

## Trait-based indicators of bird species sensitivity to habitat loss are effective within but not across data sets

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**Abstract.** Species' traits have been widely championed as the key to predicting which species are most threatened by habitat loss, yet previous work has failed to detect trends that are consistent enough to guide large-scale conservation and management. Here we explore whether traits and environmental variables predict species sensitivity to habitat loss across two data sets generated by independent avifaunal studies in the Atlantic Forest of Brazil, both of which detected a similar assemblage of species, and similar species-specific responses to habitat change, across an overlapping sample of sites. Specifically, we tested whether 25 distributional, climatic, ecological, behavioral, and morphological variables predict sensitivity to habitat loss among 196 bird species, both within and across studies, and when data were analysed as occurrence or abundance. We found that four to nine variables showed high explanatory power within a single study or data set, but none performed as strong predictors across all data sets. Our results demonstrate that the use of species traits to predict sensitivity to anthropogenic habitat loss can produce predictions that are species- and site-specific and not scalable to whole regions or biomes, and thus should be used with caution.

**Key words:** *Atlantic Forest; birds; habitat fragmentation; habitat loss; response traits; species sensitivity; transferability.*

### INTRODUCTION

Species differ in their response to habitat loss (Banks-Leite et al. 2012) and understanding the basis of this difference is vital to comprehending why species are being lost and how to concentrate conservation effort. Many studies have examined which traits make a species more sensitive to human disturbance (see Henle et al. [2004] for review), with the aim of predicting which species will require future conservation intervention. While some studies focused on just a few traits (Stouffer and Bierregaard 1995a, Castelletta et al. 2000, Ribon et al. 2003, Sodhi et al. 2004), others have considered a larger numbers of traits (Pakeman 2011, Edwards et al. 2013), trait interactions (Renjifo 1999), and multiple taxa (Faria et al. 2006, Senior et al. 2013). Regardless of breadth of analyses, taxa, and study region, previous studies have not found consistent results (Newmark 1991, Senior et al. 2013). Most importantly, a large number of studies based their conclusions on observations from a single community or region (Renjifo 1999, Kennedy et al. 2010), and generally

lacked an assessment of model transferability to estimate the reliability of traits as proxies for species sensitivity.

The most commonly explored traits include those related to population demography, dispersal, sociality, body size, trophic level and specialization, habitat usage, species interactions, and biogeography (Henle et al. 2004). These traits are believed to be reasonable proxies for species sensitivity because they are related to species adaptability or the likelihood of local extinction. Indeed, some authors have found trends to be consistent across studies and regions (Gray et al. 2007, Williams et al. 2010), such as an increased sensitivity to fragmentation in specialized taxa, including butterflies with narrow feeding niches (Ockinger et al. 2010). Others, however, have found that although traits can be useful indicators, the patterns may be specific to certain areas (Sigel et al. 2010, Thornton et al. 2011, Vetter et al. 2011). For example, birds that join mixed-species flocks are considered highly sensitive to habitat changes, but Sigel et al. (2010) only found this to be the case in one of the areas studied. Hence, while this approach may provide insight into the dynamics of local systems, contradictions arise due to species- and site-specificity in the relationship between traits and anthropogenic disturbances, or due to the different methods used by different authors.

Here, we perform a direct comparison of transferability of trait-based models across two data sets generated

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by intensive bird surveys in the Atlantic Forest of Brazil. The Atlantic Forest has been extensively studied, so provides a rich testing ground for model transferability. The data sets used follow similar experimental designs and were collected in the same study region at an overlapping sample of sites, but used different methods for data collection. Thus, we (1) investigate which traits can be used to predict bird species sensitivity to habitat loss and then (2) assess model transferability by testing whether traits that are strong predictors of species sensitivity in one data set maintain their predictive power in different data sets. We performed the above tests on four different subsets of the data: occurrence or abundance data of all recorded species or just the species that were observed in both studies. Lack of model transferability between data sets could result from traits being spuriously correlated to species sensitivity, or from differences in species sensitivities between data sets. The latter is particularly problematic to these analyses given that different survey methods were used, which influences the probability of species detection and therefore the probability of detection of ecological trends (Banks-Leite et al. 2014). For this reason, we also examined the consistency of species sensitivity to habitat change across studies.

## METHODS

### *Study area*

Our data originates from two independent studies conducted in the Atlantic Plateau of the state of São Paulo, Brazil. The survey area is broadly the same for both studies, including 19 overlapping study sites (Appendix S1: Fig. S1). Elevation ranges from 700 to 1,000 m and the original vegetation is lower montane rainforest. Both studies were designed with similar spatial sampling protocols, comparing paired 10,000-ha blocks of continuous and fragmented forest landscape, but differed in the main method of data collection.

*Mist-net study (Banks-Leite et al. 2011).*—Data were collected from 2001 to 2007 in 65 study sites varying from 5% to 100% of forest cover (800 m radius). Nearly 8,000 individuals of 140 species were sampled during 41,000 h of mist netting (Appendix S1).

*Point count study (Develey 2004).*—Data were collected from 2000 to 2003 in 32 sites varying from 20% to 100% of forest cover (800 m radius). Birds were sampled using 10-minute point counts, with 20 point counts carried out per site, resulting in estimates of abundance for 154 species. (Appendix S1).

### *Trait data*

Bird surveys produced a total list of 197 species, including 43 species unique to mist netting, 57 unique to point counts, and 97 shared across data sets. One species,

*Picumnus cirratus*, was removed from the analysis because of missing data. Our final data set contained information on 25 ecological or phenotypic variables for 196 bird species (Appendix S2: Table S1). These variables included information on geographical distribution, as well as a range of traits chosen to reflect the morphology and ecology of species, including their foraging habits and behavior. A similar mix of environmental variables and species traits are widely used to predict sensitivity to habitat change (Turner 1996, Henle et al. 2004). For convenience, we use the term “traits” when environmental variables and species traits are referred to collectively.

Global species’ distribution area was measured using ESRI ArcGIS v.10.0 (ESRI, Redlands, California, USA) from standard range polygons (BirdLife International and NatureServe 2012). We then used MaxEnt v.3.3.3k (Phillips et al. 2006) to predict the bio-climatic suitability of each survey site for all species. Species distribution models were produced using the MaxEnt auto features option and the full set of 19 temperature and rainfall derived Bioclim variables (Hijmans et al. 2005). Cost distance analysis was used to find distance to nearest terrestrial distributional range edge (i.e., proximity to the edge of distribution; PED) from the center point of both study areas. This was conducted using R v.3.3.2 (R Core Team 2016) and the packages raster (Hijmans and van Etten 2013), gdistance (van Etten 2012), and maptools (Bivand and Lewin-Koh 2013), as well as ESRI ArcGIS v.10.0., defining coastlines using the admin98 boundaries layer. Proximity to range edge (PED) and distributional range size was logarithmically transformed ( $\ln[x + 1]$  for PED).

Morphological traits were compiled by measuring museum specimens following standard protocols (Bregman et al. 2015, 2016, Ulrich et al. 2017). We used three bill measurements (length, width, and depth), tarsus length, tail length, and wing length (for a more detailed description of measurements, see Appendix S2: Table S1). We also calculated the hand wing index (HWI) as an index of dispersal ability using a combination of wing length and first secondary length, following Claramunt et al. (2012). Measurements were accurate to 0.01 mm, except tail and wing, which were to the nearest millimeter. Where possible, each measurement was averaged from four specimens with an even sex ratio. Where trait information was unavailable, values were taken from closely related and ecologically similar congeneric species, or, in the case of some hummingbird species in monotypic genera, tarsus measurements were taken from similar sized species in closely related genera. Body mass was compiled from literature (see Appendix S2: Table S1). All morphological traits including body mass were logarithmically transformed for analyses, except HWI.

Diet composition information (Appendix S2: Table S1) was subject to a PCA on the whole species pool to obtain independent variables summarizing the diet composition of each species relative to the rest of the community using the package vegan (Oksanen et al. 2013).

*Statistical analysis*

All statistical analyses were run using R v.3.3.2 (R Core Team 2016) with packages *vegan* (Oksanen et al. 2013), *caper* (Orme et al. 2013), *ape* (Paradis et al. 2004), and *phytools* (Revell 2012).

We used a novel approach to select the traits and calculate a species-specific score of sensitivity to habitat changes for each of species' abundance and occurrence (Fig. 1). The approach was based on weighted averages ordination (Gauch 1982), in which Bray-Curtis and Sørensen dissimilarity between sites was first calculated from each of the community abundance and incidence matrices, respectively. A principal coordinates analysis (PCoA) was then conducted on each dissimilarity matrix. We assumed that the position of each site along the first PCoA axis reflects its position on a gradient of habitat change based on the previous finding that over 90% of variance in the PCoA axis 1 of the mist-net data is explained by landscape metrics (Banks-Leite et al.

2011). The sensitivity of each species, or the weighted average, was then taken as the average PCoA score of the sites in which it was found, hence representing its mean position along the habitat change gradient. Where abundance data was considered, the value for a species at each site was calculated by weighting the site score by the species abundance at that site. The directionality of the ordination axes were checked (and inverted if required) to ensure that an increasing sensitivity score indicated increasing sensitivity to habitat change. This method produces results that are qualitatively similar to fourth-corner methods and RLQ (Dray et al. 2014; Appendix S3), but has the advantage of allowing us to control for phylogenetic non-independence and allows for more flexibility in model building.

First, we investigated which species traits can be used to predict species' sensitivity to fragmentation using phylogenetic generalized least squares (PGLS) models with traits as explanatory variables. Phylogenetic trees were obtained as phylogeny subsets from BirdTree.org (Jetz et al. 2012):

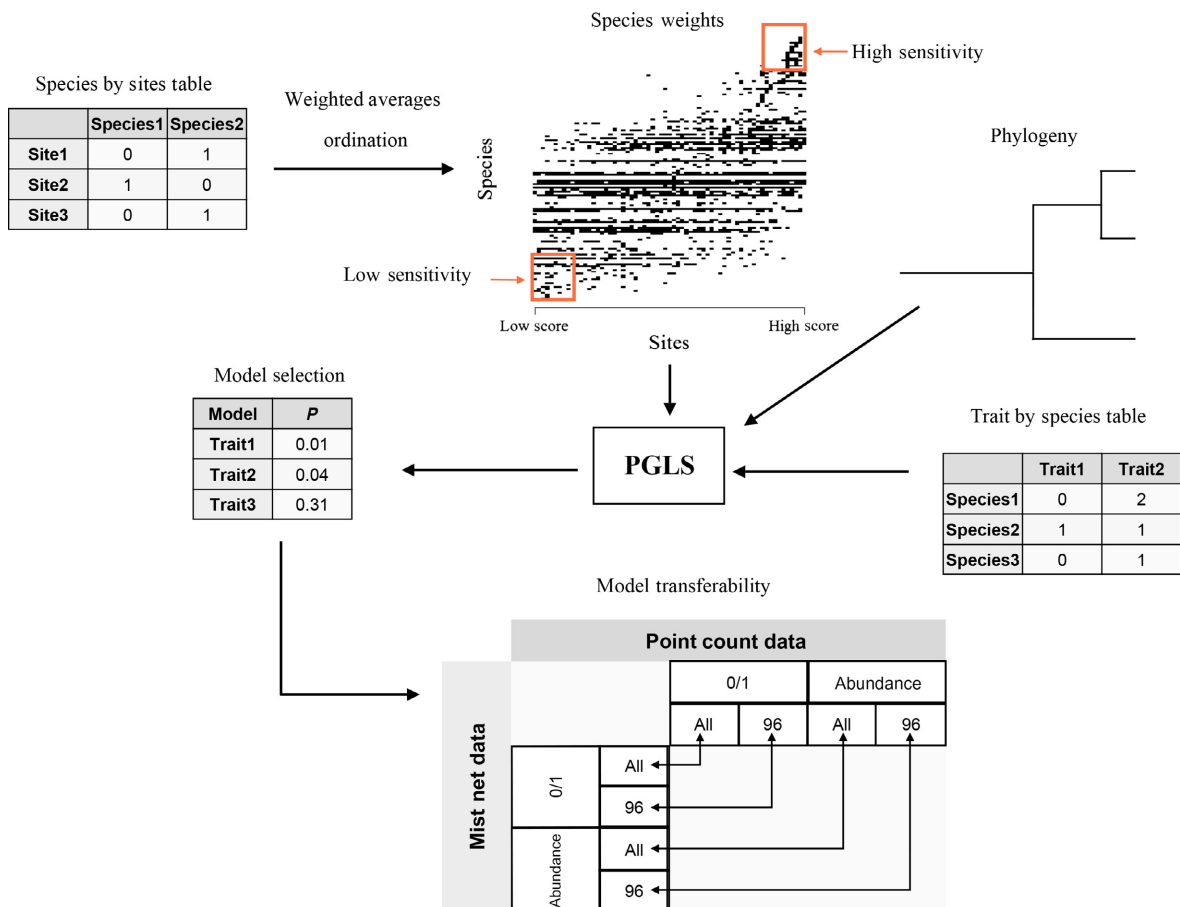


FIG. 1. Schematic of the modelling and transferability testing process. The phylogenetic generalized least squares (PGLS) analysis uses the species weights (which are derived from a species by site table using weighted averages), a species phylogeny (consensus tree), and a trait by species table as input data. After PGLS, traits are selected using stepwise backward model selection, and finally models are transferred only across similar data sets. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

this data set provides a posterior distribution of phylogenies from Bayesian analyses. For each set of species, we therefore selected 1,000 trees and calculated a consensus tree using a 10% burn-in, maximum clade credibility, median node heights, and a posterior probability limit of 0.5, using TreeAnnotator v.1.8.3 and FigTree v. 1.4.2. from the software BEAST (Drummond et al. 2012). Consensus trees calculated from a large number of trees have been found to provide the same results as model averaging over multiple trees (Rubolini et al. 2008). In this case, a consensus tree was used as it allowed greater clarity in model simplification and the influence of phylogeny used was found to be relatively low for the majority of analyses.

The traits to be included in the PGLS models were checked for collinearity. All traits that were not highly correlated ( $r < 0.7$  [Dormann et al. 2013]) were fitted to form the maximal model. The lambda value of the maximal model was determined using maximum likelihood and subsequently fixed to allow for model simplification. Step-wise simplification was conducted based upon  $P$  values, by using the anova function to compare between models. The minimum adequate model was considered to be that in which all terms were significant at the 0.05 level. This method was preferred over AIC model selection because of difficulties comparing models with different random factors (i.e., phylogenetic covariance structure). We did not fit interaction terms as the data set was not large enough.

#### *Model transferability*

We first obtained the  $R^2$  from the minimum adequate PGLS model generated by one data set, and then applied the same set of selected predictors to obtain the  $R^2$  from the other data set. The difference in  $R^2$  between these models was used to assess the retention of explanatory power for transferred predictions. This process was conducted in both directions (Fig. 1). We initially fitted the models using all of the species detected in each data set to better understand the extent to which we can generalize knowledge on response traits from a given bird community. To ensure that any differences to  $R^2$  were not simply a product of changes in phylogenetic covariance, we also re-ran models restricted to the 96 species common to both data sets. We tested for the correlation between sensitivity scores for this 96-species sample using the occurrence data and a Pearson correlation to examine whether survey method influences our measures of species sensitivity or confounds model transferability.

## RESULTS

### *Species sensitivity*

For the shared sampled ( $n = 96$ ), species' sensitivity scores were found to be highly correlated between data sets ( $r = 0.86$ ) indicating that observed species responses to habitat changes are not dependent on the sampling

method, and thus that sampling method is unlikely to influence model transferability.

### *All species*

For occurrence data, the minimum adequate model for the mist-net data contained eight variables (adjusted  $R^2 = 0.34$ ) and the model for the point count data contained six variables (adjusted  $R^2 = 0.43$ ). Some variables (number of habitats used, open habitat usage, bill width, tarsus length) were common to both models. When transferred to the other data set, the explanatory power of the model parameterized on the mist-net data increased to 0.38 (despite the inclusion of non-significant variables) but the explanatory power of the model parameterized on the point count data fell to 0.26. Hence we detected a 12% increase in explanatory power for one model, and a 38% decrease for the other model.

Using abundance data, seven traits were retained in the minimum adequate models of species sensitivity using the mist-net data (adjusted  $R^2 = 0.27$ ), and five traits were retained using the point count data (adjusted  $R^2 = 0.38$ ). When transferred, both models lost performance, with explanatory power falling to  $R^2$  values of 0.18 and 0.18, respectively (representing a drop of 35% and 53% in explanatory power). Again, the set of variables differed between models, and only ant following behavior and understory usage were significant in both models.

No variables were retained across all models (Appendix S2: Table S2).

### *Species present in both data sets*

For occurrence data, the minimum adequate model for the mist-net data contained six variables (adjusted  $R^2 = 0.46$ ) while the model for the point count data contained nine variables (adjusted  $R^2 = 0.51$ ). The variables that were consistent in significance and sign to both models were ant following behavior, diet composition, understory usage, open habitat usage, and number of habitats used. When transferred to the other data set, the explanatory power of the model parameterized on the mist-net data dropped to 0.39 and the explanatory power of the model parameterized on the point count data fell slightly to 0.47. Thus, a 14% decrease in explanatory power was found for the mist-net model and a 7% decrease for the point count model.

For abundance data, the minimum adequate model for mist-net data contained four variables (adjusted  $R^2 = 0.30$ ), while the minimum adequate model for the point count data contained five variables (adjusted  $R^2 = 0.44$ ). Again there was a considerable difference between the sets of variables (Appendix S2: Table S2); only ant following behavior was significant in both data sets. When we tested for model transferability, we found the explanatory power of these two models fell to 0.22 and 0.25, respectively (representing a 28% and 43% drop in explanatory power). Across models of abundance and occurrence data

on both data sets, only ant following behavior was found to be consistently significant and positively associated with the disturbed to intact habitat gradient.

#### *Phylogenetic non-independence*

In general, models showed little evidence of phylogenetic signal in the data ( $\lambda$ , typically  $1 \times 10^{-6}$  or lower, and not significantly different from zero). Values of  $\lambda$  were also consistent through model simplification, suggesting that variable combinations do not differ markedly in their phylogenetic pattern. The abundance data models using point count data were exceptions. The model for all species showed a range of  $\lambda$  values between the maximal and minimal models (0.547–0.562), as did the model for the species common to both data sets (0.358–0.344). However, this had minimal effects on the eventual model structure; all terms were still retained using a  $\lambda$  value calculated under maximum likelihood. This is likely due to the uncertainty associated with the phylogenetic structure of the species in this data set, but only had a slight effect upon the results.

#### DISCUSSION

Our results show that response variables can be strongly correlated to measures of species sensitivity to habitat loss and fragmentation at local scales, in line with previous studies (Stouffer and Bierregaard 1995b, Kennedy et al. 2010). However, although it is often proposed that species traits can therefore be used to predict sensitivity at wider spatial and temporal scales (Castelletta et al. 2000, Ockinger et al. 2010), our results indicate that this type of extrapolation may not be possible given the large (up to 53%) reduction in explanatory power when transferring models between data sets.

In general, we found evidence that a wide range of distributional, behavioral, dietary, and morphological variables can be used to indicate species sensitivity at least locally, corroborating the findings of previous studies (Henle et al. 2004, Sekercioglu et al. 2004, Gray et al. 2007). The best indicators in our study appear to be number of habitats used, open habitat usage, and ant following behavior, as these variables were the most consistently effective across different data sets. Nonetheless, there was a lack of consistency of trait predictors between data sets and data types, with no single trait performing as a significant predictor for all data set or data type combinations.

This level of inconsistency may help to explain why our models generally had low transferability, performing most consistently when transferred between data sets containing exactly the same species (particularly when using occurrence data). There are a number of possible reasons for limited transferability between data sets. Survey method, and its associated effects on species-specific detection probabilities, may account for some of the reduced transferability, but not all. The high correlation

in species sensitivity scores between data sets shows that the use of different survey methods is not biasing or confounding our ability to detect species sensitivity to habitat changes. Thus, the fact that we found strong explanatory power of response variables but low transferability of models suggests that trait-sensitivity correlations may be spurious and not generalizable. Another issue is the high collinearity of the response variables, which may be the reason why under certain circumstances model transfer does not lead to a large drop in explanatory power but instead to conflicting sets of variables included in final models. This was observed with occurrence data for the 96 species where the model parameterized on the point count data only suffered a minor drop in explanatory power using the mist-net data, yet the mist-net data had yielded a minimal model containing six variables, whereas the point count model contained nine variables, with five variables common to both.

The results of this study add to the growing consensus of site specificity in the literature. For example, Vetter et al. (2011) shows that vertebrate responses to fragmentation can be highly site specific. Thornton et al. (2011) went further to show that certain traits of Neotropical mammals were more or less influential across different sites in Guatemala and Mexico even when the same species are considered, thus reinforcing the idea that traits may not be consistent predictors of species responses. As for Neotropical birds, Sigel et al. (2010) showed that some response traits can be extremely site specific and that patterns of variation were best interpreted in the local context.

To conclude, our results suggest that response traits should be used with caution if the aim is to understand mechanisms of species sensitivity to habitat loss and fragmentation. In particular, our analyses indicate that even when species traits predict sensitivity to habitat change, these patterns may be inconsistent even within study communities or regions, and cannot simply be extrapolated to predict species sensitivity at broader spatial or taxonomic scales. Thus, although trait-based proxies have become popular short cuts in conservation forecasting and priority-setting exercises, their application across multiple taxa, regions, and time (Henle et al. 2004) may be more complex than first anticipated. The validity and transferability of trait-based models of species sensitivity to habitat change requires more thorough investigation.

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## SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1646/full>

## DATA AVAILABILITY

Data available from figshare: <https://doi.org/10.6084/m9.figshare.c.3899116.v1>