INTRODUCTION

Measuring the extent to which a species is specialized is a major challenge in ecology, with important repercussions for fundamental research as well as for applied ecology and conservation. Here, we develop a multidimensional index of specialization based on five sets of ecological characteristics of breeding bird species. We used two recent databases of species traits of European birds based on foraging ecology, habitat, and breeding characteristics. The indices of specialization were calculated by applying the Gini coefficient, an index of inequality. The Gini coefficient is a measure of statistical dispersion on a scale between 0 and 1, reflecting a gradient from low to high specialization, respectively. Finally, we tested the strength of the phylogenetic signal of each specialization index to understand how the variance of such indices is shared throughout the phylogeny. The methods for constructing and evaluating a multidimensional index of bird specialization could also be applied to other taxa and regions, offering a simple but useful tool, particularly suited for global or biogeographic studies, as a contribution to comparative estimates of the degree of specialization of species.

KEYWORDS
animal specialization, bird, conservation ecology, generalist, phylogenetic signal, trait-based approach
2.2 | Specialization indices and overall specialization

We estimated the degree of specialization in diet, foraging behavior, foraging substrate, habitat, and nesting site for each bird species.

### TABLE 1  Species traits used for the estimation of specialization indices in European birds, including the number of variables for each group and sources of data

| Group of species traits | No. variables | Source |
|-------------------------|---------------|--------|
| Diet (all year)         | 9             | Storchová and Hořák (2018) |
| Diet (breeding season)  | 9             | Storchová and Hořák (2018) |
| Foraging behavior      | 9             | Pearman et al. (2014)     |
| Foraging substrate     | 9             | Pearman et al. (2014)     |
| Habitat                | 15            | Storchová and Hořák (2018) |
| Nesting site           | 18            | Pearman et al. (2014)     |
using the Gini index of inequality (Colwell, 2011; Gini, 1921). The index is based on the Gini coefficient, a measurement of statistical dispersion on a scale between 0 and 1, representing low to high specialization, respectively. This measure was developed by the Italian statistician Corrado Gini in 1921 and is probably the best single measure of inequality (Gastwirth, 1972). It is commonly used in the study of economic inequalities (Lerman & Yitzhaki, 1984), and also for measuring the evenness of coverage of protected areas among habitat types (Barr et al., 2011).

The Gini coefficient is estimated with the following formula:

\[
G = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} |x_i - x_j|}{2n^2 \bar{x}}
\]

where “x” is an observed value, “n” is the number of values observed and “\(\bar{x}\)” is the mean value.

In the specific case of our table of avian traits, if every variable in a group (e.g., diet specialization) has exactly the same value or weight, the index would equal 0, indicating the maximum generalism for that trait. In contrast, the Gini coefficient would equal 1, indicating perfect inequality (high specialization), when a species has a diet entirely composed of a single type. Applying this procedure, we obtained five different specialization indices: diet specialization, foraging behavior specialization, foraging substrate specialization, general habitat specialization, and nesting site specialization.

Finally, to explore the consequences of reducing the index to a single number, an overall “specialization index” was estimated for each species, calculated as the mean, maximum, and minimum values of the five single specialization indices based on diet, foraging behavior, substrate, habitat, and nesting site, subsequently standardized between 0 (generalist species) and 1 (specialist species).

2.3 | Phylogenetic signal of specialization

The phylogenetic signal can be briefly defined as the tendency for related species to resemble each other, more than they resemble species drawn at random from a phylogenetic tree (Blomberg, Garland, & Ives, 2003). This is because all organisms descend from common ancestors and hence are related in a hierarchical fashion (Futuyma & Agrawal, 2009). A high phylogenetic signal indicates species traits that are more similar in close relatives than distant relatives, while traits that are more similar in distant than close relatives or randomly distributed species across a phylogeny suggest a low phylogenetic signal (Kamil & Cooper, 2013). Some studies have focused on quantifying these differences in phylogenetic signal among species and traits (Blomberg et al., 2003; Münkemüller et al., 2012). However, further studies have to clarify the nature of phylogenetic signal in biological or functional traits, mainly in behavioral and ecological characteristics of species (Kamil & Cooper, 2013). Here, we calculated the phylogenetic signal for all specialization indices, to test whether the indices appear to be describing an ecological phenomenon underpinned by evolution.

Considering that bird species are evolutionarily related, they cannot be treated as independent sampling units in comparative analyses (Harvey & Purvis, 1991). Thus, we modeled interspecific variation across a phylogeny, obtaining the phylogenetic relationships from “www.birdtree.org”. We downloaded 1,000 phylogenetic trees from the backbone tree based on Ericson et al. (2006) for the 365 bird species that were the focus of this study. The consensus tree was obtained applying the 50% majority rule (i.e., the proportion of a split to be present in all trees). In order to manage phylogenetic trees, we used the following R packages: “ape” (Paradis, Claude, & Strimmer, 2004), “phangorn” (Schliep, 2011), and “Rphylip” (Revell & Chamberlain, 2014).

2.4 | Statistical analysis

The Gini coefficient for each group of species traits (specialization indices) was calculated using the package “DescTools” for R (Signorell, 2019). Associations among the specialization indices for diet, foraging behavior and substrate, habitat, and nesting site were explored using correlation coefficients. A Shapiro–Wilk normality test was used to test the normality of the distribution of each specialization index, and a Spearman correlation test was used when the distribution of the specialization indices was not normal (Triola, 2012).

To measure the strength of the phylogenetic signal (Blomberg & Garland, 2003) in the five specialization indices and the overall specialization index for 365 European bird species, we used Blomberg’s K statistic and statistic \(K'\) (Blomberg et al., 2003). The K statistic works as a mean square ratio, where the numerator is the error assuming that the trait evolves independently of the phylogenetic structure, and the denominator is corrected by the phylogenetic covariances. When \(K\) approaches 1, trait evolution follows a mode of evolution that is consistent with Brownian motion. If \(K > 1\) and \(<1\), close relatives are more similar and less similar, respectively, than expected under Brownian motion, indicating a strong phylogenetic signal, while \(K\)-values closer to zero it is concluded that the trait has no phylogenetic signal (Blomberg et al., 2003). Blomberg’s K statistic was estimated using the R package “phylosignal” (Keck, Rimet, Bouchez, & Franc, 2016). Moran’s corregograms were used to assess how phylogenetic autocorrelation changes across different phylogenetic distances. Moran’s correlograms were plotted using the function “phyloCorrelogram” from the package “phylosignal” (Keck et al., 2016).

All statistical tests were performed with R software version 3.2.4 (R Development Core Team, 2017).

3 | RESULTS

We calculated six specialization indices for each bird species, considering different functional dimensions (diet all year, diet during the breeding season, foraging behavior, foraging substrate, habitat, and nesting site) by estimating the Gini coefficient (Table S2). All specialization indices showed a non-normal distribution (Shapiro–Wilk normality test for all specialization indices, p-values < 0.05). The most strongly correlated specialization indices among species traits were the indices...
for diet all year and diet during the breeding season, followed by
habitat specialization with nesting site specialization (Figure 1, Table S3).
Foraging behavior specialization was also correlated with foraging sub‐
strate specialization and foraging substrate specialization with nesting site
specialization (Figure 1, Table S3). Nesting site specialization was signifi‐
cantly correlated with all the other specialization indices, while other
specialization indices were not statistically significantly correlated
among themselves (Figure 1, Table S3). Considering the strong cor‐
relation between diet all year and diet during the breeding season
(correlation coefficient = 0.833, \( p < 2.2\text{e}^{-16} \)), we use only diet during
year for further analysis.

Analyzing specialization separately for each functional dimen‐
sion, 111 species were classified as diet specialists (30.4%), 143 as
foraging behavior specialists (39.2%), 68 as foraging substrate spe‐
cialists (18.6%), 96 as habitat specialists (26.3%), and two as nesting
site specialists (0.5%; Table S2).

Additionally, we calculated the overall specialization index by
normalizing the mean values of the five specialization indices be‐
tween 0 and 1 (Table S2). Marked generalism occurred in several clades such as
tits, thrushes, and crows (Figure 2). The five most generalist species
were common chaffinch *Fringilla coelebs*, European pied flycatcher
*Ficedula hypoleuca*, common crane *Grus grus*, carrion crow *Corvus
corone*, and European robin *Erithacus rubecula* (Table S2).

Analysis of the phylogenetic signal in all five specialization index
values returned the following statistically significant \( K \) and \( K' \) values
(all \( p < 0.01 \)): \( K = 1.082 \) for diet specialization, \( K = 0.917 \) for foraging
behavior specialization, \( K = 0.879 \) for foraging substrate specialization,
\( K = 1.375 \) for habitat specialization, and \( K = 0.777 \) for nesting site spe‐
cialism, suggesting a generally high degree of phylogenetic signal
(Table 2, Figure 3). For habitat specialization and nesting site specialization,
the \( K \)-values were lower than 1 (\( K = 0.753–0.777 \)) and statistically
significant, suggesting that a model similar to Brownian motion is
likely, although closely related species are slightly less similar in the
two specialization indices than expected based on phylogenetic
relatedness alone (Table 2). Also the index of overall specialization
was characterized by a statistically significant phylogenetic signal
(Table 2, Figure 3).

4 | DISCUSSION

The use of niche or functional dimensionality in the study of wild‐
life ecology dates back more than 100 years to the classical work
by Grinnell (1917). Species diversification, changes in species traits, and niche evolution across the tree of life are mainly due to the process of adaptive radiation (Castiglione, Mondanaro, Carotenuto, & Passaro, 2017; Schluter, 2000). As a result, traits of species provide a tool for understanding—and potentially classifying—such species in terms of a specialization gradient. Here, we have provided and tested a simple framework for calculating specialization indices based on species traits.

We calculated five different indices of specialization, focusing on five different groups of readily available species traits or “natural history” dimensions of European birds and applying the Gini coefficient to each set of traits. We also explored how the specialization indices in different functional dimensions are correlated. Among the five specialization indices estimated for European birds, diet specialization calculated for the entire year and diet specialization calculated for the breeding season were the most tightly correlated (Table S3). This result could be interpreted in ecological terms as confirming a relatively constant diet composition through the year in European breeding birds, but it could be also interpreted in methodological terms, suggesting that just one dimension (e.g., diet throughout the year) is sufficient to characterize dietary specialization in this group of birds. However, although many indices were positively correlated with one another, only a few were strongly related, highlighting the importance of assessing specialism in a number of different dimensions without reducing specialization to a single overall index value. Using a diverse set of traits permits a better description of each dimension characterizing the species, as well as the overall level of specialism. This is also important for conservation since different

**FIGURE 2** Fan dendrogram representing the overall specialization index, in a colored gradient from generalist (dark blue) to specialist species (red). Tips represent the avian phylogeny of the 365 European bird species that were the focus of this study. The bird silhouettes used in this figure represent four specialists and four generalists.

**TABLE 2** Phylogenetic signal of five specialization indices based on diet, foraging behavior, foraging substrate, habitat, and nesting site and the overall specialization index for 365 European bird species included in this study

| Specialism index          | K statistic | p value | K’ statistic | p value |
|---------------------------|-------------|---------|--------------|---------|
| Diet specialization       | 1.082       | <0.01   | 1.081        | <0.01   |
| Foraging behavior specialism | 0.917   | <0.01   | 0.919        | <0.01   |
| Foraging substrate specialism | 0.879 | <0.01   | 0.872        | <0.01   |
| Habitat specialism       | 0.753       | <0.01   | 0.755        | <0.01   |
| Nesting site specialism  | 0.777       | <0.01   | 0.780        | <0.01   |
| Overall specialism       | 0.892       | <0.01   | 0.889        | <0.01   |

Note: The table shows K statistic, K’ statistic, and associated p-values for each index.
sets of traits can help identify a broader range of species’ vulnerabilities, and hence which species might be most sensitive to which anthropogenic threats (Allan et al., 2019; Hatfield, Orme, Tobias, & Banks-Leite, 2018; Henle, Davies, Kleyer, Margules, & Settele, 2004).

All indices estimated in this study showed a strong phylogenetic signal, indicating that more closely related species tended to show more similar levels of specialization. This is further confirmation that the specialization indices calculated in this study, by applying the Gini coefficient on groups of species traits, are describing ecological phenomena congruent with evolutionary principles. The continuous traits of closely related species in a phylogeny tend to be similar, mainly because such traits are derived from a common ancestor and because they were shaped by selection originating from the environment (Keck et al., 2016). The Brownian motion model assumes that the correlation among trait values is proportional to the extent of shared ancestry for pairs of species, or, in other words, that “members of lineages that have only recently diverged will necessarily (on average) tend to be similar, as compared with more distantly related lineages” (Blomberg et al., 2003). Our results suggest that the five specialization indices estimated for European birds operate in a similar manner, even if for some specialism indices close relatives were more similar (diet specialism) or less similar (other specialism indices) than expected under a Brownian motion model of trait evolution (Blomberg et al., 2003).

The use of specialization indices based on species traits raise the possibility of robustly comparing results across studies and regions, and updating the indices as additional information becomes available. In comparison with previous approaches (e.g., methods for calculating the Species Specialization Index; Julliard et al., 2006), our method does not need de novo data collection.

In conservation ecology, a deep understanding of the characteristics that make a species susceptible to extinction is essential. Ecological specialization is generally thought to be a key contributor to a species’ risk of extinction, although while paleoecological studies investigating longer term survival have confirmed this hypothesis, other comparative studies focusing on the history of entire lineages, suggest that specialist species could be more ecologically "plastic" than expected, sometimes able to become generalists (Clavel et al., 2011; Colles et al., 2009). With the tool presented in this study, we expect to forge a deeper understanding of the level of specialization of species, by focusing on the relative specialization in different trait dimensions and pointing out how this multidimensional gradient of specialization can be used to assess the overall conservation status of different species. However, although the proposed methodology is useful for measuring the level of specialization of species, we
highlight potential drawbacks and finally provide some thoughts for optimizing the potential of this approach.

An important point is that species classified as a specialist in at least one category (e.g., diet specialist and habitat specialist) could, and perhaps should, be considered a specialist species overall. For example, extreme specialization in just one category of species traits (e.g., diet) could determine the level of extinction risk for a species, much more so than the value of the overall specialization index, in which extreme values are averaged away. While we recognize the convenience of deriving a single index of specialization (e.g., overall specialization index, created in our study only for reference), we consider it preferable to work with the five constituent specialization indices. So, we suggest assessing the level of specialization of species by considering separately each dimension of specialization or bundle of traits. We also suggest treating the specialization indices as a package or bundle, in a similar way as proposed for the multidimensional indices for estimating functional diversity (Villéger, Mason, & Mouillot, 2008). Loss of information that is potentially useful for conservation will occur if we only consider the reduced subset of dimensions of the overall specialization index.

An index of specialization is only as reliable as the underlying data. The quality of information about traits varies from species to species, might be incomplete or inaccurate in some cases, depending on the quality and number of studies conducted on each species (Ducatez & Lefebvre, 2014; Garamszegi & Möller, 2012; McKenzie & Robertson, 2015). Furthermore, the type of variable used to fill out the trait-features can also influence the index. In this study, we estimated the Gini coefficient using binomial traits (based on a characterization of the trait initially made explicit as yes/no. For example, diet specialization was assessed using nine categories (folivore, frugivore, granivore, arthropods, etc.) and such categories were filled out by determining whether at least 10% of the diet during the year is composed of each type of food. It would also be possible to directly estimate the percentage of the diet made up of each food type, and this data structure would be even better suited for summarizing the Gini coefficient, which works best on continuous data. However, significant uncertainty could exist across such a large number of possible categories. For example, the diet of Sylvia atricapilla changes over time, the species being more insectivorous during the breeding season and frugivorous during autumn and winter. The habitat of Fringilla coelebs could be more variable than is easily expressed by these traits, because it inhabits forests during the breeding season and more open-country habitats during autumn and winter. A parameter could be devised to take into account this temporal variability in some species, when calculating the specialization indices. Also, other indices could be applied to estimate specialization, as has been done for size and fecundity specialization in plant communities, where the Lorenz asymmetry coefficient has been used to understand how inequality is distributed across a set of communities or species (Damgaard & Weiner, 2000).

Finally, although we focused on five bundles of species traits of avian species, we recognize that specialization can also be measured in other dimensions. For example, further studies on degree of specialization could introduce gradients of specialization in brood parasitic species, by considering the number of host species, host preferences, or interspecific relationships between pollinator species and plants.

In conclusion, we propose the more widespread use of multidimensional gradients of species specialization, especially for the assessment of the conservation status of species. For example, a metric indicating the level of species’ specialization based on a trait-based approach could be included in the protocol for IUCN Red List assessments. In the same way that niche size change was recently incorporated in such assessments (Breiner et al., 2017), we propose that information on species specialization is also included, because it might predict other dimensions of extinction risks, as suggested in many studies (Colles et al., 2009; Devictor et al., 2008; McKinney, 1997).

ACKNOWLEDGMENTS
We are grateful to Luis Maria Carrascal for fruitful and stimulating discussions during the initial stage of this study. F.M. and Y.B. were financially supported by the Czech Science Foundation GAČR (project number 18-16738S).

CONFLICT OF INTEREST
None declared.

AUTHOR CONTRIBUTIONS
F.M., Y.B. and R.A.F. conceived the idea and designed methodology; F.M. and Y.B. prepared the data and performed data analyses. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY
The datasets generated during and/or analyzed during the current study is provided in the Appendix.

ORCID
Federico Morelli https://orcid.org/0000-0003-1099-1357
Yanina Benedetti https://orcid.org/0000-0003-1600-2310
Anders Pape Møller https://orcid.org/0000-0003-3739-4675
Richard A. Fuller https://orcid.org/0000-0001-9468-9678

REFERENCES
Allan, J. R., Watson, J. E. M., Di Marco, M., O’Bryan, C. J., Possingham, H. P., Atkinson, S. C., & Venter, O. (2019). Hotspots of human impact on threatened terrestrial vertebrates. PLoS Biology, 17, 1-18. https://doi.org/10.1371/journal.pbio.3000158
