drastically. While species richness is a continuous variable that can provide a continuous output of species occurrence probabilities, using a single species' occurrence as a predictor can only provide a binary output, i.e. species richness is a certain amount higher or lower when the species occurs. From a practical point of view for the prediction of biodiversity-rich areas using the occurrence of only one species, this hence narrows down to a prediction that can only provide information on high or low biodiversity, based on a single-value difference. With sufficient statistical power (which is amongst others related to the sample size), any effect size will become statistically significant, and knowledge on the magnitude of the effect and the explained variation hence becomes vital to interpret the ecological significance (Koricheva et al., 2013; Parker et al., 2018). In other words, depending on the characteristics and amount of sample data, statistically 'significant' effects of species occurrence on species richness might actually be ecologically meaningless (e.g. 'species-rich' areas have 1 species more than 'species-poor' areas). While such small differences between species richness could even be meaningful in certain contexts, they should be studied, presented, and interpreted accordingly. As such, using a model to predict the occurrence of species based on species richness to substantiate the effect of the occurrence of that species on species richness provides insufficient detail and evidence to be able to interpret whether or not the results are meaningful for the suggested reverse relationship.

4.4. Single-species surrogates versus multi-species surrogates for species richness estimation

While surrogate approaches are widely used in biodiversity conservation, the surrogate species or species groups have been and

continue to be mainly selected based on a priori criteria, e.g. rarity or charisma, instead of on evidence-based data-driven empirical assessments of effectiveness (Jyväsjärvi et al., 2018). Not surprisingly then, the reported effectiveness of surrogates for species richness has been highly variable, and the topic continues to be highly debated (Carrascal et al., 2012; Sætersdal and Gjerde, 2011). In particular, the usefulness of single-species surrogates for biodiversity richness estimation and ultimately conservation has been strongly questioned before, if not completely dismissed (Cushman et al., 2010; Gross and Noon, 2015; Roberge and Angelstam, 2004). Contrary to single-species, multi-species surrogate approaches do offer more compelling evidence of being useful under certain circumstances (Fleishman et al., 2018; Roberge and Angelstam, 2004), and are able to provide more continuous estimates of species richness. Yet, even multi-species surrogate approaches for species richness estimation are likely to be limited in both space (Billeter et al., 2008; Mac Nally and Fleishman, 2002) and time (Fleishman et al., 2018) due to the different relation of all species (and even populations) with the environment and the continuously changing relationships between species. Given robust statistical testing and explicit independent validation in space or time, multi-species surrogates may, however, be useful for species richness estimations (Fleishman et al., 2018), but their limitations or the uncertainties in space and time should always be acknowledged and where possible quantified.

5. Conclusions

The common cuckoo has recently been repeatedly suggested to be an excellent single-species surrogate of avian biodiversity. Altogether, these studies suggest that the common cuckoo is an effective and inexpensive surrogate for several aspects of avian biodiversity over multiple scales, from the local to the inter-continental scale. Being both a charismatic and relatively easy to monitor species, including also possibilities for citizen science, this would in effect mean that the holy

grail of avian biodiversity has been found. I have presented compelling evidence, however, to strongly doubt the statistical and ecological significance of much of the evidence presented in these studies. As such, I hope to be able to discourage conservation scientists and practitioners from investing time, effort, and money in using the common cuckoo as a single-species surrogate for avian biodiversity conservation. Instead, I suggest the search for surrogates of (avian) biodiversity further focusses on data-driven empirical selection of multi-species surrogates, with an emphasis on appropriately demonstrated and validated transferability in space and time.

Acknowledgements

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