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Multiple species of cuckoos are superior predictors of bird species richness in Asia

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Abstract. The abundance and the presence of common cuckoos Cuculus canorus have been shown to predict species richness of birds across Europe, while there are no such analyses available for other continents where species richness of parasitic cuckoos is larger. Here, we tested whether species richness of birds increased with the number of cuckoo species in two study areas in China and one in Japan. We also tested whether species richness of birds can be predicted by the number of cuckoo individuals. Furthermore, we compared the strength of association between overall bird species richness and species richness of cuckoos, Paridae, Corvidae, and birds of prey. This is the first study demonstrating that cuckoo species richness is more strongly associated with overall bird species richness than richness of species belonging to other families, and rather than occurrence of a single cuckoo species, as already demonstrated for the common cuckoo in Europe. The number of cuckoo species was positively associated with both non-host and host species richness. We found evidence of the number of cuckoo species being associated with species richness of birds independently of country and year, while abundance of individual cuckoos was not a statistically significant predictor. Furthermore, we showed that richness of host species is strongly positively correlated with overall bird species richness in both countries. This implies that the high species richness of cuckoos in South-East Asia is a reliable predictor of overall bird species richness.

Key words: bioindicators; birds; brood parasite; multiple cuckoos; taxonomic diversity.

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INTRODUCTION

Biodiversity and its conservation rely heavily on assessment of species diversity and its component parts, but also on the ability to quantify these components (Gaston and Spicer 2004). Species richness provides one of the simplest univariate measures of community diversity (Magurran 2004), but the assessment of species richness and abundance require reliable methods with little or no error due to methodology or among-observer variability (Møller 1983, Bibby et al. 2005, Voríšek et al. 2010), and merging such data is even a greater cause of concern. Furthermore, the direct assessment of diversity metrics is often difficult and time-consuming. An alternative way for assessment of biodiversity and its component parts is to rely on surrogates or bioindicators.
They are variables that reflect species diversity, their abundance, or other biological phenomena that reveal diversity, abundance, phenology, or other features of natural, man-made, or otherwise perturbed habitats (Burger 2006, Armon and Hänninen 2015). There is a high diversity of bioindicators (review in Armon and Hänninen 2015), raising questions about which have superior efficiency. This will depend on efficiency of conducting research, but also on time and other resources used for assessment of biodiversity, or important features of the living environment. Such indicators require cross-validation, but also links between measures of diversity and actual diversity measured at the ground level.

The use of surrogates or bioindicators represents shortcuts in ecology: a cost-effective strategy to study complex systems (Rodrigues et al. 2007, Lindenmayer et al. 2015). Among the numerous surrogates developed in the last decades, the occurrence and distribution of bird species is one of the potentially most useful surrogates for several reasons: Birds are widely distributed, and breeding bird records are among the easiest species distribution data sets to obtain, thanks to the presence of birding across the world (Padoa-Schioppa et al. 2006, Carrascal et al. 2012).

Cuckoos are unlikely, but highly efficient bioindicators of species richness and abundance of birds (Morelli et al. 2015, 2017c, Tryjanowski and Morelli 2015). In fact, they could be more efficient indicators than alternative taxa used previously, such as raptor species (Sergio et al. 2005, 2008a, b), woodpeckers (Mikusinski et al. 2001, Drever et al. 2008), and combinations of birds and small mammals (Chase et al. 2000) or invertebrates (Báldi 2003). There are steep latitudinal clines in cuckoo species richness in Asia, Africa, South America, and Australia (Erritzøe et al. 2012). Why that is the case remains an open question and is currently a research subject of intense scrutiny. Independently of the origin of this diversity, there is every reason to pose the question how this efficiency of cuckoos as a bioindicator has evolved.

Some studies in Europe and Asia, where our previous studies have been made, indicate that the presence of the common cuckoo and its abundance are reliable bioindicators of bird species richness, much more so than alternative bioindicators such as raptor abundance (Morelli et al. 2015, 2017b, c, Tryjanowski and Morelli 2015).

Among the ecological reasons for cuckoo surrogacy, we have highlighted that the distribution of these parasitic birds is driven not only by climate and trophic availability, but mainly by the presence of their host species (Ducatez 2014, Lee et al. 2014), and the number of host species is positively correlated with overall bird species richness (Morelli et al. 2015). However, until now no study has yet focused on whether cuckoo richness could constitute a reliable bioindicator in Asia, where multiple cuckoo species co-occur. If the previously published studies show that the presence or the absence of cuckoos at a given census point is the basis for cuckoos being a reliable bioindicator, then we should also expect that to be the case when there are more sympatric cuckoo species present.

The objectives of the present study were (1) to analyze the associations between bird species richness and cuckoo species richness and cuckoo abundance, respectively, and (2) compare the strength of these associations also using other bird groups as control. First, we tested whether bird species richness increased with the number of cuckoo species. Second, we compared the strength of associations between overall bird species richness and cuckoo richness, Paridae, Corvidae, and raptor richness. Third, we tested whether the abundance of cuckoo individuals rather than cuckoo species richness was an indicator of bird species richness. Finally, we related the richness of host and non-host species to overall bird species richness and cuckoo species richness.

**Materials and Methods**

**Study sites**

The breeding bird census points were made in China and Japan (Appendix S1: Fig. S1), in three different types of environments: mainly forested areas in Fukushima (Japan), urban forests in Beijing (China), and subtropical moist broadleaf and mixed forests in Guizhou (China). All data were collected during the breeding season. Data were collected in forested areas west of the exclusion zone around the Fukushima Daiichi power plants in 2011–2016 (see more details in Möller et al. 2015a, b). The study in Beijing was conducted during June 2016 in 10 city urban parks across the metropolis (see more details in Morelli et al. 2017a). The study in Guizhou was performed...
during June 2015 in the Kuankuoshui National Nature Reserve, southwestern China, in a subtropical moist broadleaf and mixed forest, interspersed with abandoned tea plantations, shrubby areas, and open fields used as cattle pastures (see more details in Yang et al. 2010a, b). These three areas were selected because they constitute suitable habitat for many cuckoo species, and because they were subject to our previous studies.

**Bird census work**

We conducted standard point counts of breeding birds. The observer started at a randomly chosen site where he recorded all birds seen or heard during a 5-min period in a buffer of 50 m around the observer, before moving at least 100–200 m to the next census point. All sites were visited once. The separation among point counts was useful to avoid any bias related to double counts of cuckoo individuals. Additionally, during field work, we paid special attention to the direction of the origin of cuckoo calls in order to quantify the abundance of cuckoos and to avoid potential double counting. With these precautions, we obtained good results for bird community determination (Møller et al. 2015b, Morelli et al. 2017b). All observers, who have exceptional field skills in the study sites, started early in the morning, and all observations were made under conditions of warm and calm weather. This method has been demonstrated to provide reliable information on relative occurrence of birds (Blondel et al. 1970, Bibby et al. 2005). Extensive national monitoring programs for breeding birds based on point counts occur in many different European countries, as part of environmental monitoring by the European Union (Vorísek et al. 2010).

We directly tested the reliability of our counts by letting two persons independently perform counts, and the degree of consistency was high in terms of species richness, total abundance, and abundance of individual species (details are reported by Møller and Mousseau 2007).

**Statistical analyses**

In this study, for each sample site, we estimated overall bird species richness, cuckoo species richness, and cuckoo individual abundance. Furthermore, we calculated the number of species of Paridae, Corvidae, and birds of prey (species richness). These groups were treated as controls for comparing cuckoo species richness surrogacy of overall bird species richness. These groups were selected for two main reasons: because they have widespread distributions (Paridae and Corvidae), or because they are traditionally used as bioindicators (Sergio et al. 2008a, b). In order to explore the strength of associations between overall bird species richness and cuckoos, Paridae, Corvidae, and raptor species richness, we used Spearman’s correlation coefficients. In order to avoid over-inflated correlations during modeling, we calculated bird species richness deducting the number of species of cuckoos from the total number of bird species at each site, and the same procedure was performed when comparing Paridae, Corvidae, and raptor species richness with overall species richness. Furthermore, bird species richness was decomposed into host and non-host species richness, considering bird species assumed to be host species for each cuckoo species (see details in Yang et al. 2012).

In order to explore the association between host species richness, non-host species richness, and overall bird species richness, we used Pearson’s correlation coefficient.

We used generalized linear mixed models, to account for variation in bird species richness in relation to cuckoo species richness, in two areas in China and one in Japan. The interactions between the three surveyed sites and year of survey were added as random factors in the statistical models (groups = 7; Bolker et al. 2009). A second model was fitted using cuckoo abundance (number of individuals) as predictors, while interactions between site and year were added as random factors. In order to control for the strong correlation between cuckoo abundance and cuckoo species richness ($R^2 = 0.90$, $P < 0.05$), the second model was made only for a subset of data in which cuckoo species richness equaled one.

Models were fitted assuming a Poisson distribution after having explored the distribution of variables as suggested by Box and Cox (1964) using the packages “MASS” (Venables and Ripley 2002), and “glmmADMB” in R (Fournier et al. 2012, Skaug et al. 2013). In this study, Akaike’s information criterion was used to determine the model that “best” explained variation in the data (Burnham and Anderson 2002). Confidence intervals for the significant variables were calculated by the Wald method from the
package “MASS” (Venables and Ripley 2002). All statistical tests were performed with R software (R Development Core Team 2017).

RESULTS

The minimum value of species richness was 0 in point counts from Guizhou and Fukushima, while the maximum was 14 bird species in a point count from Guizhou (Table 1). The average number of bird species richness per point count was slightly higher in Beijing (Table 1).

Bird species richness and cuckoo species richness

Overall bird species richness was positively correlated with host species richness ($r = 0.71$, $P < 0.05$), as well as with non-host species richness ($r = 0.75$, $P < 0.05$; Appendix S1: Fig. S2).

A total of four cuckoo species were recorded in this study in China and Japan: *Cuculus poliocephalus*, *Cuculus canorus*, and *Cuculus saturatus* in Guizhou and Fukushima, while *C. poliocephalus*, *C. canorus*, and *Cuculus micropterus* occurred in Beijing (Appendix S1: Table S1). Areas where cuckoo species were present had a larger number of bird species than areas where cuckoos were absent (Fig. 1A). Bird species richness increased with cuckoo species richness in the three sites, and these differences were statistically significant (Table 2A, Fig. 1A). In fact, bird species richness doubled or tripled when the number of cuckoo species increased from one to four.

When comparing the correlation between overall bird species richness and species richness for each group separately, we found that the strongest correlation was found for cuckoo species richness (Fig. 1A; Appendix S1: Table S2), followed by Corvidae species richness (Fig. 1C; Appendix S1: Table S2), while raptor species richness and Paridae species richness were uncorrelated to overall species richness (Fig. 1B, D; Appendix S1: Table S2). Furthermore, the association between cuckoo species richness and overall species richness was constant in all three localities, while the same associations for Paridae, Corvidae, or raptor species were variable (see Fig. 1A–D).

Bird species richness increased with the number of cuckoo individuals (Appendix S1: Fig. S3), although the effect of cuckoo abundance was not statistically significant (Table 2B). Cuckoo species richness was also positively associated with both host species richness and non-host species richness in all countries (Appendix S1: Table S3, Fig S2A, B).

DISCUSSION

The main finding of this study was that a large species richness of cuckoos during the breeding season was positively associated with bird species richness in three independent study sites in Asia. This is the first study demonstrating that cuckoo species richness mirrors overall bird species richness. Previous studies in Europe have found that even the occurrence of a single cuckoo species, the common cuckoo, also predicts overall bird species richness (Morelli et al. 2015, 2017c, Tryjanowski and Morelli 2015, Møller et al. 2016). Furthermore, we found that species richness of cuckoos was strongly correlated with overall bird species richness and much more so than species richness of other groups such as Paridae, Corvidae, and raptors. We have shown here that bird species richness more than doubled across the range of cuckoo species richness in two sites in China and one in Japan, thereby considerably extending previous findings from Europe of cuckoos as efficient bioindicator of bird species richness. Given that total species richness of cuckoos ranges from one to 17 sympatric species in parts of Asia and Africa (Erritzøe et al. 2012), this may imply that cuckoos are reliable bioindicators even in these areas rich in cuckoo species that are likely characterized by extremely high bird species richness (Gaston 2000).

Perhaps not surprisingly, in this study, we also demonstrated a strong positive correlation between bird species richness and the number of host species in bird communities. Additionally, we demonstrated that cuckoo species richness

| Site               | Years | N  | Mean | SE  | Min | Max |
|--------------------|-------|----|------|-----|-----|-----|
| Guizhou (China)    | 2015  | 205| 4.11 | 0.17| 0   | 14  |
| Beijing (China)    | 2016  | 95 | 5.36 | 0.20| 1   | 11  |
| Fukushima (Japan)  | 2011–2015 | 400| 3.60 | 0.04| 0   | 9   |

Note: In Fukushima were performed 400 bird point counts, repeated once per year during the period 2011–2015.
Fig. 1. Bird species richness in relation to (A) the number of cuckoo species, (B) the number of Paridae species,
was positively associated with both non-host and host species richness. These findings imply that it is not only the interaction between cuckoos and their hosts, but even the presence of non-hosts that is the mechanistic basis for the positive association between bird species richness and cuckoo species richness. These findings also support results from previous studies, specifically for *Cuculus canorus* in Europe (Morelli et al. 2015, 2017c). We hypothesize that the correlation between cuckoos and non-host species may be associated with indirect biotic interactions, or possible direct or indirect interactions between host and non-host bird species (Wisz et al. 2013, Morelli and Tryjanowski 2015).

In contrast to cuckoo species richness, the abundance of cuckoos alone was not predictive of overall bird species richness when analyzed separately after statistically removing the effect of cuckoo species richness. A decrease in the predictive power of cuckoo occurrence and cuckoo species richness in areas with few cuckoo species, but large numbers of individuals of one preferred host species, is not unexpected and is likely a simple product of the lack of statistical power when species richness is minimal (i.e., one). For example, in some urban forests in Beijing, we found wetlands with low levels of overall bird species richness, but a high density of Oriental reed warblers, *Acrocephalus orientalis*, the most frequent host for the common cuckoo *C. canorus* in this region (Yang et al. 2012). In these areas, we found a wide distribution and high density of the common cuckoo, with low cuckoo species richness. Sites with such relationships lead to a decrease in the predictive power of cuckoo occurrence and cuckoo richness as a surrogate for overall bird species richness, constituting a limitation to the methodology of using cuckoos as a surrogate of biodiversity.

Further analyses focusing on the surrogate value of cuckoos for bird diversity or richness may consider the partitioning of each bird community in terms of abundance of species classified by trophic guilds (seed-eaters, insectivores, fruit-eaters, carnivores, and omnivorous birds). These analyses could reveal new insights about the complex mechanisms which appear to play a role in habitat selection of brood parasite species as cuckoo species. Cuckoos show a high diversity of breeding strategies within a single bird family with differences in parental care strategies characterized by facultative and obligate brood parasitism (Krüger and Davies 2002). In parasitic cuckoos, it is well known that selection of host species depends on the capacity of hosts to deliver food to the young in the nest (Grim 2006, Yang et al. 2013). Both the quantity and quality of food provided through parental provisioning significantly influence offspring success (Yang et al. 2013). Thus, we can expect part of the effect on cuckoo surrogacy of bird species richness is associated with the relative composition of carnivorous, insectivorous, and seed-eating host bird species in a given community.

In conclusion, here we have shown that bird species richness is reliably predicted by species richness, with modest variation in relation to cuckoo species richness (A) and the number of cuckoo individuals (cuckoo abundance) (B) in China and Japan. The box plots show medians, mean (yellow rhombus), quartiles, 5 and 95 percentiles, and extreme values.

Table 2. Results of fixed-effect parameters in a generalized linear mixed models, accounting for variation in bird species richness in relation to cuckoo species richness (A) and number of cuckoo individuals (cuckoo abundance) (B) in China and Japan.

| Variable                      | Estimate | CI     | SE   | z     | P       |
|-------------------------------|----------|--------|------|-------|---------|
| (A)                           |          |        |      |       |         |
| Intercept                     | 1.368    | 1.23, 1.51 | 0.070 | 19.43 | <0.00001|
| Cuckoo species richness       | 0.217    | 0.17, 0.26 | 0.023 | 9.36  | <0.00001|
| (B)                           |          |        |      |       |         |
| Intercept                     | 1.625    | 1.37, 1.88 | 0.129 | 12.56 | <0.00001|
| Cuckoo abundance              | 0.021    | –0.08, 0.12 | 0.050 | 0.412 | 0.681   |

*Notes:* The interaction between surveyed sites and year was added as random factors in the model (groups = 7). Model B was performed for a subset where maximum cuckoo richness was one.
richness of parasitic cuckoos in three study areas in Asia characterized by different habitat types. Cuckoo surrogacy, regardless of habitat type, should reflect avian diversity, being associated with both host and non-host bird species. These findings extend previous research in Europe showing that even a single common parasitic cuckoo can reliably predict species richness and that multiple species of cuckoos also imply a higher bird species richness of other bird species. Last but not least, our findings also suggest new perspectives for the use of simple procedures for determining “hotspots” of bird species richness through the simultaneous occurrence of a few bioindicator species (i.e., cuckoos), that are characterized by a very loud and distinctive song, which provides the opportunity for future citizen science projects.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2003/full