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Reassessment of the conservation status and protected area coverage of Taiwanese birds: How distribution modelling can help species conservation

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Summary

Taiwan has 145 breeding bird species, but so far no comprehensive attempt has been made to model their distributions. For the first time, we bring together various datasets to model the distributions of the 116 bird species with sufficient sampling coverage. We improved on previous limited modelling efforts by using ensemble modelling, based on five well-performing modelling approaches: multiple discriminant analysis, logistic regression, genetic algorithm for rule-set production, ecological niche factor analysis and maximum-entropy. We then used these ensemble models to improve our knowledge of the status of each bird species by (1) calculating each species's coverage of Taiwan, (2) calculating each species's coverage by Taiwan's protected area network, and (3) comparing these two conservation-relevant measures with already established measures to highlight those species whose status may need to be reassessed. We categorised each species's coverage of the entire study area as measured by their modelled distributions into four quartiles, thus establishing a new measure of rarity called 'range quartile' which we used to highlight the 22 species with a limited distribution on mainland Taiwan. We also calculated that overall, 29.8% of the distribution ranges of the 116 modelled species are covered by Taiwanese protected areas. We then identified those species whose status may need to be reassessed because of possible conflicts between the respective conservation-relevant measures. Thus we identified 10 species which are first-quartile species < 5% of whose distributions are protected, of which only five are considered threatened. We also identified another 12 species with limited distributions, 30 species with limited protection and 19 species whose status may need to be reassessed for various reasons. We recommend that range quartile and protected area coverage be incorporated into future assessments of the conservation status and protected area coverage of Taiwanese birds.

Introduction

Taiwan is an important hotspot of endemism for many taxa, including birds. While Taiwan has a relatively well established protected area network which covers almost 20% of its area, it also faces multiple challenges to its biodiversity due to unsustainable economic growth and its environmental consequences. Therefore, studies of the conservation status of Taiwan's avifauna are urgently needed.

More than 570 bird species have been recorded in all of Taiwan (Chinese Wild Bird Federation 2010), and 145 species breed on mainland Taiwan (Fang 2008) of which 17 species (12%) are endemic (Chinese Wild Bird Federation 2010). The first comprehensive avifauna of Taiwan was recently published (Severinghaus *et al.* 2010) and, correspondingly, location databases on Taiwanese birds have grown to such an extent that data coverage for most species is now sufficient to use statistical approaches to model their distributions.

Efforts to use this newly available information for macroecological and conservation-related studies have so far been incomplete. Previous studies focused only on species richness patterns without the use of distribution modelling: in a local region (Hsu *et al.* 2004, Ko 2004, Peng 2008), Taiwan's mountains (Shiu and Lee 2003) or all of Taiwan (Lee *et al.* 2004). Early modelling techniques were then used to study bird distributions in a local region (Koh *et al.* 2006a, Koh *et al.* 2006b) or of a single species or subfamily (Ko *et al.* 2009a). A hotspot analysis using Taiwan's birds was restricted to 14 out of the 17 endemic bird species (Ko *et al.* 2009b).

Here for the first time we model the distributions of all Taiwanese breeding bird species with sufficient sampling coverage. We improved on previous modelling efforts by choosing the best models from several model runs with the help of AUC scores and then combining these chosen models into an ensemble model (Araújo and New 2007, Barbet-Massin *et al.* 2009, Thuiller *et al.* 2009). We then used these ensemble models to improve our knowledge of the status of each bird species by (1) calculating each species's coverage of the entire study area, mainland Taiwan, (2) calculating the proportion of each species's range covered by Taiwan's protected area network, and (3) comparing these two conservation-relevant measures with already established measures to highlight those species whose status may need to be reassessed in light of this new information.

Methods

Study area

Our study area is the island of Taiwan which covers latitudes 22°–25°18′N and longitudes 120°27′E–122°E with a maximum elevation of 3,952 m (Figure 1a). It can be roughly divided into an almost flat western plain, which has been highly modified by humans, and the mountainous areas in central and eastern Taiwan which comprise almost 65% of the island and are much less developed, and in some parts almost inaccessible to humans. The climate ranges from tropical in the south to subtropical in the north and alpine in the high mountains, with a mean annual temperature of 18.0°C and an average annual precipitation of 2,510 mm. The natural vegetation is almost exclusively forest, except at high elevations and river floodplains. Except for some almost inaccessible mountain areas, all parts have been heavily modified by human influence. We divided our study area into a total of 36,022 grid cells of 1 x 1 km.

Determining species status

For this study, we selected the 145 bird species (Appendix S1) that are listed as breeding species on the main island of Taiwan (Fang 2008). To determine the status of each species regarding its endemicity, rarity, global and Taiwanese status, we consulted a variety of sources (see Appendix S1). In general, the status of Taiwan's fauna is based on the Wildlife Conservation Act of Taiwan (http://www.forest.gov.tw/ct.asp?xItem=21726&ctNode=249&mp=1). This states that all wildlife shall be classified into two categories: A) protected species, which are either (1) endangered species, (2) rare and valuable species, or (3) other conservation-dependent wildlife; and B) all other species not covered by these three definitions. To distinguish between categories A and B, the Directions for Evaluating Wildlife Categories (http://www.afasi.gov.tw/ct.asp?xItem=28569&ctNode=1917&mp=1) state that the following criteria should be evaluated for each avian species: 1) distribution, 2) abundance of adult individuals, 3) population trends, 4) taxonomic status, and 5) the combined threat from hunting pressure, capture for trade and the rate of habitat loss. The Wildlife Conservation Advisory Committee is then charged with determining which species falls into category A, while the National Principal Authority is responsible for the compilation of the

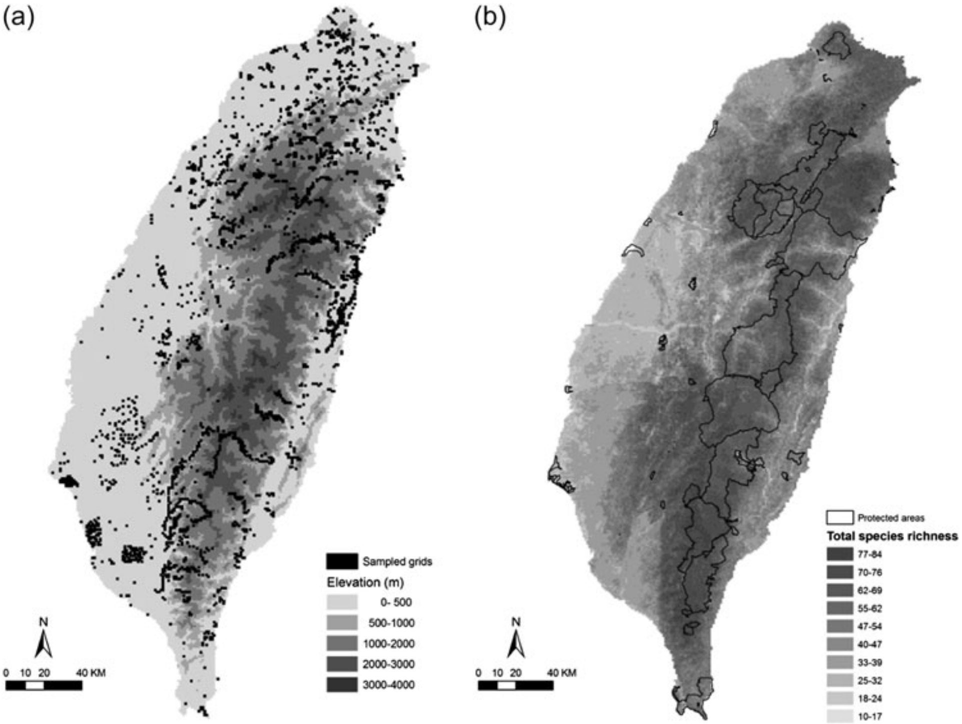

Figure 1. (a) Topography of Taiwan showing elevational ranges and the locations of the 2,455 sampled 1 x 1 km grid cells used in this study. The total number of grid cells is 36,022, meaning that 6.8% of all grid cells were covered by bird surveys. (b) Map of total species richness overlaying all 116 bird species distributions resulting from ensemble models of each species. Dark colours correspond to high species richness (maximum 84 species) and light colours to low species richness. For the different types of protected area, see Figure S1.

Schedule of Protected Species (Council of Agriculture of Executive Yuan 2009) whose update from 1 April 2009 was used in this study.

Distributional data

We derived distributional data from a variety of sources to build the first comprehensive distributional dataset of the breeding birds of Taiwan, including data from bird census projects conducted in 1993-2004 (Endemic Species Research Institute unpubl. data), 1999-2003 (Koh *et al.* 2006a), 2002-2003 (P.-F. Lee unpubl. data), 2003-2004 (Ko 2004; P.-F. Lee unpubl. data), 2006-2007 (Peng 2008), and 2008 (W.-J. Chih, C.-J. Ko & M.-Y. Yang, unpubl. data) (see the online supplementary material for details). For each record, we entered the following information into the database: (1) species; (2) number of individuals recorded if available, otherwise only presence recorded; (3) day, month and year; (4) geographical coordinates; and (5) sources (see above).

We *a priori* excluded the White Wagtail *Motacilla alba* from all analyses because it is not possible to visually distinguish breeding individuals and winter visitors, some of which extend their stay in Taiwan into the breeding season.

To verify the distributional data, records of each species were plotted using ArcGIS and checked for unusual records. First, any record that was outside of Taiwan was deleted. Second, we restricted records to the months of March to July, which is the main breeding season of most species, leaving us with 96,783 records among the remaining 144 species.

Third, we examined each sampling point to eliminate unreliable records which were likely erroneous, such as: 1) the recorded place name and geographical coordinates were not consistent; 2) the avifauna recorded at a single sampling point was highly unusual for the specific habitat type and elevational range (Wang *et al.* 1991, Shiu 2003, Fang 2008; W.-J. Chih, pers. comm., pers. obs.); for example, if several farmland species typical of low elevations had been recorded together in mountain forest, we would evaluate all the records of that single sampling point as unreliable and consequently delete them. As a result, we deleted all the records from 28 sampling points (with each point containing several to tens of species). The remaining number of records was 88,646 (91.6% of the original 96,783 records).

For each species, we then coded each 1 x 1 km grid cell as either present (presence recorded ≥ 1 visit) or absent (absence recorded ≥ 5 visits). Finally, we excluded those species for which < 30 grid cells had been coded as present, because distribution models usually do not perform well at low sample sizes (Stockwell and Peterson 2002, Wisz *et al.* 2008). This left us with 116 species (Appendix S1) with 33,785 presence records within the 1 x 1 km grid, and a total of 2,455 grid cells containing presence records of ≥ 1 species (Figure 1a).

Combining habitat data with environmental data

To build distributional models for each bird species, we used 120 environmental data layers compiled by the Spatial Ecology Lab of National Taiwan University (for details, see Lee *et al.* 1997) which were updated in 2008 by the same lab. These environmental data layers fall in to eight categories and cover the entire mainland of Taiwan with 36,022 1x1 km grid cells (Figure 1a), all of which overlay perfectly with each other and the bird distribution grid. We then selected a subset of data layers relevant to the ecology and behaviour of each bird species (*sensu* Elith and Leathwick 2009; see online supplementary material for details), which resulted in a minimum of 30 to a maximum of 37 data layers associated with each of our 116 species (e.g. 35 in the case of the Taiwan Magpie *Urocissa caerulea*). To eliminate variables, we first used a two-tailed t-test to test each of the selected environmental variables for significant association with the presence or absence of the species using a $P < 0.05$ significance level; only significantly associated variables were retained. We further eliminated variables by running an Unweighted Pair Group Method with Arithmetic Mean (UPGMA) Tree in ENFA to avoid autocorrelation between the remaining variables. If two variables had a correlation coefficient > 0.9, we retained only one of the two variables, chosen randomly. This elimination procedure resulted in a minimum of nine to a maximum of 25 data layers associated with each of our 116 species (e.g. 17 in the case of the Taiwan Magpie) which we then used to build the distribution models for each species. Further variables were eliminated automatically by the black-box procedures integrated in some of the distribution models described below.

Building distribution models

To produce one modelled distribution (the 'final map') for each species, we first produced five probabilistic distribution models for each species by using the environmental data layers described above (see also Table S1 and Appendix S1) and the following methods: multiple discriminant analysis (MDA) (Johnson and Wichern 1998), logistic regression (LR) (Austin 2002), genetic algorithm for rule-set production (GARP) (Stockwell *et al.* 2006), ecological niche factor analysis (ENFA) (Hirzel *et al.* 2002), and maximum-entropy (MAXENT) (Phillips *et al.* 2006). We built MDA and LR models with SAS 9.0, and GARP, ENFA, MAXENT models with the DesktopGARP software (www.nhm.ku.edu/desktopgarp), Biomapper 3.1 software (www2.unil.ch/biomapper) and maxent 3.3.0 software (www.cs.princeton.edu/~schapire/maxent), respectively (see supplementary material for details). These methods were chosen because several reviews of modelling performance had verified the good overall performance of these particular methods (Elith *et al.* 2006, Hernandez *et al.* 2006, Guisan *et al.* 2007, Wisz *et al.* 2008). Each of these methods was used to model each species's distribution using 50% of all presence and 50% of all absence records (training data) and then evaluated with the remaining 50% of presence and absence records (testing data). Dividing the data randomly into training and testing data is a prerequisite for calculating evaluation metrics such as MaxKappa and the AUC score (Fielding and Bell 1997, Pepe 2000).

Using the AUC score, we ranked the performance of the five models for each species. We then produced an ensemble model for each species using a variant of the frequency histogram method (Figure 1 in Araújo and New 2007) by summing up the three best performing models for each species based on their respective AUC scores, thus avoiding over-fitting by eliminating the two worst performing models (M. Araújo *in litt*. 2012). To add up the three models, we chose the MaxKappa threshold recommended by Freeman and Moisen (2008) to turn the probability surface of each model into a binary presence-absence map (resulting in a distribution map of each species coded 0, 1, 2 or 3). We then re-coded codes 0 and 1 into absence (0) and codes 2 and 3 into presence (1). We chose not to re-code 1 into presence because we wanted our distribution models to be conservative.

Finally, we deleted over-prediction for 11 of the 116 species by comparing the modelled distributions with published distribution maps (Severinghaus *et al.* 2010). Over-prediction refers to the distribution model extending into areas where the species has never been observed (e.g. because of interspecific competition, see Discussion). Any region of Taiwan where the species had never been observed was converted into absence by using a variety of appropriate shape files (elevation, ecoregions, counties).

All further analyses were done on these 'final maps' (shown in Appendix S3). We calculated the Kappa values of the five models and the final maps of the 116 species based on the observed present (presence recorded ≥ 1 visit) or absent (absence recorded ≥ 5 visits) grid cells. Furthermore, we subdivided species into four quartile categories whereby first, second, third and fourth quartile species correspond to the modelled distribution of the respective species covering 0–25%, 25–50%, 50–75% and 75–100% of all cells of our study area, respectively (corresponding to almost 9,006 cells or 9,006 km^2 per quartile). Appendix S2 gives the exact percentage coverage for each species; note that none of the species fell exactly on the 25%, 50% and 75% dividing line. This categorical measure is called 'range quartile' hereafter.

Protected area coverage of Taiwan

We used shape files of each of Taiwan's protected areas which were created by the Spatial Ecology Lab of National Taiwan University (Figure S1). These protected areas are categorised into five different types (Forestry Bureau of Council of Agriculture 2011): (1) national parks, (2) nature reserves, (3) forest reserves, (4) wildlife refuges, (5) major wildlife habitats. We further subsumed these five types into three categories: (1) highest protection (national parks only), (2) medium-to-high protection (all protected areas except major wildlife habitats) and (3) low-to-high protection (all protected areas). Placing national parks into the highest protection category is justified because they cover the largest areas of all protected areas as they must be > 1,000 ha according to IUCN (2011a) criteria and are overall the best protected by Taiwan's government. We categorised major wildlife habitats into the lowest protection category because they are the only type of protected area that allows people to enter without a government permit.

Taiwan's laws for setting up protected areas predate the establishment of IUCN's (2011a) six protected area categories. Therefore, Taiwan's protected area criteria are somewhat inconsistent with the IUCN criteria. Nevertheless, the Taiwanese government insists that their criteria are sufficient to cover the six types of IUCN criteria. A comparison between these categories and the IUCN categories, published in Chinese (Lee and Chao 2005), suggests that Taiwan's national parks are almost equivalent to IUCN category II, nature reserves are consistent with IUCN category I, forest reserves cover IUCN categories I, IV and VI, wildlife refuges cover IUCN categories I, IV and VI, and major wildlife habitats cover IUCN categories IV and VI.

Results

Evaluating model performance

Overall model performance using mean AUC scores averaged over all species ranked models as follows: MDA, LR, GARP, ENFA, and MAXENT (Table S2). Therefore, our overall model performance falls into the upper half of the AUC interval from 0.7 to 0.9, which Pearce and Ferrier (2000) labelled as 'reasonable' model performance.

For almost all subcategories (such as endemic species status, conservation status, and so on), MDA was also the best and LR the second best performing technique. GARP and ENFA performed worse than MDA and LR, but better than MAXENT which was the worst performing model in eight out of 14 subcategories, and never performed better than third best except for endemic species.

Kappa values decreased in the same order as model performance: from 0.69 for MDA to 0.54 for ENFA (Table S2). We could not obtain Kappa values for Maxent because all the observed grid cells (present or absent) were predicted as present in Maxent. The Kappa value for the final maps (0.69) was equal or better than the five models. Our overall Kappa value falls into the upper half of the Kappa interval from 0.4 to 0.75, which Landis and Koach (1977) labelled as "good" agreement. For almost all subcategories, Kappa values decreased in the same order as model performance except for the 4th quartile of range quartile rarity where the Kappa value for ENFA was higher than GARP. The Kappa values of each of the final maps of the 116 species are shown in Appendix S3.

Status of Taiwanese breeding birds

Appendices S1 and S2 list all 145 recognised breeding bird species of Taiwan (Fang 2008, Chinese Wild Bird Federation 2010). Seventeen species have full endemic status, while 62 belong to a recognised endemic subspecies. Only two species are listed as globally threatened: Fairy Pitta *Pitta nympha* and Taiwan Bulbul *Pycnonotus taivanus* which are 'Vulnerable' and five as 'Near Threatened' (IUCN 2011b). However, more species are considered threatened within Taiwan: five are listed as endangered (Australasian Grass-Owl *Tyto longimembris*, Black Eagle *Ictinaetus malayensis*, Mountain Hawk-Eagle *Nisaetus nipalensis*, Black-naped Oriole *Oriolus chinensis*, and Russet Sparrow *Passer rutilans*); 33 as rare and valuable, and 11 as conservation-dependent species. In all, 26, 30 and 89 species were recorded as rare, uncommon and common, respectively. Considering range quartile, 22, 50, 35 and 9 species fell into the first, second, third and fourth quartiles, respectively.

Coverage of species modelled distributions by protected areas

Protected areas cover 19.25% of mainland Taiwan, and the five different types (namely, national parks, nature reserves, forest reserves, wildlife refuges, and major wildlife habitats) cover 8.63%, 1.80%, 0.59%, 0.71%, and 9.06%, respectively (these percentages do not add to 19.25% because in a few cases two or more categories of protected areas overlap). Most protected areas in Taiwan are found at mid-elevation (Figure 2), but there is also a peak at the lowest elevation which results from the existence of some coastal protected areas (Figure 1b).

Overall, 29.8% of the distributional ranges of the 116 modelled species are covered by Taiwanese protected areas (Table 1). This percentage drops to 16.9% for medium-to-high protected areas and to 12.5% for national parks. Looking at species of global or Taiwanese conservation concern, coverage of protected species ranges from 17.0% to 46.7% for all protected areas, but this drops to from 5.8% to 20.6% for national parks. Coverage of non-threatened species is 27.0% to 29.6% for all protected areas, but drops to 11.5% to 12.5% for national parks.

There is an inverse relationship between the degree of conservation status and coverage by protected areas, for both global and Taiwanese conservation status (Table 1). The situation is

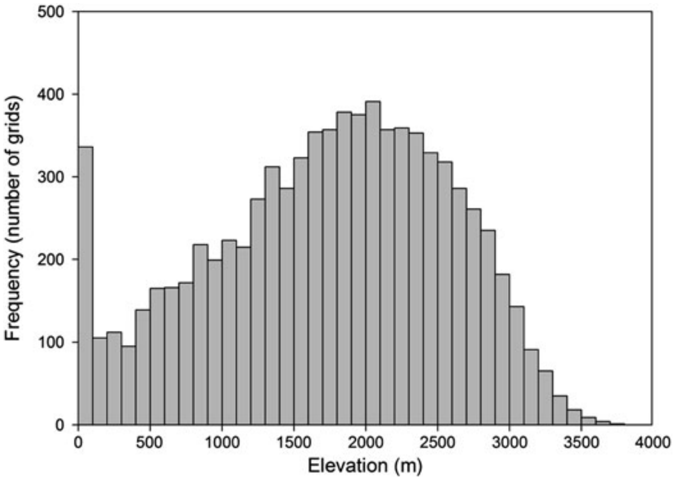

Figure 2. Number of grid cells (n = 8,240) of Taiwan's protected areas falling into various elevational bands.

reversed for endemic species, whereby endemic species are best covered, followed by endemic subspecies and then non-endemic species. Finally, for range quartile, we find a slightly different pattern, with decreasing coverage from the first to the third quartile but then slightly increased coverage for the fourth quartile.

The relationship between the percentage of each species's coverage of our study area and the percentage of that species's distribution covered by protected areas (Figure 3) clearly shows that there is an upper boundary for species well covered by protected areas, but also that there are many species not well covered by protected areas at all (see Appendix S2 and Table S3). We categorised those species whose distributions are covered by < 5% by the highest protection category as 'badly protected.' We chose this 5% threshold because it is about one-eighth of the coverage of species with the highest cover and it encompasses about one-third (40 out of 116) of all species; using a higher threshold would have included too many species. In this case, there is no need to consider the other protection categories, as the percentage cover of all three categories are highly correlated across species (linear regression for highest versus medium-to-high: $n = 116$, $F = 6{,}021.9$, $r^2 = 0.98$, $P < 0.0001$; for highest versus low-to-high: $n = 116$, $F = 4{,}397.9$, $r^2 = 0.98$, $P < 0.0001$; for medium-to-high versus low-to-high: $n = 116$, $F = 29{,}882.9$, $r^2 = 1.00$, $P < 0.0001$). Therefore, essentially the same species would be 'badly protected' regardless of which protection category we chose.

Comparing range quartile, Taiwanese conservation and endemic status

Comparing range quartile with endemic species status, we found that no endemic species is a fourth quartile species, while endemic subspecies are found in all four quartiles (Figure 4). Comparing range quartile with Taiwanese conservation status (Figure 5), we found an overall agreement between these two measures, with endangered species found only in the first quartile, and other conservation-dependent species found in all quartiles except the fourth. Rare and valuable species appear in all quartiles, but at a much higher percentage in the first and second quartiles. Similarly, the four categories of Taiwanese conservation status are related to the number of grid cells where the respective species were recorded and predicted, with these rankings being significantly different from being equal (Table 2; Kruskal-Wallis, df = 3; $n = 144$, $H = 34.40$, $P < 0.0001$, $n = 116$, $H = 15.98$, $P = 0.001$ and $n = 116$, $H = 9.08$, $P = 0.03$, respectively). The latter analyses demonstrate that the Taiwanese conservation categories correspond, as would be expected, to the

Table 1. Percentage cover of the distribution of 116 modelled species by the protected areas of Taiwan, classified into three categories (see Methods). In each cell, we first give the mean percentage ± SD, then the 95% confidence interval range in brackets. For definitions of categories in column 1, see Appendices S1 and S2.

Category	Sample size	Highest protection	Medium-to-high protection[a]	Low-to-high protection
Taiwanese conservation status				
Endangered	1	5.8	14.0	27.5
Rare and valuable	19	12.9 ± 7.3 (9.4-16.5)	18.3 ± 9.4 (13.8-22.9)	32.6 ± 18.4 (23.8-41.5)
Other conservation-dependent species	11	20.6 ± 11.6 (12.8-28.4)	26.0 ± 12.5 (17.6-34.4)	46.7 ± 23.9 (30.6-62.7)
Non-threatened	85	11.5 ± 9.6 (9.4-13.5)	15.4 ± 11.6 (12.9-17.9)	27.0 ± 22.0 (22.2-31.7)
IUCN Conservation Status				
'Vulnerable'	1	7.2	14.0	17.0
'Near Threatened'	4	15.4 ± 6.4 (5.1-25.6)	21.1 ± 7.5 (9.2-33.0)	37.8 ± 15.4 (13.3-62.3)
'Least Concern'	111	12.5 ± 9.9 (10.6-14.3)	16.7 ± 11.8 (14.5-19.0)	29.6 ± 22.4 (25.4-33.8)
Endemism				
Endemic Species	16	18.7 ± 9.4 (13.7-23.7)	24.6 ± 9.6 (19.5-29.7)	43.8 ± 18.8 (33.8-53.8)
Endemic Subspecies	53	15.1 ± 9.8 (12.4-17.8)	19.9 ± 11.4 (16.7-23.0)	35.6 ± 21.4 (29.7-41.5)
Non-endemic	47	7.5 ± 7.5 (5.3-9.7)	10.8 ± 9.7 (8.0-13.7)	18.4 ± 18.9 (12.8-23.9)
Recorded rarity				
Rare	6	18.4 ± 12.8 (5.0-31.8)	24.3 ± 14.2 (9.4-39.3)	45.6 ± 27.2 (17.0-74.2)
Uncommon	23	14.9 ± 7.3 (11.7-18.0)	20.7 ± 9.3 (16.6-24.7)	37.2 ± 18.1 (29.4-45.0)
Common	87	11.5 ± 10.0 (9.4-13.6)	15.4 ± 11.8 (12.8-17.9)	26.7 ± 22.1 (22.0-31.4)
Range quartile				
1st quartile (0-25%)	22	16.6 ± 15.6 (9.7-23.5)	20.6 ± 17.4 (12.9-28.3)	36.5 ± 32.7 (22.0-50.9)
2nd quartile (25-50%)	50	13.0 ± 9.1 (10.4-15.6)	17.9 ± 11.8 (14.5-21.3)	32.0 ± 22.6 (25.5-38.4)
3rd quartile (50-75%)	35	9.8 ± 5.6 (7.8-11.7)	13.7 ± 7.1 (11.3-16.1)	23.6 ± 13.4 (19.0-28.2)
4th quartile (75-100%)	9	10.4 ± 2.5 (8.5-12.3)	14.4 ± 2.8 (12.2-16.6)	25.1 ± 5.1 (21.2-29.0)
All species	116	12.5 ± 9.8 (10.7-14.3)	16.9 ± 11.7 (14.7-19.0)	29.8 ± 22.2 (25.7-33.8)

total area in which the species was recorded and predicted to be present. However, there are a number of species which fall outside of these general trends (see below).

Species whose status may be reassessed

Using the analyses above, we identified those species whose status may need to be reassessed because of possible conflicts between the respective conservation-relevant measures (Table S3). As with any categorisation, we made some arbitrary decisions about how to categorise species. For example, we only considered first quartile species to be threatened because of a small distributional range, or we categorised those species whose distributions had < 5% cover by the highest protection category as 'badly protected' (see above). Nevertheless, we considered these categories as helpful to focus attention on those species that may need to be reassessed most urgently. While the process of classifying a species's conservation status has become more and more formalised (Mace *et al.* 2008), this process still includes some arbitrary categorisations. Therefore, the examples below are not meant as descriptive recommendations, but as suggestive pointers as to which species should be further investigated and why.

Category 1: Species of limited distribution and protection: 10 species are all first quartile species and < 5% of their distributions are protected. Only four of these have a Taiwanese conservation status of rare and valuable (Ring-necked Pheasant *Phasianus colchicus*, Greater Painted-snipe *Rostratula benghalensis*, Collared Scops-owl *Otus lettia*, Crested Myna *Acridotheres cristatellus*) and one of conservation-dependent (Oriental Pratincole *Glareola maldivarum*). The remaining

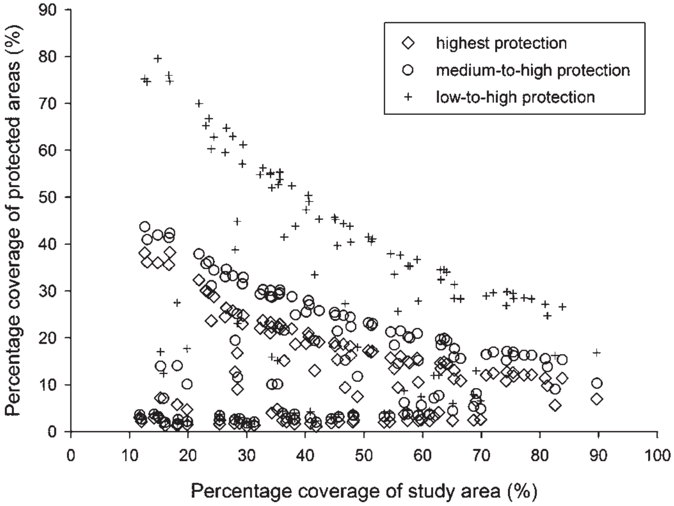

Figure 3. Relationship between the percentage of each species's coverage of our study area (mainland Taiwan) and the percentage of that species's distribution covered by the highest, medium-to-high, and low-to-high levels of protection.

five species (Yellow Bittern *Ixobrychus sinensis*, Cinnamon Bittern *I. cinnamomeus*, Malayan Night-Heron *Gorsachius melanolophus*, Ruddy-breasted Crake *Porzana fusca*, and Black-billed Magpie *Pica pica*) deserve special attention.

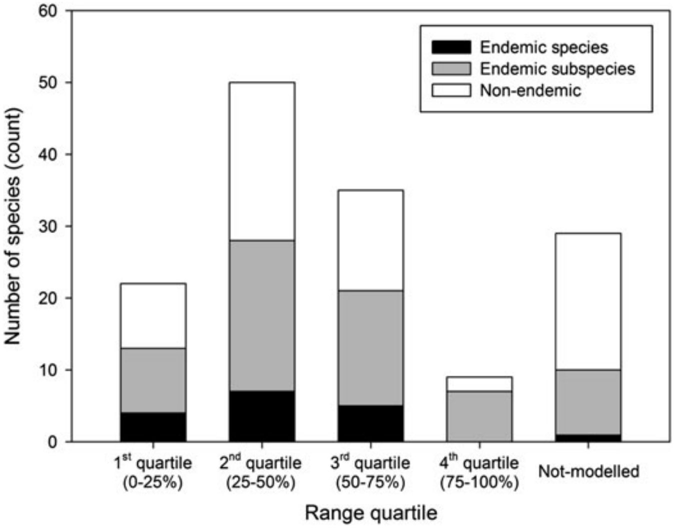

Figure 4. Comparison of Taiwanese endemic status (see Appendix S1) versus range quartile (see Appendix S2). Quartiles 1-4 correspond to the percentage coverage of the study area by each species (see Methods). 'Not modelled' means the sample size was insufficient to model the species's distribution (see Methods and Appendix S1). The distribution of endemic status categories is not distributed randomly amongst the four categories of range quartile (likelihood ratio chi-square $G^2 = 5.04$, df = 6, $n = 116$, $P = 0.54$).

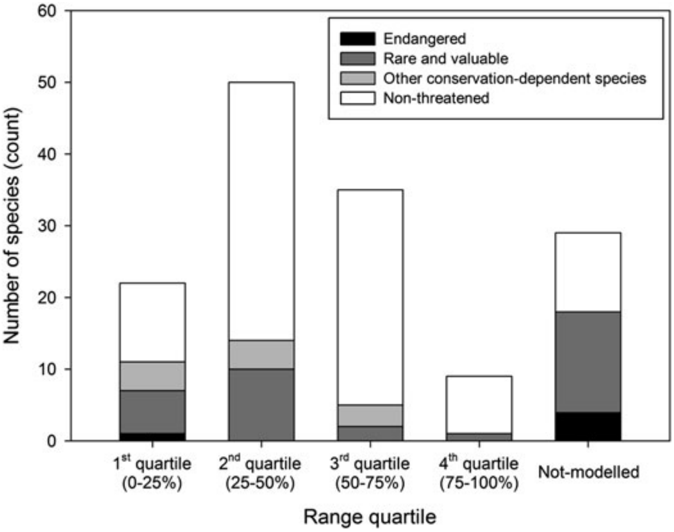

Figure 5. Comparison of Taiwanese conservation status (see Appendix S1) versus range quartile (Appendix S2). Quartiles 1–4 correspond to the percentage coverage of the study area by each species (see Methods). 'Not modelled' means the sample size was insufficient to model the species's distribution (see Methods and Appendix S1). The distribution of conservation status categories is not significantly different from random (likelihood ratio chi-square $G^2 = 12.74$, df = 9, $n = 116$, $P = 0.17$).

Category 2: Species of limited distribution: There remain 12 first quartile species. Except for the Black Eagle, Gray-faced Woodpecker *Picus canus* and White-browed Bush-Robin *Tarsiger indicus*, they were all recorded as common by the Chinese Wild Bird Federation (2010). As the definition

Table 2. Mean, median and range of recorded and predicted grid cells for four different categories of Taiwanese conservation status (Appendix S1) for all breeding species ($n = 144$) and all modelled breeding species ($n = 116$). Recorded cells are those where a species was recorded in our database, and predicted cells are those where a species was predicted to be present in our final maps.

Taiwanese conservation status	Breeding species		Modelled breeding species			
	Number of grid cells recorded		Number of grid cells recorded		Number of grid cells predicted	
	Mean (n)	Median (range)	Mean (n)	Median (range)	Mean (n)	Median (range)
Endangered (EN)	12.0 (5)	9 (3-30)	30.0 (1)	30	6,516.0 (1)	6,516
Rare and valuable (RV)	81.3 (33)	43 (1-555)	132.0 (19)	86 (30-555)	13,099.2 (19)	12,262 (5,500-27,166)
Other conservation-dependent species (CD)	158.5 (11)	124 (47-359)	158.5 (11)	124 (47-359)	12,456.8 (11)	12,350 (5,333-21,277)
Non-threatened (NT)	312.1 (95)	185 (0-1,204)	347.1 (85)	213 (33-1,204)	17,015.3 (85)	16,443 (4,229-32,308)

of common is "the respective bird species was recorded in > 70% of suitable habitats" (Appendix S2), we suggest that these suitable habitats may be relatively rare within the study area. Furthermore, while six of these species are categorised as threatened in Taiwan, another six species are considered non-threatened (Spotted Nutcracker *Nucifraga caryocatactes*, Taiwan Bush-Warbler *Bradypterus alishanensis*, Grey-hooded Fulvetta *Alcippe cinereiceps*, Winter Wren *Troglodytes troglodytes*, Collared Bush-Robin *Tarsiger johnstoniae* and Vinaceous Rosefinch *Carpodacus vinaceus*); given their restricted distributions, their status may need to be reassessed. Finally, all of these species except the Black Eagle and the Gray-faced Woodpecker are endemic species or endemic subspecies, further emphasising their conservation value.

Category 3: Species of limited protection: There remain another 30 species whose distributions are protected by < 5%. All of these are either second or third quartile species, and they are also all recorded as common, except the Emerald Dove *Chalcophaps indica* and Golden-headed Cisticola *Cisticola exilis* which were recorded as uncommon. Meanwhile, the Taiwan Magpie *Urocissa caerulea*, albeit recorded as common, is a conservation-dependent and second quartile species. More protected areas may need to be established for these three species.

Category 4: Species which may need to be reassessed: Here we summarise species whose assessment categories are not in agreement. The Taiwan Partridge *Arborophila crudigularis* is considered uncommon and conservation-dependent but is a third quartile species. The Crested Serpent-Eagle *Spilornis cheela* and Crested Goshawk *Accipiter trivirgatus* are considered rare and valuable species but are recorded as common and are a fourth and third quartile species, respectively. The Mountain Scops-Owl *Otus spilocephalus* is considered a rare and valuable species but is recorded as common and a third quartile species. The Plumbeous Water-redstart *Rhyacornis fuliginosa* is considered conservation-dependent but is recorded as common and a third quartile species. The White-tailed Robin *Cinclidium leucurum* is recorded as uncommon and considered conservation-dependent but is a third quartile species. The Green-backed Tit *Parus monticolus* and the Taiwan Barwing *Actinodura morrisoniana* are considered conservation-dependent but are recorded as common and second quartile species. Another 11 species are recorded as common while being only second quartile species. All of these species may need to be reassessed.

Discussion

Ideally, a distribution model of a biological species should be a geographic representation of its ecological niche (Peterson *et al.* 2011). Because the data to build the model can only come from the species's realised niche, the model should represent the realised niche, but may also extend into the species's fundamental niche. This can be a desirable feature, e.g. to predict into which areas invasive species may spread (Gallien *et al.* 2012, Václavík and Meentemeyer 2012) or where a new population of an endangered species may be introduced (Pérez *et al.* 2011).

However, in some cases, distribution models over-predict the distribution of a species because they do not take into account factors that limit the realised niche, e.g. interspecific competition. For example, the Light-vented Bulbul *Pycnonotus sinensis* and the Taiwan Bulbul are sister species which hybridise along their contact zone within Taiwan, with each species probably being excluded from the range of the other by interspecific competition (Severinghaus *et al.* 2010). Therefore, it is to be expected that the modelled distribution of the Light-vented Bulbul incorporates the modelled distribution of the Taiwan Bulbul, and vice versa. To deal with this obvious problem in 11 of our species, we corrected over-prediction by cutting out regions where the species had never been observed (previously done, e.g. for migratory birds, see Walther *et al.* 2004, Walther *et al.* 2007, Wisz *et al.* 2007, Walther *et al.* 2010).

Given that our distribution models are based on the most comprehensive avian database of Taiwan, and are the first to be based on an ensemble approach and to correct for over-prediction, and have yielded reasonable AUC scores, our distribution maps of Taiwanese birds (Appendix S3) are currently the best available. There is ongoing discussion about both the best evaluation metrics (Fielding and Bell 1997, Pepe 2000, Anderson *et al.* 2003, Austin *et al.* 2006, Lobo *et al.* 2008, Liu *et al.* 2009) for evaluating model performance, as well as the best thresholds for converting probabilistic into binary maps (Manel *et al.* 2001, Liu *et al.* 2005, Hernandez *et al.* 2006, Jiménez-Valverde and Lobo 2007, Pearson *et al.* 2007, Freeman and Moisen 2008, Nenzén and Araújo 2011, Bean *et al.* 2012). Our study was not designed to answer these questions, but we tried to minimise any concerns by combining ensemble modelling with the AUC evaluation technique and the MaxKappa threshold.

These maps allowed us to calculate the protected area coverage of Taiwan's bird species, which is major improvement in assessing the status of each species status as well as the overall performance of the protected area network in maintaining the long-term survival of Taiwan's avifauna. Currently, Taiwan's protected areas cover almost 30% of the distributional ranges of the 116 bird species that we modelled. However, this figure dropped to 16.9% for areas with medium-to-high and to 12.5% for the highest protection (Table 1).

Species with low protected area coverage (Appendix S2, Figure 3) should be of special concern which is why we point them out for reassessment (Table S3). Of course, some of these 'badly' protected species survive well in human-modified landscapes, e.g. Malayan Night-Heron and Black-billed Magpie (both category 1 species; Table S3), and are therefore hardly dependent on natural landscapes found in protected areas for long-term survival. None of the five criteria used to evaluate each species's status from the Directions for Evaluating Wildlife Categories (see Methods) so far considers either the protected area coverage (this study) or the percentage human-modified landscape covered by the species's distribution (see Discussion below), although the fifth criterion incorporates the rate of habitat loss. Therefore, the use of GIS mapping could enhance the Wildlife Conservation Advisory Committee's ability to categorise objectively the status of Taiwan's bird species (as well as other taxa).

Given that we now have distribution maps of each bird species, we could also quantify the amount of human-modified versus natural landscapes used by each bird species through overlay analyses. However, we first have to define which habitats are more or less modified by humans which would require more expert consultation and research (such as by quantifying the human appropriation of net primary production, e.g. Haberl *et al.* 2010).

Our distribution maps have another benefit, i.e. a more realistic estimate of the area occupied by a species, which we then divided into four quartiles in accordance with other macroecological studies (Jetz and Rahbek 2002, Wisz *et al.* 2007). The size of a species's distribution is *per se* an important criterion for determining conservation status because smaller occupied areas are at larger risk of being subject to catastrophes droughts, fires, epidemics, etc; e.g., Mace and Lande 1991), regardless of how much of the occupied area overlaps with protected areas, natural or human-modified habitats.

Based on our modelled distributions, we investigated how categories of conservation status and endemism established by the Wildlife Conservation Advisory Committee relate to each species's occupied area and range quartile. As one might expect, no relationship was found between range quartile and endemic status (Figure 4) indicating that endemic species and subspecies range from narrowly to widely distributed species. Also as expected, we found that a general relationship exists between range quartile and conservation status with narrowly distributed birds being overall more endangered (Table 2, Figure 5). However, there is considerable variation in range quartile among the categories of Taiwanese conservation status, with some first quartile species considered non-threatened and some fourth quartile species considered rare and valuable (Figure 5). Likewise, the numerical ranges of predicted cells among the categories of Taiwanese conservation status (Table 2) suggest that there are species whose status may need to be reassessed.

To help with such a reassessment, we here made an initial attempt to select those species that, based on range quartile and protected area coverage, may be more threatened by local or national extinction than previously realised (Table S3). While such species may need to be uplisted, we also pointed out a number of species which could be downlisted (e.g. threatened species that are recorded as common and are in the fourth quartile). We refrain from making definite recommendations here because (1) additional criteria, as stated in the Directions for Evaluating Wildlife Categories, need to be considered and (2) our suggested criteria have not yet been accepted by the Wildlife Conservation Advisory Committee. Therefore, they only remain recommendations for the moment. Further discussion of this complex topic is provided in Walther *et al.* (2011).

As pointed out above, our cut-off points for including species in Table S3 were arbitrary. For example, first quartile species in our study have a distribution of < 9,006 km^2 (see Methods), while the cut-off points for Endangered and Vulnerable species under the IUCN criteria are 5,000 km^2 and 20,000 km^2, respectively (Mace *et al.* 2008). There are only four species (Cinnamon Bittern, Black-billed Magpie, Winter Wren, Vinaceous Rosefinch) with a distribution of < 5,000 km^2 in our assessment but 79 species with a distribution of < 20,000 km^2 (Appendix S1) while 22 species are first quartile species. Any of these cut-off points is as justifiable as any other; however, 22 species represents about 19% of the 116 modelled species which seems a more reasonable cut-off point than 3% or 68% which would have resulted from using the IUCN criteria. We therefore chose to keep to with our own cut-off criterion of first quartile species.

Finally, our distribution maps allow us to pinpoint sampling gaps both within and outside of protected areas, which should be subject to further fieldwork, for example, much of Taiwan's central mountain range which has almost no records but is predicted to have high species richness (Figure 1a, 1b). Better data coverage will result in even better models, which in turn will result in even better conservation assessments.

We recommend that the species' potential distribution (measured continuously as the number of predicted cells, and categorically as the range quartile) and the protected area coverage be incorporated into future assessments of the status of Taiwanese birds, and that assessments of current and future land-use and threats from climate change, direct persecution and invasive species should also be considered.

Supplementary Material

The supplementary materials for this article can be found at journals. cambridge.org/bci

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