Can traits predict species’ vulnerability? A test with farmland passerines in two continents

Michael J. O. Pocock*

School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK

Species’ traits have been used both to explain and, increasingly, to predict species’ vulnerability. Trait-based comparative analyses allow mechanisms causing vulnerability to be inferred and, ideally, conservation effort to be focused efficiently and effectively. However, empirical evidence of the predictive ability of trait-based approaches is largely wanting. I tested the predictive power of trait-based analyses on geographically replicated datasets of farmland bird population trends. I related the traits of farmland passerines with their long-term trends in abundance (an assessment of their response to agricultural intensification) in eight regions in two continents. These analyses successfully identified explanatory relationships in the regions, specifically: species faring badly tended to be medium-sized, had relatively short incubation and fledging periods, were longer distant migrants, had small relative brain sizes and were farmland specialists. Despite this, the models had poor ability to predict species’ vulnerability in one region from trait–population trend relationships from a different region. In many cases, the explained variation was low (median $R^2 = 8\%$). The low predictive ability of trait-based analyses must therefore be considered if such trait-based models are used to inform conservation priorities.

Keywords: agricultural intensification; ecological correlate; farmland birds; life history; phylogenetic analysis; trait

1. INTRODUCTION

Biodiversity faces extraordinary threats owing to environmental change, and many species are suffering rapid declines although some species are faring worse than others. Variation in vulnerability can be partially explained by species’ traits [1]. Trait-based research has undergone a rapid expansion in recent years [2]; it can be explanatory (e.g. to allow mechanisms causing species’ vulnerability to be inferred; [1]), or predictive. Predictions from trait-based research have been used to focus conservation priorities, e.g. by efficiently identifying vulnerable species [3] or potential bioindicators [4], and by predicting changes in ecosystem function under realistic (i.e. trait based) scenarios of biodiversity loss [5].

Here, I test the ability of species’ traits to predict species’ vulnerability. I undertook this analysis on farmland passerine birds in eight regions (four in Europe and four in the USA), using quantitative estimates of long-term population trends (i.e. trends in abundance throughout each region) as an assessment of vulnerability. These replicated datasets allowed trait–population trend models developed in each region to be tested in each other region. With these models, I therefore assessed trait–vulnerability relationships in a narrow range of species subject to a single threat, which is important given the taxon-specificity and threat-specificity of comparative analyses [6,7].

Agricultural intensification is one of the major drivers of global environmental change [8]. Its impacts on birds are well known, and include population declines in Europe and North America [9,10]. As a result, farmland bird population trends are used as one indicator of changes in the ‘health’ of agro-ecosystems [11]. Previous studies on a wide range of traits have shown that farmland birds faring badly are specialized, have small relative brain size and atypical resource use [12–14]. However, to my knowledge, all such research on farmland birds has been carried out with the same dataset: trends in English farmland bird species populations from 1968 to 1995. The current study allowed the generality, across regions, of these explanatory relationships to be tested.

The objectives of this study were twofold. For the first objective, I tested relationships between 11 traits and population trends of farmland passerine bird species in eight regions in two continents. I used phylogenetically informed analyses and for each trait tested the consistency of the effect between the regions. I predicted that species at the slow end of the fast–slow life-history continuum, which tend to have low reproductive rate and high parental investment, and also to be relatively large-bodied, are most vulnerable because they are least able to compensate for increased mortality (e.g. owing to declining habitat quality) through increased recruitment [1,15]. I also tested for a curved response of vulnerability with body size, given the finding of Amano & Yamaura [16], although the mechanisms causing for medium-sized species to be most vulnerable are unclear. I predicted that species with traits associated with increased flexibility are less vulnerable. Specifically, I tested whether farmland passerines that are faring best are habitat generalists, which benefit from their use of habitats other than farmland [1], and behaviourally flexible species, i.e. those having relative large brains, given that they can best

*michael.pocock@bristol.ac.uk

Table 1. Sources of data on population trends of farmland passerines in the eight northern temperate regions used in the analysis. The order of the American states is the same as that of the European regions to which they were matched based on land-use data (electronic supplementary material, table S1).

<table>
<thead>
<tr>
<th>region</th>
<th>number of species</th>
<th>years</th>
<th>median population trend in % yr $^{-1}$ (min, max)</th>
<th>source for population trends</th>
<th>source for definition of farmland passerines</th>
</tr>
</thead>
<tbody>
<tr>
<td>England</td>
<td>31</td>
<td>1980–2005</td>
<td>0.31 (−10.64, 3.17)</td>
<td>[41]</td>
<td>[13]</td>
</tr>
<tr>
<td>Netherlands</td>
<td>26</td>
<td>1984–2004</td>
<td>0.68 (−5.21, 10.70)</td>
<td>[42]</td>
<td>[42]</td>
</tr>
<tr>
<td>Denmark</td>
<td>20</td>
<td>1976–2001</td>
<td>0.56 (−3.80, 4.68)</td>
<td>[43] calculated with the method of [39]</td>
<td>[43]</td>
</tr>
<tr>
<td>Sweden</td>
<td>15</td>
<td>1976–2001</td>
<td>−1.83 (−5.10, 0.86)</td>
<td>[39]</td>
<td>[39]</td>
</tr>
<tr>
<td>Oklahoma</td>
<td>26</td>
<td>1980–2005</td>
<td>0.25 (−9.40, 9.60)</td>
<td>[44]a</td>
<td>[10]</td>
</tr>
<tr>
<td>South Dakota</td>
<td>22</td>
<td>1980–2005</td>
<td>0.70 (−8.50, 8.10)</td>
<td>[44]a</td>
<td>[10]</td>
</tr>
</tbody>
</table>

*Excluding species for which data quality was poor (these are called ‘red-coded’ by Sauer [44]).

adapt to novel resources [17]. Given concerns over the vulnerability of long-distance migrants [18,19], I also tested the generality of the finding that long-distance migrants are faring worse than sedentary birds and short-distance migrants. For the second objective of this study, I used the model-averaged trait–trend relationships from each region to predict population trends in each other region, in order to test the predictive ability of the models. I also constructed ensembles of predictive models because such ensembles provide a robust approach to predictive modelling [20].

2. MATERIAL AND METHODS

I obtained quantitative information on farmland bird population trends over 20–25 years in eight northern temperate regions, four in Europe and four in non-adjacent North American states within the eastern and central Breeding Bird Survey regions (table 1). The four states were chosen because they each matched one of the European regions in their size and agricultural land use (electronic supplementary material, table S1). The species chosen were ‘farmland birds’, i.e. species that commonly occur in farmland, for which robust data on population trends were available from regional monitoring schemes (electronic supplementary material, appendix S2). These species included both farmland generalists and specialists (as per [14]; electronic supplementary material, figure S4). Branch lengths were assumed to be one, and polytomies were retained. In addition, I tested the sensitivity of the results to the phylogeny used (electronic supplementary material, appendix S5). Each analysis tested an a priori hypothesis, so correction for multiple tests was not applied. For each region, I calculated the AICc weight for each trait–population trend model, i.e. its probability of being the best approximating model in the set of candidate models. I tested the significance of the consistency of the relationships of each trait with population trend in the eight regions, by using Stouffer’s method to combine p-values and testing against a z distribution [30].

In the predictive analysis, I predicted farmland bird population trends in each region with the explanatory relationships derived from the data from each other region. There were 12 trait–trend relationships for each region: the intercept-only model, and 11 models with traits. The predictions from each model were weighted according to the model’s AICc weight. This approach for predictive modelling avoids the problem of colinearity of predictor variables, unlike stepwise model selection. There were, therefore, eight sets of predictions for each of the eight regions (one self-predictive model and seven between-region predictive models). For comparison, I also made predictions with a full multivariate model, containing a set of non-correlated traits and a ‘minimum adequate model’ derived from the full multivariate model by stepwise regression (electronic supplementary material, appendix S6).

As well as using single region models to make predictions, I created an ensemble prediction for each region from the
tests. I used ranks throughout because the results of the observed population trends with Spearman’s rank correlation (cross-continent ensemble) and one based on the four regions in the other continent 

regions in the same continent (within-continent ensemble), ensembles: one based on the predictions from the three population trends for each species. I created two other total ensemble prediction was the sum of ranked predicted 

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3. RESULTS

Few relationships between species’ traits and population trends were significant (14% of the 88 relationships at $p < 0.05$) and there was substantial variation in the effect size and direction (figure 1) and in the model weight (electronic supplementary material, table S3) between regions. Of the 11 traits that I considered, four were significantly related to population trend in more than one region: log-transformed body mass$^2$ and relative brain size in two regions and log-transformed incubation period and farmland specialization in three regions. The minima of log-transformed body mass$^2$ varied between 40 and 100 g (electronic supplementary material, figure S7). Four traits (annual productivity, egg mass, clutch size and fledging period, all log transformed) showed no significant relationship with population trend in any region.

Testing the consistency of the relationships across regions (using Stouffer’s method), there was strong evidence that those farmland passerines that are faring worst are farmland specialists, medium-sized, have longer distance migration, have short fledging and incubation periods (relative to body mass) and have small brain sizes (all $p < 0.05$; figure 1).

Most PGLS models showed no phylogenetic autocorrelation ($\lambda = 0$). In some cases, phylogenetic autocorrelation was moderate (electronic supplementary material, table S4), but in no case were the PGLS results substantively different from those of the OLS regressions. The source of the phylogeny had no substantial effect on the results (electronic supplementary material, appendix S5). I therefore used OLS regressions (treating species as independent data points) to predict population trends.

Model averaging provided reasonable explanatory power (average $R^2$ for the self-predictive models = 30%), but most between-region models and ensembles performed more poorly and in most cases just a few per cent of the variance between predicted and observed values was explained (table 2). Nine per cent of rank correlations of the cross-region predictive models were negative (but close to zero), indicating that models were mis-specified.

The fit, assessed by rank correlation coefficients, of the cross-region predictions was significantly greater than zero (one-sample $t$-test of $r$: $t_{55} = 11.968$, $p < 0.001$; mean $r = 0.27$) but fits were close to significantly lower than those from the self-predictive models (Welch two-sample $t$-test of $r$: $t_{6.3} = -3.543$, $p = 0.006$). There was no evidence that predictions of population trends in European and North American regions, paired for

Figure 1. Results of the PGLS regression. Error bars indicate twice the standard error of the estimate, hence if error bars do not overlap $y = 0$ then the value of estimate is significant at $p < 0.05$. The significance values written above each plot show the overall significance of the effect (the individual $p$-values combined by Stouffer’s method). European regions are numbered 1–4 (England, Netherlands, Denmark and Sweden, respectively). American states are numbered 5–8 (Oklahoma, South Dakota, Illinois and Michigan, respectively) and are presented in the same order as the European regions to which they are matched based on land-use data (i.e. England is matched with Oklahoma, and so on).

seven model-averaged cross-region predictions [20]. The total ensemble prediction was the sum of ranked predicted population trends for each species. I created two other ensembles: one based on the predictions from the three regions in the same continent (within-continent ensemble), and one based on the four regions in the other continent (cross-continent ensemble).

I compared the ranks of the species’ predicted and observed population trends with Spearman’s rank correlation tests. I used ranks throughout because the results of the ensemble models were ranks.
Table 2. The percentage variance of observed farmland passerine population trends in each of eight regions that is explained by predictions from trait–population trend models in the same region, each other region and ensembles. (Values given are derived from Spearman’s rank correlations. (negative.)

<table>
<thead>
<tr>
<th>Region</th>
<th>England</th>
<th>Netherlands</th>
<th>Denmark</th>
<th>Sweden</th>
<th>Oklahoma</th>
<th>South Dakota</th>
<th>Illinois</th>
<th>Michigan</th>
<th>Total within-continent</th>
<th>Total between-continent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Self</td>
<td>27.7***</td>
<td>31.8***</td>
<td>31.8***</td>
<td>27.7***</td>
<td>11.0</td>
<td>2.5</td>
<td>44.6</td>
<td>27.6</td>
<td>29.1***</td>
<td>20.2***</td>
</tr>
<tr>
<td>England</td>
<td>10.8***</td>
<td>5.1</td>
<td>5.1</td>
<td>10.8***</td>
<td>3.7</td>
<td>6.4</td>
<td>1.9</td>
<td>6.4</td>
<td>3.7</td>
<td>2.4</td>
</tr>
<tr>
<td>Netherlands</td>
<td>8.6</td>
<td>17.1</td>
<td>17.1</td>
<td>8.6</td>
<td>3.0</td>
<td>3.0</td>
<td>8.3</td>
<td>3.0</td>
<td>8.3</td>
<td>8.3</td>
</tr>
<tr>
<td>Denmark</td>
<td>3.7</td>
<td>8.0</td>
<td>8.0</td>
<td>3.7</td>
<td>9.0</td>
<td>4.8</td>
<td>4.8</td>
<td>9.0</td>
<td>4.8</td>
<td>4.8</td>
</tr>
<tr>
<td>Sweden</td>
<td>6.0</td>
<td>3.6</td>
<td>3.6</td>
<td>6.0</td>
<td>1.5</td>
<td>1.5</td>
<td>3.6</td>
<td>1.5</td>
<td>3.6</td>
<td>3.6</td>
</tr>
<tr>
<td>Oklahoma</td>
<td>14.0***</td>
<td>3.6</td>
<td>3.6</td>
<td>14.0***</td>
<td>1.5</td>
<td>1.5</td>
<td>3.6</td>
<td>1.5</td>
<td>3.6</td>
<td>3.6</td>
</tr>
<tr>
<td>South Dakota</td>
<td>11.0</td>
<td>3.0</td>
<td>3.0</td>
<td>11.0</td>
<td>4.8</td>
<td>4.8</td>
<td>9.0</td>
<td>4.8</td>
<td>9.0</td>
<td>4.8</td>
</tr>
<tr>
<td>Illinois</td>
<td>4.8</td>
<td>3.0</td>
<td>3.0</td>
<td>4.8</td>
<td>4.8</td>
<td>9.0</td>
<td>9.0</td>
<td>9.0</td>
<td>9.0</td>
<td>9.0</td>
</tr>
<tr>
<td>Michigan</td>
<td>8.3</td>
<td>8.3</td>
<td>8.3</td>
<td>8.3</td>
<td>9.0</td>
<td>9.0</td>
<td>9.0</td>
<td>9.0</td>
<td>9.0</td>
<td>9.0</td>
</tr>
</tbody>
</table>

The ensemble models substantially varied in their performance, at best being as good as self-predictive models ($R^2 = 0.47$; table 2). The total ensemble predicted rank population trends significantly well for three regions (mean $r_s$ for the eight regions = 0.35). The within-continent and between-continent ensembles predicted rank population trends significantly well for three and four regions, respectively (mean $r_s$ across the eight regions = 0.35 and 0.39, respectively), but were not significantly different from each other (paired $t$-test: $t_7 = 0.138$, $p = 0.894$). None of the three ensembles performed significantly better than the between-region predictive models (Welch two-sample $t$-tests of $r_s$: minimum $p = 0.087$). The predictive power of the full multivariate models and the minimum adequate models was not substantially different to the model averaged predictions from the univariate models (electronic supplementary material, appendix S6).

4. DISCUSSION

Making predictions, and thus informing conservation priorities, is one of the goals of trait-based analyses [1]. I found that, when predicting farmland passerine declines from trait–population trend relations in other regions, trait-based analyses often performed poorly. This has serious implications if decisions were based on trait-based research.

I also used comparative analyses to infer the intrinsic (i.e. trait based) mechanisms related to farmland passerine declines. Given the importance of farmland birds as putative bioindicators and hence their role in directing policy (e.g. [11]), the explanatory relationships are of practical importance. Trait–population trend relationships had poor explanatory power when considered individually for each region (i.e. few relationships were significant), but the results showed that, across the eight regions, species faring badly tended to be farmland specialists have medium body size, relatively short incubation and fledging periods and small relative brain sizes and be longer distant migrants.

Many of the explanatory variables of farmland passerine declines found in this study have been discussed in depth elsewhere (e.g. [12–14]). However, a strength of considering several different regions is that the generality of explanatory effects can become clearer (figure 1), even if their predictive power is low.

Being a farmland specialist is an important explanatory factor, as expected [1]: in every region, farmland specialists are faring worse than farmland passersines that are generalists, but only in three regions was this significant. Farmland passerines that are habitat generalists use habitats other than farmland, e.g. woodland patches, and this appears to buffer them from the most negative effects of the intensification of managed cropland and grassland, despite agricultural intensification reducing the amount of non-farmed habitats.

Many previous researchers have discovered a negative relationship between body size and vulnerability [1],
which is probably owing to the association of large body size with slow life history and thus the reduced ability to compensate for increased rates of mortality [15]. However, the current study provided strong evidence that the relationship of body mass with population trend of farmland passerines was concave, not a monotonic decline, with medium-sized species faring worst. This relationship was strongly influenced by large-bodied Corvidae that are faring well, but I suggest that the relative vulnerability of medium-sized bird species is not an artefact of these data for three reasons. Firstly, the concave relationship was present even with the appropriate degree of phylogenetic correction in PGLS regressions (figure 1 and electronic supplementary material, figure S7). Secondly, several large-bodied non-passerine species are also faring well in the UK [13]. Thirdly, Amano & Yamaura [16] also found that medium-sized birds (ca 70 g) were faring worst. The reasons for the concave relationship are unclear, but one possibility is that separate mechanisms decrease vulnerability in small and large birds: e.g. if the large-bodied farmland passerines that can persist in farmland are, by necessity, more generalist and hence less vulnerable than would be expected (e.g. by the action of an extinction filter; [31]), then this would transform a monotonic decline to a concave relationship. Including non-monotonicity in comparative analyses is potentially fruitful for future research because it would determine the prevalence of concave responses and allow possible mechanisms to be inferred.

High parental investment (long incubation and fledging periods relative to body size) was positively related to population trend. High parental investment is regarded as at the slow end of the life-history continuum, so this was contrary to initial expectations. High parental investment is empirically related to high juvenile survival but low adult survival in birds [32]. This suggests that low juvenile survival may be an important mechanism causing increased vulnerability. Given that empirical data on survival rates are difficult to obtain, this result confirms the benefits of comparative analyses in constructing hypotheses about the mechanisms that cause vulnerability.

Relative brain size was relatively strongly positively related to population trend. Relative brain size is positively related to behavioural flexibility, which allows species to adapt to changes in resources and to take advantage of novel resources [17]. This appears, in its own right, to be advantageous in the rapidly changing and dynamic agro-environment [14], at least partly through enhancing adult survival rates [33]. Passerine birds, being altricial, do not show the association between large brain size and low maximal reproductive rates present in other birds, which otherwise, would have created a direct trade-off between the two advantageous traits of behavioural flexibility and a high reproductive rate [34].

Geographically replicated datasets provide an ideal test of the generality of comparative analyses, but few have been previously considered [7, 35, 36]. The current study had a clearly defined focus (population trends of farmland passerines subject to agricultural intensification), thus aiding the identification of trait–population trend relationships [6,7,35]. Few relationships were significant and effects often varied between regions, which is analogous to regional variation in farmland bird habitat associations [37]. The results clearly demonstrate that trends in the abundance of farmland passerines are not predictable between the regions in this study (table 2). Previous studies have considered this where species are shared between the regions [38, 39], but considering trait–trend relationships allows this conclusion to be made between continents where there are few-shared species.

There are at least three possible reasons why there was geographical variation in the size and significance of the trait–trend relationships. Firstly, it could be a result of spatial variation in the environment (e.g. amount of forest or urban habitat for species that are not farmland specialists or climate) or rate of agricultural intensification (electronic supplementary material, table S1). Secondly, species may respond idiosyncratically to different aspects of agricultural intensification [4], e.g. by being limited by mortality in one region and by reproductive recruitment in another [40], or by using non-farmed habitat to different extents. Thirdly, sample size (the number of species from each region) was low and was limited by considering only passerines, but this should have made relationships easier to discern. Discovering more about why these population trends and these trait–trend relationships vary even in related species subject to a single threat is a valuable topic for future research.

Trait–vulnerability relationships are potentially valuable tools for conservation scientists, and the use of trait-based research, including for predicting species vulnerability, is rapidly growing. My findings clearly show that although trait-based research has good explanatory power, the power of single models and ensembles of models to predict population trends in other regions varies substantially and is generally quite low. It is clear that (to echo the conclusion of Whittingham [37] on habitat association models) ‘ecologists should beware of placing too much confidence in the use of’ trait-based models. Many conservation decisions need to be made with limited evidence, and trait-based research can provide valuable information, but the limitations of this approach should be recognized and should continue to drive future research.

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