Cuckoo and biodiversity: Testing the correlation between species occurrence and bird species richness in Europe

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\textbf{A B S T R A C T}

The use of biodiversity surrogates is an increasingly popular tool, because it provides strong results while reducing the costs of conservation studies. Here, we hypothesize that cuckoo (\textit{Cuculus canorus}) occurrence may correlate with high bird species richness based on the assumption that their presence should mirror the richness of their potential avian hosts and the overall bird community. Specifically, we assessed the association between species occurrence and taxonomic diversity patterns on a multi-spatial scale using datasets from seven European countries. Our results show that high bird species richness is a good proxy for cuckoo occurrence, and the best results were based on data from point counts. The species was almost absent at sites with low species richness, suggesting that the presence of cuckoo is an appropriate surrogate of bird biodiversity. The accuracy of the models ranged from 0.68–0.71 (for large spatial scale) to 0.86 (for local spatial scale) and provided valuable indications of bird taxonomic diversity distribution on all different types of environments monitored in each country. These associations are possibly related to co-evolutionary relationships with host species (correlated with overall species richness) and the cuckoo’s preference for sites that are attractive to many other bird species, due to high habitat diversity or abundant food resources. Our findings highlight how conservation planners can use cuckoo occurrence as a surrogate to maximize efficiency when studying bird species richness patterns. These results also demonstrate the advantages of using the cuckoo rather than top predators as a potential surrogacy tool for citizen scientist programs.

1. \textbf{Introduction}

Conservation planning and management strategies are fundamentally based on spatial information of biodiversity distribution (Margules and Pressey, 2000; Rodrigues and Brooks, 2007; Wiens et al., 2008). Biodiversity has a critically important role in the conservation of ecosystem function, and biologists and managers now recognize that species conservation involves more than simply observing the presence of threatened species (Clark et al., 2014; Geiger et al., 2010; Schwartz et al., 2000; Sol et al., 2014). While different facets of biodiversity are recognized (i.e. phylogenetic, taxonomic, and functional diversity) (Devictor et al., 2010; Zupan et al., 2014) in space and time (Baselga, 2010), species richness remains one of the most important and widely used measures for quantifying biological diversity on Earth. Species richness is also considered a basic surrogate for more complex concepts of ecological diversity and has been successfully applied to assess

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the habitats of different taxa (Boch et al., 2013; Freemark et al., 2006; Maes et al., 2005; Magurran, 2004; Thomas and Mallorie, 1985; Young et al., 2013). Furthermore, many criteria used to study sustainable agriculture practices are based on species richness, alone or in combination with the occurrence of specialist species (Andersson and Lindborg, 2014).

Nevertheless, the study of species richness requires a particularly complex methodology and significant investments of time, effort, and funds. Therefore, an effective indirect method that would suitably account for species richness would be useful (Yoccoz et al., 2001). The use of surrogates to identify hotspots of species richness is a common practice in conservation biology (Carrascal et al., 2012; Roth and Weber, 2008; Sattler et al., 2014; Sergio et al., 2005). Priority areas for conservation are often designed based on the distribution of biodiversity surrogates or bioindicators (Larsen et al., 2012). There are several advantages associated with surrogate use in ecological studies, including the ability to simplify, represent, and assist in complex system management (Lindenmayer et al., 2014); the ease of use, which reduces monitoring costs (Rodrigues and Brooks, 2007); and the predictive capacity for modelling (Mellin et al., 2011). In brief, surrogates can be divided into two main categories (Granath et al., 2010): (1) taxonomic or biotic surrogates and (2) environmental surrogates. Taxonomic surrogates are based on biological data, for example, as a species or groups of species. Environmental surrogates are typically abiotic parameters such as climate (temperature, precipitation, solar radiation), elevation, soil type (Garnier-Géré and Ades, 2001; Sarkar et al., 2005), and various landscape metrics including measures of spatial heterogeneity (Batáry et al., 2010; Morelli et al., 2013; Schindler et al., 2015).

Cross-taxon surrogates are substantially more effective than surrogates based on environmental data (Rodrigues and Brooks, 2007). Among the recent candidates considered as taxonomic surrogates of species diversity, birds are among the most used. They are widely distributed and can be readily identified with numerous monitoring schemes (Kissling et al., 2012; Larsen et al., 2012). Top predators are a good example of bird species that can be used as surrogate bioindicators of species richness. They are one of the best documented avian indicators in terms of both potential and limitations (Cabeza et al., 2007; Kéry et al., 2007; Roth and Weber, 2008; Sergio et al., 2008). The effectiveness of biodiversity surrogates continues to be debated (Granath et al., 2010; Marfil-Daza et al., 2013), but it is widely acknowledged that there is a need for more effective and reliable surrogates in conservation biology. Species richness patterns could be non-concordant on different spatial scales (e.g. local or regional), thus creating conflicts when establishing goals for conservation plans (Ricketts, 2001) and necessitating a multi-scale approach. Alternatively, other bird species or groups of species may be employed as suitable surrogates for species richness, potentially due to co-evolutionary factors. Because biotic interactions affect species’ spatial distributions via several mechanisms such as predation, competition, resource–consumer interactions, host–parasite interactions, mutualism, and facilitation (Bascompte, 2009; van Dam, 2009; Wisz et al., 2013), co-evolutionary considerations may provide insight into the causes of biodiversity distribution (Poulin and Morand, 2005; Thompson, 2005).

The cuckoo Cuculus canorus is a brood parasite that exploits the reproductive behaviors of numerous host species to incubate its eggs and raise its chicks (Davies, 2011; Soler et al., 1999; Weibergen and Davies, 2012). As such, these birds have a specific relationship with potential host populations (Stokke et al., 2007; Wesołowski and Mokwa, 2013). Most insectivorous passerines in Europe have an history of interacting with the common cuckoo, and these pairwise interactions possibly indicate tight co-evolution (Krüger et al., 2009). Cuckoos are also characterized by particularly high detectability due to their distinctive and loud vocalisation, which greatly enhances survey effectiveness. The distinctiveness and popularity of its song also make the cuckoo an effective species to encourage people who are not experienced birdwatchers to participate in a wide-scale volunteer survey under the umbrella of citizen science initiatives.

In the present study, we tested the hypothesis that C. canorus may serve as an effective taxonomic surrogate for bird species richness based on the assumption that the presence of this avian parasite breeder would mirror the richness of its potential avian host community and the local bird community as a whole. We evaluated this hypothesis by measuring whether cuckoo occurrence is related to sites with greater bird biodiversity in different European countries at both small and large spatial scales. Our primary goal was to demonstrate this as an effective approach for assessing taxonomic biodiversity distribution.

2. Methods

2.1. Study area, spatial scales, and environments

The study was carried out using different datasets on bird species’ presence–absence collected in seven European countries (Fig. 1). The data on bird species distribution cover two different spatial scales: (1) local scale, mainly small or medium-size areas (approximately 61.2–3500 km²) in central Greece, central Italy, western Poland, San Marino Republic, and southern Switzerland (1216 sites in total, Table 1) and (2) large scale (from 78,870 to 671,308 km²) in France and the Czech Republic (Table 1).

The sampled sites in western Poland (51.73 N, 17.49E) were mainly distributed on farmlands. The sampled sites in central Italy (43.36 N, 12.50E) were largely grassland with shrublands and scattered woodland patches. In San Marino Republic (43.92 N, 12.43E), the sampled sites were distributed on a mosaic of different land-use typologies, with a greater prevalence of agricultural and small- or medium-size woods mixed with urban and peri-urban patches. The sampled sites in the Prefecture of Trikala, Greece (39.82 N, 21.72E) were distributed on intensified agriculture fields with scattered shrubs and few patches of forestal vegetation. The sampled sites in southern Switzerland (46.04 N, 8.92E) were distributed on managed (open) and unmanaged (closed) chestnut forests.

The sampled sites in France were randomly distributed throughout the country and included agricultural landscapes with gradients of management intensity ranging from intensively managed to high nature value (HNV) farmlands. These areas included mosaics of meadows and pastures, arable fields, midfield woodlots of different ages, scattered trees, and discontinuous linear habitats (mainly mixed rows of trees and shrubs).

The transects surveyed in the Czech Republic covered all the main typologies of environments present in the country.

2.2. Bird data collection

Point counts were carried out each month during the 2010 breeding season (April–June) in all countries, except for Switzerland (samples were collected in different survey campaigns during 2006 and 2013) and Greece (surveyed in two campaigns in 2008 and 2010). All points were visited once between 06:00 and 10:00 for 5 min, only during favorable weather conditions without rain or strong wind. Point counts provide highly reliable estimates of relative population density and are a standardized practical method to compare bird communities among habitats and temporal scales (Bibby et al., 1992). All diurnal bird species detected visually and acoustically were recorded. In France, counts were
obtained during 5 min at 10 points distributed within a 2 × 2 km² area randomly selected for each observer. The detailed method is available in Jiguet et al. (2012). Each transect used to survey the Czech Republic contained 20 census points, with data recorded for 5 min in the morning at approximately 300-m intervals. The transects were visited twice per breeding season by the same observer to sample both early and late breeders (Reif et al., 2013).

2.3. Biodiversity measures

2.3.1. Direct measures

Bird species richness (BSR) was used as a basic surrogate for biodiversity (Magurran, 2004) in all countries and for all spatial scales. At each sampled site, species richness was expressed as the maximum number of recorded bird species.

The French dataset was the largest in the study and included abundance values per species data. For the French dataset, were calculated other biodiversity measures.

Bird diversity (BD) was estimated using the Shannon–Weaver diversity index ($H = \sum p_i \ln (p_i)$, where $p_i$ is the abundance of each bird species in the sampled sites). Host species richness (HSR) was calculated as the sum of all host species present in the sampled site. Finally, the host species were ranked with respect to their published parasitization frequencies (Brooke and Davies, 1987; Davies and Brooke, 1988; Makatsch, 1955; Moskát, 2005; Wesolowski and Mokwa, 2013) (Table 2). The rank values for all the host species present in the bird community were summed and used to classify each sampled site (host species rank, HSRank).

2.3.2. Indirect measures (surrogates)

Two different measures were calculated for the French dataset. They were derived from landscape metrics, which are classically associated with biodiversity in a territory. The types of land use considered in this study were based on the CORINE land-cover vector data derived from 25-m resolution satellite data. CORINE is a

Table 1
Summary of collected observations for Cuculus canorus.

<table>
<thead>
<tr>
<th>Study area</th>
<th>Spatial scale</th>
<th>Sampled sites</th>
<th>Survey type</th>
<th>Cuckoo freq. (%)</th>
<th>Main environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Central Greece</td>
<td>Local</td>
<td>285</td>
<td>Point-count</td>
<td>15.0</td>
<td>Intensive farmland</td>
</tr>
<tr>
<td>Central Italy</td>
<td>Local</td>
<td>287</td>
<td>Point-count</td>
<td>14.5</td>
<td>Grassland</td>
</tr>
<tr>
<td>Western Poland</td>
<td>Local</td>
<td>79</td>
<td>Point-count</td>
<td>21.1</td>
<td>Farmland</td>
</tr>
<tr>
<td>San Marino</td>
<td>Local</td>
<td>250</td>
<td>Point-count</td>
<td>45.2</td>
<td>All environments</td>
</tr>
<tr>
<td>Southern Switzerland</td>
<td>Local</td>
<td>115</td>
<td>Point-count</td>
<td>17.4</td>
<td>Chestnut forests</td>
</tr>
<tr>
<td>France</td>
<td>Large</td>
<td>1153</td>
<td>Point-count</td>
<td>76.2</td>
<td>Farmland</td>
</tr>
<tr>
<td>Czech Republic</td>
<td>Large</td>
<td>101</td>
<td>Transect</td>
<td>35.6</td>
<td>All environments</td>
</tr>
</tbody>
</table>

Fig. 1. Study area and geographic position of the sampled areas in the seven European countries. Gray polygons correspond to countries where large spatial scale analysis was carried out, while black dots indicate local-scale analyses. The gray dots in the right panel represent the distribution of sampled sites in France.

Table 2
List of bird species used as hosts by cuckoo Cuculus canorus.

<table>
<thead>
<tr>
<th>Species</th>
<th>Frequency of host (%)</th>
<th>Rank</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acrocephalus scirpaceus</td>
<td>32.4</td>
<td>10</td>
</tr>
<tr>
<td>Lanius colurio</td>
<td>16.9</td>
<td>10</td>
</tr>
<tr>
<td>Acrocephalus palustris</td>
<td>8.5</td>
<td>10</td>
</tr>
<tr>
<td>Phylloscopus sibilatrix</td>
<td>6.3</td>
<td>10</td>
</tr>
<tr>
<td>Motacilla alba</td>
<td>5.6</td>
<td>10</td>
</tr>
<tr>
<td>Phoenicurus ochruros</td>
<td>4.9</td>
<td>1</td>
</tr>
<tr>
<td>Erithacus rubecula</td>
<td>4.2</td>
<td>1</td>
</tr>
<tr>
<td>Prunella modularis</td>
<td>3.5</td>
<td>1</td>
</tr>
<tr>
<td>Sylvia communis</td>
<td>2.4</td>
<td>0.1</td>
</tr>
<tr>
<td>Hirundo rustica</td>
<td>2.1</td>
<td>0.1</td>
</tr>
<tr>
<td>Saxicola rubetra</td>
<td>2.1</td>
<td>0.1</td>
</tr>
<tr>
<td>Acrocephalus arundinaceus</td>
<td>2.1</td>
<td>0.1</td>
</tr>
<tr>
<td>Anthus trivialis</td>
<td>1.4</td>
<td>0.1</td>
</tr>
<tr>
<td>Phoenicurus phoenicurus</td>
<td>1.4</td>
<td>0.1</td>
</tr>
<tr>
<td>Sylvia curruca</td>
<td>1.4</td>
<td>0.1</td>
</tr>
<tr>
<td>Troglytes troglodytes</td>
<td>1.4</td>
<td>0.1</td>
</tr>
<tr>
<td>Alauda arvensis</td>
<td>1.2</td>
<td>0.1</td>
</tr>
<tr>
<td>Muscicapa striata</td>
<td>1.2</td>
<td>0.1</td>
</tr>
<tr>
<td>Turdus merula</td>
<td>1.2</td>
<td>0.1</td>
</tr>
<tr>
<td>Hippolais icterina</td>
<td>0.7</td>
<td>0.1</td>
</tr>
<tr>
<td>Phylloscopus collybita</td>
<td>0.7</td>
<td>0.1</td>
</tr>
<tr>
<td>Motacilla flava</td>
<td>0.7</td>
<td>0.1</td>
</tr>
<tr>
<td>Sylvia atricapilla</td>
<td>0.7</td>
<td>0.1</td>
</tr>
<tr>
<td>Sylvia borin</td>
<td>0.7</td>
<td>0.1</td>
</tr>
<tr>
<td>Sylvia nisoria</td>
<td>0.7</td>
<td>0.1</td>
</tr>
</tbody>
</table>

* Data from previous studies were used for the relative frequency of parasitization, and ranking was performed to classify the sampled sites on the presence of potential hosts.
national georeferenced land-cover database that is based on satellite digital images for all of France. This land-cover layer uses remote sensing to classify landscape units larger than 25 ha into 44 classes (Boscard et al., 2000).

Land-uses diversity (LUD) is a surrogate of available trophic niches and therefore of potential biodiversity (Kisel et al., 2011). LUD was calculated using the Shannon–Weaver diversity index with the formula \( H = \sum p_i \ln (p_i) \), where the \( p_i \) values are the proportions of the different land-use types within a 1-km radius surrounding the sample site.

The weighted edge density (WEDG), which is considered a good surrogate of ecological diversity because it indicates landscape heterogeneity (Morelli et al., 2013; Schindler et al., 2015), was calculated as the sum of the perimeters of all polygons in the buffer zone per number of land-use types/buffer surfaces (Hargis et al., 1998).

2.4. Statistical analyses

The sampled sites at the local scale were treated as statistically independent observations because the spatial autocorrelation values were not significant. A Mantel test was performed on different subsets of the sampled sites between geographic distances and bird species richness dissimilarities (Manly, 2006). Dissimilarity indices among sampled sites were calculated using the “vegdist” function of the vegan package for R software (Oksanen, 2014) by applying the Sørensen index of dissimilarity between pairwise sites for bird species richness.

The correlations between biodiversity measures in France (BSR, BD, HSR, HSRank) were studied by means of linear regression because the variables are nested. The nature and strength of the relationship between cuckoo occurrence and species richness at each sample site (both local and large scale) were examined using generalized linear models (GLMs) (McCullagh and Nelder, 1989). The ecological rational for the models was that cuckoo occurrence is sensitive to bird species richness variations. Therefore, cuckoo occurrence was used as the response variable, assuming a binomial distribution, while biodiversity measures (bird species richness, bird diversity, and host species richness) were used as predictors. Because predictors are correlated, the models were carried out separately using only one predictor. The confidence intervals for each model are based on the profiled log-likelihood function.

An additional set of GLM models were generated for the large French dataset. We used taxonomic biodiversity (bird species richness) as the response variable, assuming a Poisson distribution, and the predictors were landscape heterogeneity measures (LUD: land-use diversity, WEDG: weighted edge density) and cuckoo occurrence.

We provided two measures of model performance: the overall goodness of fit (explained deviance) and the ability of the model to discriminate between the two groups defined by the response variable (discrimination skills). The amount of deviance each logistic model accounted for was estimated using the D\textsuperscript{2}quared function in the modEvA package for R (Barbosa et al., 2014) and calculated as the Nagelkerke pseudo R\textsuperscript{2} for logistic regression models (Nagelkerke, 1991). However, pseudo R\textsuperscript{2} statistics in logistic regression is not equivalent to the R-square means in OLS regression (the proportion of variance of the response variable explained by the predictors) (Hu et al., 2006), and for this reason we suggest interpreting this statistic with great caution. For the Poisson models, the amount of deviance each model accounted for was estimated as \( D = (\text{null deviance} - \text{residual deviance})/\text{null deviance} \).

The measure of a statistical model’s discrimination skill evaluates the discrepancy between observed and expected values (Hosmer et al., 1997). The predictive power of the bird species richness as a surrogate of cuckoo occurrence was quantified using the area under the receiver-operating characteristic (ROC) curve (AUC) of the logistic models in the ROCR package for R (Sing et al., 2015). The AUC indicates for each model the predictive performance expressed as an index ranging from 0 to 1 (DeLong et al., 1988). However, when considering the predictive power, the useful range is between 0.5 (random) and 1 (perfectly accurate predictions in binomial response variables). The measure of AUC accuracy can be summarized as follows: 0.90–1.00, excellent; 0.80–0.90, good; 0.70–0.80, fair; 0.60–0.70, poor; and 0.50–0.60, fail (Swets, 1988). All statistical tests were performed with R software (R Core Team, 2014).

3. Results

A total of 54,568 records from 2270 sample sites in different environmental typologies following similar sampling design (point count or transects) were collected from seven European countries (Table 1). The frequency of cuckoo occurrence in the different countries ranged from 14.5% for grasslands in central Italy to 76.2% for cultivated landscapes in France. The average BSR per sampled site ranged from a minimum of four species (min: 2, max: 16 species) for intensively cultivated arid zones in central Greece to a maximum of 36 species (min: 5, max: 58 species) in France.

3.1. Correlation between cuckoo occurrence and bird species richness on a local scale

The average BSR at the local/small scale was higher at sites where cuckoos were present (Fig. 2). In the five countries where local-scale analysis was performed, the models developed using BSR as a predictor of cuckoo occurrence were significant, with BSR always correlating with the response variable (Table 3). The models showed good discrimination performance with goodnesses of fit ranging between 0.74 and 0.86 (Fig. 3).

3.2. Correlation between cuckoo occurrence and bird species richness on a large scale

Cuckoos in the Czech Republic and France were mainly distributed at the sampled sites with greater bird diversity values. In France, the species was only present when bird species richness was at least 15 species. Conversely, cuckoos were absent at sites with lower bird diversity values (Fig. 4).

The correlation between cuckoo occurrence and measures of bird diversity was significant for both diversity index and species richness (Table 3, Fig. 5). Furthermore, host species richness and sampled sites ranked on host species were predictive of cuckoo occurrence (Table 3). The discrimination performance of models using BSR as surrogate of cuckoo presence ranged from 0.68 for the Czech Republic to 0.71 for France (Table 3, Fig. 3).

The four measures of bird diversity correlated with one another; the highest correlations were observed between bird diversity and bird species richness and between host species richness and BSR (BD-BSR: 0.67, HSR-BSR: 0.61, HSRank-BSR: 0.36, HSR-BD: 0.43, HSRank-BD: 0.20, HSRank-BSR: 0.43, all \( p < 0.05 \), \( n = 1153 \)). The models using bird species richness as the response variable showed an increase on performance, and it was nearly 21% greater when adding cuckoo occurrence as a predictor compared with the model using only landscape heterogeneity measures (Table 4).

4. Discussion

4.1. Cuckoo as a multi-scale surrogate of bird species richness

In this work, we suggest that the cuckoo possesses several attributes that make it an attractive bioindicator (Bani et al., 2006;
The cuckoo is a trans-Saharan migratory bird that arrives late in the breeding season, which allows the potential host species the opportunity to start breeding prior to their arrival (Saino et al., 2009; Tryjanowski et al., 2005). This would translate into a specific pattern of landscape-scale cuckoo distribution localized to sites of high bird species richness.

In this study, we hypothesized that cuckoo presence is sensitive to variations in bird species richness due to co-evolution with host species. Our findings provide strong evidence that cuckoos are mainly distributed among sites with high bird species richness. Based on this, we can conclude that cuckoo presence would be a good surrogate of bird biodiversity. The models’ performances were convincing, even when they were based on a single predictor, showing good discrimination capacities (AUC). However, the pseudo $R^2$ value used to measure the variance in this study was based on comparisons between the log-likelihood from the null model (with intercept alone) and the log-likelihood from the full model (with predictors included). This reduces the potential for a straightforward interpretation. Hosmer and Lemeshow (2005) demonstrated that pseudo $R^2$ measures are more appropriate for evaluating multiple models that predict the same outcome for the same dataset, rather than comparing different models or measuring the overall goodnesses of fit. Mittlböck and Schemper (1996) explained that the pseudo $R^2$ depends on the range and distribution of explanatory factors. That is, with binary responses, the values tend to be low even for an underlying perfect regression relationship. Some criticisms moved on use AUC measures to assess models accuracy were highlighted by Lobo et al. (2008), and are related mainly to: AUC could inflate slightly the discrimination skill of models performed on dataset with too many zeros; AUC weights omission and commission errors.

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### Table 3

Results of GLM logistic models relating cuckoo occurrence to biodiversity measures at different spatial scales and measures of goodness of fit.

<table>
<thead>
<tr>
<th>Study area</th>
<th>Predictor</th>
<th>Scale</th>
<th>ES</th>
<th>CI</th>
<th>SE</th>
<th>z</th>
<th>p</th>
<th>Pseudo $R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Central Greece</td>
<td>BSR</td>
<td>Local</td>
<td>0.40</td>
<td>(0.22–0.57)</td>
<td>0.08</td>
<td>4.4</td>
<td>&lt;0.05</td>
<td>0.26</td>
</tr>
<tr>
<td>Central Italy</td>
<td>BSR</td>
<td>Local</td>
<td>0.37</td>
<td>(0.26–0.48)</td>
<td>0.05</td>
<td>6.3</td>
<td>&lt;0.05</td>
<td>0.51</td>
</tr>
<tr>
<td>Western Poland</td>
<td>BSR</td>
<td>Local</td>
<td>0.21</td>
<td>(0.08–0.35)</td>
<td>0.07</td>
<td>3.1</td>
<td>&lt;0.05</td>
<td>0.40</td>
</tr>
<tr>
<td>San Marino</td>
<td>BSR</td>
<td>Local</td>
<td>0.18</td>
<td>(0.14–0.24)</td>
<td>0.02</td>
<td>6.1</td>
<td>&lt;0.05</td>
<td>0.53</td>
</tr>
<tr>
<td>Southern Switzerland</td>
<td>BSR</td>
<td>Local</td>
<td>0.29</td>
<td>(0.13–0.48)</td>
<td>0.08</td>
<td>3.4</td>
<td>&lt;0.05</td>
<td>0.44</td>
</tr>
<tr>
<td>Czech Republic</td>
<td>BSR</td>
<td>Large</td>
<td>0.10</td>
<td>(0.02–0.12)</td>
<td>0.02</td>
<td>2.9</td>
<td>&lt;0.05</td>
<td>0.21</td>
</tr>
<tr>
<td></td>
<td>BSR</td>
<td>Large</td>
<td>0.10</td>
<td>(0.09–0.11)</td>
<td>0.01</td>
<td>10.1</td>
<td>&lt;0.05</td>
<td>0.38</td>
</tr>
<tr>
<td>France⁵</td>
<td>BD</td>
<td>Large</td>
<td>2.51</td>
<td>(2.05–3.00)</td>
<td>0.24</td>
<td>10.3</td>
<td>&lt;0.05</td>
<td>0.43</td>
</tr>
<tr>
<td></td>
<td>HSR</td>
<td>Large</td>
<td>0.20</td>
<td>(0.14–0.24)</td>
<td>0.02</td>
<td>7.8</td>
<td>&lt;0.05</td>
<td>0.35</td>
</tr>
</tbody>
</table>

Abbreviations: ES, estimate; CI, confidence interval; SE, standard error; BSR, bird species richness; HSR, host species richness.

* Only significant variables are shown in the table.

⁵ In France, each predictor corresponds to a separate model.
equally, and AUC could be biased in the case of small datasets. However, in our case study (with large dataset and a gradient of presence/absence cases) we retain that AUC is an adequate tool, based on the proportion of correctly classified subjects.

The cuckoo occurrence was also a better surrogate of BSR than habitat heterogeneity measures, which are often used as proxy. Likewise, it is important to be cautious with extrapolations for conservation purposes because species richness hotspots may not show perfect congruence among taxas. Previous studies have focused on these aspects of ecology and highlighted the primary concerns (Prendergast et al., 1993; Ricketts, 2001).

Spatial patterns of species richness are strongly dependent on spatial scale (Lennon et al., 2001). For this reason, effective conservation strategies should also rely on multi-spatial scales (Devictor et al., 2010). If this approach is employed, it offers a powerful ecological tool by providing a single surrogate can be used on multiple spatial scales. The proposed methodology offers a very simple and cost-effective alternative to predict potential sites with high bird species richness.

**Fig. 3.** Predictive performance of taxonomic biodiversity (bird species richness) as a surrogate of cuckoo occurrence in different European countries at local and large scales. The lines represent the area under the curve (AUC) that indicates how well the model fits a set of observations using the selected predictor.

**Fig. 4.** Count of cuckoo’s occurrence in the sampled sites ordered by values of bird species richness for the large-scale analysis in France (n = 1153). The heights of the bars represent the counts of cases in each group, where 1 is the maximum height of the bar corresponding to the 100% of cases. Cuckoos were absent in all sites with low bird species richness.
species richness, independent of the environment. An important characteristic, considering that the distribution of biological diversity often changes along environmental gradients, which affects the use of certain predictive tools (Meynard et al., 2011; Morelli et al., 2013).

Furthermore, our results support recent studies conducted on a local spatial scale in farmlands of Poland, where the efficiency of cuckoo as surrogate of bird species richness was 27% higher than the best performance using top predators as a surrogate (Tryjanowski and Morelli, 2015).

4.2. Ecological reasons for cuckoo surrogacy

The relationship between cuckoo occurrence and bird diversity is also related to host species richness patterns, which are strongly correlated with bird species richness. In our study, this correlation was quantified at a large spatial scale in France, with significant results higher than 0.67. The direct relationship between avian brood parasites and the occurrence of host species is an important characteristic in their life history, defining the realized niche for the former. In fact, the patterns of parasite distribution are driven by their own ecological needs (climate and food availability) and also those of their host species (Ducatez, 2014; Lee et al., 2014).

From a co-evolutionary perspective, the long-term ebb and flow of co-evolutionary selection might be an important source of ecological dynamics that increases biodiversity (Thompson and Cunningham, 2002). Sites with higher avian diversity are characterized by both higher cuckoo host species diversity and higher host abundance (Hochberg and van Baalen, 1998). The correlation between cuckoo occurrence and bird diversity in this study might result from a co-evolutionary relationship with hosts (more species of hosts resulting in a higher probability of cuckoo presence).
a cuckoo preference for sites that are attractive to many other bird species because of favorable environmental characteristics (e.g. high habitat diversity, abundant food resources, etc.), and/or the heterospecific attraction hypothesis (Monkkonen et al., 1999; Thomson et al., 2003). These factors may provide insight into the cuckoo’s presence at sites with greater species richness. A possible cascade of interactions involving several important hosts of the cuckoo (e.g. Acrocephalus scirpaceus, Lanius collurio, Phylloscopus spp., Sylvia spp., Erithacus rubecula, etc.) and other bird species could help explain the observed patterns. Recent studies highlighted that positive heterospecific interactions can affect bird species distribution (Morelli and Tryjanowski, 2015).

Additionally, the cuckoo is well adapted to live in several kinds of habitats including forests, farmlands, grasslands, open lands, and marshes (Erritzøe et al., 2012). Its potential use as a surrogate is strengthened by the fact that it is a widespread species.

4.3. Conservation implications

Given that biodiversity is dynamic, ever changing in response to the environmental pressures, it is necessary to monitor its status quo in time and space, and, subsequently, monitor variations in order to identify changes and assess their impacts (Green et al., 2009). Monitoring species diversity allows to quantify temporal and spatial fluctuations of species richness over different spatial scales and along gradients of pressure such land use and climate changes. National biodiversity monitoring programs are important instruments that allow to verify the achievement of international agreements among countries worldwide (e.g. Conventions on Biological Diversity of Nagoya) and all of them include species richness as one of the most important components of biodiversity. Then, a surrogate of species richness constitutes an useful tool for the general public and politicians, often forced to work following rigid timescale and moderate costs, then focus only few elements (Weber et al., 2004). Indeed, surrogates are commonly used to reduce the complexity of quantifying biodiversity for conservation purposes (Sattler et al., 2014).

Attributes that can improve the effectiveness of an ecological surrogate include the use of species that are well known, conspicuous, and readily measurable (Cabeza et al., 2007). The cuckoo falls under the flagship species definition suggested by Samways et al. (1995): a known charismatic species that serve as a symbol or focus point to raise environmental consciousness. The species’ charisma is essential to its selection as a flagship. Its recognition by the population potentially guarantees its use on a large scale (Home et al., 2009; Segura et al., 2014). Importantly, the cuckoo is relatively easy to detect due to its conspicuous song. The public’s strong knowledge of the species and familiarity with its vocalisations is spread over a wide geographical area. The name of this bird is highly similar across several languages, because it is based on the bird song, which further demonstrates the public’s familiarity with this species. These onomatopoetic names, probably derived from continuous exposure to the bird song through the centuries, have approximately the same pronunciations in different languages (English: cuckoo, Italian, cuculo; French, coucou; Spanish, cuco; Polish, kukulka; Dutch, koekoek; German, kuckuck; Russian, kukushka; Japanese, kak-ko). The appeal of the cuckoo song, which further demonstrates the public’s familiarity with this species means that there is no variation in detection probability, and uncorrected values are acceptable for identifying ecological patterns and general responses (Bas et al., 2008).

On the basis of our results, we suggest the development of a cheap and effective method to quickly assess the overall bird species richness patterns in a local or regional territory. For example, the methodology could survey cuckoos as a surrogate of bird community diversity during the breeding season by recording call songs. Such a method would be suitable for most of the common natural or semi-natural environments (e.g. farmlands, grasslands, forest). The use of species song would also make the method suitable for citizen scientists. As part of the proposed methodology, we suggest performing a partial (20–25%) traditional bird census (recording all detected bird species) to verify the performance of cuckoo surrogacy in real time. The method would be also valuable because it would improve general awareness about changes in species richness at local and regional levels. In addition, the use of a high acceptance species like the cuckoo, which is recognized by politicians and policy makers, may help achieve conservation goals and increase public acceptance of expensive measures for conserving biodiversity and species richness. Valuable, also considering that biodiversity surrogates need simple definitions and should be easy to communicate (Weber et al., 2004).

In conclusion, the proposed methodology is acceptable for both local and large spatial scales, with better results for data obtained by means of point counts. This is an alternative method to assessing hotspots of bird species richness, less complicated than the approach based on top predators, group of species or focal species.

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