Taiwania, 57(4): 342–358, 2012

Modeling the Distribution of Rare or Cryptic Bird Species of Taiwan

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(Manuscript received 29 May 2012; accepted 14 August 2012)

ABSTRACT: For the study of the macroecology and conservation of Taiwan's birds, there was an urgent need to develop distribution models of bird species whose distribution had never before been modeled. Therefore, we here model the distributions of 27 mostly rare and cryptic breeding bird species using a statistical approach which has been shown to be especially reliable for modeling species with a low sample size of presence localities, namely the maximum entropy (Maxent) modeling technique. For this purpose, we began with a dedicated attempt to collate as much high-quality distributional data as possible, assembling databases from several scientific reports, contacting individual data recorders and searching publicly accessible database, the internet and the available literature. This effort resulted in 2022 grid cells of 1 × 1 km size being associated with a presence record for one of the 27 species. These records and 10 pre-selected environmental variables were then used to model each species' probability distribution which we show here with all grid cells below the lowest presence threshold being converted to zeros. We then in detail discuss the interpretation and applicability of these distributions, whereby we pay close attention to habitat requirements, the intactness and fragmentation of their habitat, the general detectability of the species and data reliability. This study is another one in an ongoing series of studies which highlight the usefulness of using large electronic databases and modern analytical methods to help with the monitoring and assessment of Taiwan's bird species.

KEY WORDS: Biogeography, conservation status, GIS, rarity, Taiwan avifauna.

INTRODUCTION

Taiwan is an important biodiversity hotspot of endemism for many taxa. One of the most visible and well-documented taxa of Taiwan's fauna is its avifauna, with more than 589 bird species having been recorded in all of Taiwan, including its outlying islands (Chinese Wild Bird Federation, 2011) and 145 species having been reported as breeding birds on Taiwan's mainland (Fang, 2008). Recently, the first comprehensive avifauna of Taiwan was published (Severinghaus et al., 2010, abbreviated as AT from hereupon), and constant-effort monitoring schemes have been set up, such as the Taiwan Breeding Bird Survey (BBS Taiwan) and the Monitoring Avian Productivity and Survivorship in Taiwan (MAPS Taiwan) project (Lin, 2012). Therefore, more and more information is now available to assess the status of Taiwan's bird species, such as their rarity and threat of extinction (AT; Council of Agriculture of Executive Yuan, 2009; Ko et al., 2009b; Chinese Wild Bird Federation, 2010; Walther et al., 2011; Wu et al., in press; in review).

Species are rare for different ecological and evolutionary reasons, and, consequently, also display different kinds of rarity: they have small ranges, they occur in few habitats, they have small population sizes, or any combination of these (Rabinowitz, 1981; Kunin and Gaston, 1993; Kunin and Gaston, 1997). Moreover, they may not be rare at all as defined above, but simply appear rare because they are difficult to record for various reasons, e.g., being cryptic, difficult to identify or occurring in inaccessible regions.

In this study, our only criterion of rarity is the number of geographically separated localities where a species was recorded. We do not assume that a low number of such records necessarily implies that the species is ecologically rare as defined above. However, most of the species with a low number of records will also be ecologically rare although some may simply be difficult to record (see Discussion for species-specific details).

With the growing availability of locational databases on Taiwanese birds, there is also a growing need to analyze this information. In an effort to collate much of the available distributional data on Taiwanese birds, Wu et al. (in press) recently built statistical distribution models for 116 out of the total of 145 Taiwanese breeding bird species. The models were used to highlight areas of high avian species richness (Wu et al., in review) and to reassess the conservation status of Taiwan's avifauna (Wu et al., in press). These 116 species were chosen because they had been recorded in ≥ 30 geographically separated localities within a grid of 36022 pixels of 1 × 1 km size covering mainland Taiwan.

Most of these 116 species are the more common or more easily recorded species of Taiwan, while the remaining 29 species are mostly rare or cryptic species.

Because conservation recommendations and efforts should pay close attention to these species, there was an urgent need to improve our database to allow us to model the distribution of these remaining species.

Therefore, we made a dedicated attempt to collate additional high-quality distributional data which was previously unavailable to us. We then modeled the distribution of 27 of the 29 remaining species using the maximum entropy (Maxent) modeling technique (Phillips et al., 2006). To our knowledge, this is the first attempt to model these species' distributions except for six previously modeled species: Mikado Pheasant (Ko et al., 2009b), Mountain Hawk-Eagle (Ho, 2006; Hung, 2009), Tawny Fish-Owl (Hong et al., In press), Fairy Pitta (Ko et al., 2009a), White-throated Laughingthrush (Liao, 1997) and Russet Sparrow (Lu, 2004).

The Maxent modeling technique was chosen after an extensive literature review of rare species modeling (Walther, in prep.). After reviewing approximately 150 relevant studies, it became apparent that, for the moment, Maxent is the most reliable technique for modeling species for which only a small number of presence records is available when compared to the performance of other modeling techniques (Hernandez et al., 2006; Guisan et al., 2007; Pearson et al., 2007; Wisz et al., 2008; Costa et al., 2010; Marini et al., 2010; Gastón and García-Viñas, 2011). Therefore, we relied exclusively on modeling species distributions with Maxent in this study.

MATERIALS AND METHODS

Study area

The island of Taiwan covers latitudes 22°-25°18'N and longitudes 120°27'E-122°E with a maximum elevation of 3952 m. The climate ranges from tropical in the south to subtropical in the north and alpine in the high mountains, a mean annual temperature of 18.0°C and an average annual precipitation of 2510 mm. The natural vegetation is almost exclusively forest, with great variation due to Taiwan's variable topography and human influence which has dramatically changed many of its landscapes. We divided our study area into a total of 36022 grid pixels of 1 × 1 km size.

Rationale for this study

Our original data set was derived from a variety of sources to build the first comprehensive distributional dataset of the breeding birds of Taiwan. Data came from bird census projects conducted in 1993–2004 (Endemic Species Research Institute, unpublished data), 1999–2003 (Koh et al., 2006), 2002–2003 (P.-F. Lee, unpublished data), 2003–2004 (Ko, 2004; P.-F. Lee, unpublished data), 2006–2007 (Peng, 2008), and 2008 (W.-J. Chih, C.-J. Ko & M.-Y. Yang, unpublished data). A much more detailed account of the data sources and verification is published in Wu et al. (in press). For each record, we entered the following information into a database: (1) Bird 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 used these data to model the distributions of Taiwan's breeding bird species with ≥ 30 records within the 36022 grid pixels which cover mainland Taiwan (see Wu et al., in press for details and maps). However, 28 out of the total of 145 Taiwanese breeding bird species had < 30 records, which means they were too 'rare' to be modeled only in the sense of having insufficient sample size for reliable distribution modeling. Therefore, we did not model these 28 species at the time (Wu et al., in press; in review). In these two studies, we also excluded the White Wagtail because it is not possible to visually distinguish breeding individuals and wintering visitors.

Given the urgent need to model these remaining species for ecological and conservation purposes, we recently undertook a concerted effort (1) to increase the data coverage of these 28 remaining bird species (but not the White Wagtail which already had sufficient data coverage) and (2) to choose a modeling technique which is especially robust and reliable when modeling species with low sample sizes.

Increasing sample sizes for 29 bird species

First, one of us (JLW) performed a data search for these bird species from January to April 2011 within the Chinese Wild Bird Federation database. To increase spatial accuracy, recorders (see Acknowledgements) of records were personally contacted to provide additional locational information which allowed us to place each record within a specified 1 × 1 km grid pixel.

Second, one of us (BAW) conducted a search for which all species names (see Table 1 for all English and Latin names and synonyms) were entered into the following search engines (Global Biodiversity Information Facility Species Data Portal, Google, Google Scholar, Web of Science) to find additional data. Furthermore, reference lists in published studies were checked for additional published studies with distributional data.

Third, one of us (RSL) provided additional data for the Fairy Pitta, Da-Ching Chou for the Black-shouldered Kite and Yuan-Hsun Sun for the Tawny Fish-Owl, Black-naped Oriole and Brown Wood-Owl, and Chie-Jen Ko for several species.

To verify the distributional data, records of each species were plotted using ARCGIS and checked for unusual records. First, any record which was outside of Taiwan was deleted. Second, any record whose accuracy was insufficient to be placed within a 1 × 1 km grid pixel was deleted. Third, we examined each sampling point to eliminate unreliable records which were likely erroneous records (e.g., when the recorded place name and geographical coordinates were inconsistent); for more details, see Wu et al. (in press).

All these additional data were then added to our original database. We then restricted records to the months of March to July, as these correspond to the main breeding season of most species. However, for the Tawny Fish-Owl, we defined the breeding season to be from February to May (Yuan-Hsun Sun, in litt. 2012), and for the Black-shouldered Kite, we added all definite breeding records even from outside of March to July (Da-Ching Chou, in litt. 2012). Despite all these efforts, two species could not be modeled because of insufficient data: we obtained only one record each for the Small Buttonquail (Koh et al., 2006) and the Water Rail (http://nc.kl.edu.tw/bbs/archive/index.php/t-43948-p-4.html).

For some species, it is not possible to visually distinguish between breeders and wintering individuals that extend their stay into the breeding season (specifically, White Wagtail) or migrants passing through Taiwan during the start of the breeding season of some species (specifically, Striated Heron, Mandarin Duck, Pheasant-tailed Jacana, Northern Boobook, Black-naped Oriole). However, we kept all records for modeling because we often had no additional information to distinguish records.

Our efforts to collate additional data represent a significant increase to the amount of data available previously (Wu et al., in press; in review). Excluding the White Wagtail (whose database was not increased, see above), the mean sample size increased from 12.0 (n = 28, range 0–28) in Wu et al. (in press; in review) to 63.1 (n = 28, range 1–806) in this study. The mean increase of data availability was 720% (median = 214%) over the original data base (Wu et al., in press; in review).

Choosing environmental data layers

Statistical distribution models require environmental data layers that contain the values of environmental variables for the study area. We began with 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 cover the entire mainland of Taiwan with 36022 grid pixels of 1 × 1 km size, with all layers overlaying perfectly. Because the modeling of species with low sample sizes requires a correspondingly low number of environmental data layers to avoid overfitting of models (Phillips et al., 2004; Gastón and García-Viñas, 2011; Frederic Jiguet, Morgane Barbet-Massin, in litt. 2012), we reduced the number of layers in two steps. First, one of us (TYW) pre-selected 12 out of the 120 variables based on a literature review of which variables had previously been selected as the most important predictor variables in distribution models of Taiwanese bird species (Shiu, 2003; Lee et al., 2004; Ding et al., 2006; Koh et al., 2006) and terrestrial species worldwide (Elith and Graham, 2009; Elith and Leathwick, 2009). Second, these 12 variables were then all correlated with each other using a Pearson correlation coefficient test to avoid autocorrelation between them. If two variables were correlated with a correlation coefficient > 0.9, one of the two variables was chosen randomly and eliminated. Consequently, two variables (standard deviation of elevation, temperature) were eliminated, leaving us with 10 variables for species distribution modeling: distance to river, distance to sea, mean elevation, forest density, mean NDVI, annual precipitation, road density, mean slope, human population density, and ecoregion (classified by Su, 1992 into 41 ecoregions). The variables "distance to river" and "distance to sea" were, however, used only for those species whose main habitats are coasts, rivers or wetlands (for more details, see Wu et al., in press).

Building distribution models

Given the results of the literature review (Walther, in prep.), we chose one particular distribution modeling technique, namely Maxent (Phillips et al., 2006; Phillips and Dudík, 2008; Elith et al., 2011) which one of us (TYW) used to model each of the 27 bird species. We used version 3.3.3k downloaded from http://www.cs.princeton.edu/~schapire/maxent/.

Maxent is not a discriminative method (e.g., general linear models such as logistic regression), but instead Maxent is a generative approach which estimates the probability distribution of maximum entropy, such as the spatial distribution of a species, that is most spread out but subject to constraints imposed by the information available regarding the known observations of the species and environmental conditions across the study area (for details, see Phillips et al., 2006; Phillips and Dudík, 2008; Elith et al., 2011). Maxent transforms environmental variables into feature vectors and then uses entropy as the means to generalize specific observations of presence of a species and does not require absence points within its theoretical framework. Using presence data is an advantage for modeling rare species, because absence records are notoriously difficult to establish for rare species.

Moreover, Maxent uses regularization principles to avoid overfitting which occurs when a model is excessively complex, such as having too many parameters relative to the number of observations. Many alternative models, such as logistic regression, continue to be hampered by the problem of overfitting (but see Gastón and García-Viñas, 2011). For these reasons, Maxent is an appropriate method to model biological species, and especially rare species, as it avoids fitting too many parameters to few observations (Walther, in prep.).

To evaluate the predictive performance of each species' model, we used a random subset of 75% of the data to calibrate every model (training data), and used the remaining 25% of the data for the evaluation (testing data). The predictive performance of the model was estimated using a threshold independent method called the area under the relative operating characteristic (ROC) curve (AUC). We replicated the random data splitting five times and then calculated the average AUC. This cross-validation method yields a more robust estimate of the predictive performance of each model. Recommended default values for the Maxent modeling procedure were used for the maximum number of background points (10,000), the convergence threshold (10-5), and maximum number of iterations (500). Suitable regularization values which are used to reduce overfitting were selected automatically by Maxent. Selection of "features" (environmental variables or functions thereof) was also carried out automatically, following default rules dependent on the number of presence records (Phillips et al., 2006; Phillips and Dudík, 2008; Elith et al., 2011).

The primary output of most species distribution models returns a probability of species occurrence for each grid pixel. However, it is often necessary to select a threshold of probability to divide pixels into binary categories, e.g., present or absent, or suitable or unsuitable. The question of the most suitable threshold is a concern of ongoing research (Manel et al., 2001; Liu et al., 2005; Hernandez et al., 2006; Pearson et al., 2007; Freeman and Moisen, 2008; Nenzén and Araújo, 2011). In this study, we used the 'lowest presence threshold' (LPT) which is defined as "the lowest predicted value associated with any one of the observed presence records". Pearson et al. (2007) recommended LPT as suitable for modeling rare species.

RESULTS

Status of modeled species

Out of the 27 species, one species (3.7%) has full endemic status, while nine species (33.3%) belong to a recognized endemic subspecies (Table 1). Furthermore, among the 27 species, the following species are considered threatened within Taiwan: five (18.5%) are listed as endangered (Australasian Grass-Owl, Black Eagle, Mountain Hawk-Eagle, Black-naped Oriole, Russet Sparrow), 14 (51.9%) as rare and valuable, but none as a conservation-dependent species (Table 1). Finally, among the 27 species, 18 (66.7%), 7 (25.9%) and 2 (7.4%) species were recorded as rare, uncommon and common, respectively (Table 1).

Model performance

For the 27 species, overall model performance using mean AUC scores averaged 0.891 with a range from 0.702 to 0.985 (Table 1); such values are considered to be 'reasonable' to 'very good' model performance (Pearce and Ferrier 2000). We present our 27 modeled distributions as probability maps, but with any probabilities falling below the lowest presence threshold converted to absent grid pixels (Figs 1–3). Using these distribution maps, we then calculated the number of grid pixels predicted as present (i.e., all grid pixels above the threshold) as well as the percentage coverage of the study area (Table 1). The mean (and range) of the number of predicted pixels is 11743.6 (1692–31128), while it is 15851.1 (4229–32308) for the remaining 116 breeding species of Taiwan (Wu et al., in press).

Environmental variables selected by distribution models

We obtained two metrics, namely percent contribution and permutation importance, of the relative importance of the environmental variables to each species' distribution model (Table 2). The percent contribution is the sum of the contribution of the corresponding variable and of the increase in regularized gain, in each of the 500 iterations of the training algorithm. These percent contribution values are only heuristically defined: they depend on the particular path that the Maxent code uses to get to the optimal solution, and a different algorithm could get to the same solution via a different path, resulting in different percent contribution values. In addition, when there are highly correlated environmental variables, the percent contributions should be interpreted with caution. To estimate the permutation importance, the contribution of each variable is determined by randomly permuting the values of that variable among the training points (both presence and background) and measuring the resulting decrease in training AUC. A large decrease indicates that the model depends heavily on that variable. Values are normalized to give percentages. This measure depends only on the final Maxent model, not the path used to obtain it.

Summing up the contributions of each of our 10 variables to the 27 species models, two variables, namely mean elevation and ecoregion, are the variables of highest importance to most species (Table 2). For some species, the variables forest density, road density and mean slope also make significant contributions. For most species, two variables contribute most with the remaining variables contributing far less, while for a few species, three variables are about equally important (e.g., Tawny Fish-Owl), and for a few other species, one variable predominates (e.g., Alpine Accentor).

Species accounts

Because the interpretation of each distribution model is different given the species' habitat requirements and threats, we below discuss the results for each species individually in taxonomic order. In the Discussion, we then interpret our findings by placing each species into one of five groups based each species' habitat requirements, detectability and data reliability. For ease of placing species, we give the group number at the end of each species account.

Blue-breasted Quail: Swinhoe (1863) claimed this species to be "widely distributed." Nowadays it is rarely observed in grasslands, fields and along rivers (AT) and has been recorded in only 7 grids (Table 1). The distribution map (Fig. 1A) predicts the species to be present only in lowland areas, with a particular high probability in Hualien county because four out of the seven recorded grids are found there (Group 3).

Mikado Pheasant: This endemic species is found in high-altitude forests all across Taiwan except the most northern and southern forests (AT) and has been recorded in 39 grids (Table 1). The distribution map predicts the species to be present mostly in high altitude forests with some mid-altitude forests also predicted, albeit at lower probabilities (Fig. 1B) (Group 1).

Mandarin Duck: This species has been recorded in southern and central Taiwan, but by far the most records are from northeastern Taiwan. However, southern records are exclusively wintering records, with breeding records restricted to mountainous regions in north-central to northern Taiwan. Correspondingly, our 23 recorded grids (Table 1) all represent high-altitude lakes, reservoirs, streams and rivers located in north-central to central Taiwan. Our distribution map predicts the species to be present exclusively in mountainous regions (Fig. 1C) (Group 1).

Striated Heron: This species is found in lowland to mid-altitude habitats all across Taiwan and has been recorded in 60 grids (Table 1). The distribution map correspondingly predicts the species to be present across all of Taiwan, but with higher probabilities predicted in river systems of low-altitude mountains (Fig. 1D) (Group 4).

Black-shouldered Kite: This species has recently colonized the mainland of Taiwan, with the first record in 1998 and the first breeding recorded in 2001 (AT). It has since spread into lowland regions along the central western coastline (AT; Da-Ching Chou, in litt. 2012) so that it has now been recorded in 105 grids (Table 1). The distribution map (Fig. 1E) predicts the species to be present within the same lowland region. However, it is possible and even probable that the species will spread further given its large distribution across Southeast Asia (AT) which indicates that the species has a large environmental niche. To predict the species' future range within Taiwan, one could model the species' distribution across Southeast Asia and then project this model across Taiwan which should result in a much larger distribution than the one shown in Fig. 1E (Group 5).

Black Kite: This species used to be common in all lowland regions prior to the 1980s when rapid urbanization and agricultural modernization rapidly destroyed most of its preferred habitat (AT). Nevertheless, the Black Kite has been recorded in 73 grids (Table 1) all across Taiwan in lowland to mid-altitude habitats. Our distribution map predicts the species' presence in both southern and northern Taiwan, with no presence in central and eastern Taiwan (Fig. 1F) (Group 3).

Mountain Hawk-Eagle: This species is found in mid- to high-altitude forests all across Taiwan and has been recorded in 44 grids (Table 1). The distribution map predicts the species to be present in such mountainous regions, but with higher probabilities in central and southern Taiwan (Fig. 1G). However, the species is sensitive to habitat fragmentation as well as human activity and disturbance (AT). Therefore, high-probability areas within our distribution map may not hold breeding pairs if these conditions apply (Group 4).

Slaty-legged Crake: This species has been recorded in 44 grids (Table 1) scattered all across Taiwan's mountain foothill regions. The distribution map (Fig. 1H) predicts the species to be present across all these areas of Taiwan, with higher probabilities away from the coastline in low-altitude foothill habitats (Group 2).

Slaty-breasted Rail: This species is found in wet, grassy and agricultural lowland habitats and has been recorded in 36 grids (Table 1) in northern and central Taiwan, with very few records from southern Taiwan (AT). The distribution map (Fig. 1I) predicts the species to be present only in lowland areas usually close to the coast except for the East Rift Valley (Group 2).

Watercock: Swinhoe (1863) claimed it to be "not a rare bird on the rice-fields and marshy tracts." This species is nowadays found rarely in wet and grassy habitats and has been recorded in 12 grids (Table 1) usually close to the coastline all across Taiwan. The distribution map (Fig. 2A) correspondingly predicts the species to be present only in lowland areas (Group 2).

Pheasant-tailed Jacana: This species was first recorded by Swinhoe in 1865 when it was breeding commonly across lowland Taiwan in freshwater wetlands and ponds with sufficient floating vegetation (AT). Because of habitat destruction, it gradually disappeared from most of its historical range: breeding was last recorded in eastern Taiwan in the 1950s, and in northern, central and southern Taiwan in the 1980s until only one population of < 100 individuals spread over a number of artificial water chestnut (*Trapa bicornis*) ponds remained in Tainan county in the 1990s (Chang, 2005; Ueng and Yang, 2008). Due to vigorous conservation efforts, the breeding population has recently increased to almost 300 individuals (282 and 323 individuals in 2010 and 2011, respectively; Jung-Hsuan Weng, in litt. 2012), but the breeding distribution is still restricted to Tainan county. Because our database contains historical and current records as well as some possible migrant records, our distribution model was based on 22 grids (Table 1) widely scattered across all lowland regions of Taiwan. The distribution map (Fig. 2B) correspondingly predicts the species to be present in several lowland regions even outside of its current very restricted distribution (Group 4).

Australasian Grass-Owl: This species is the only grassland-dependent owl species of Taiwan which has now a very restricted distribution with only 5 recorded grids (Table 1) located within two small areas in southwestern Taiwan (AT). Its distribution has become restricted because of widespread disappearance of appropriate grassland habitats, use of rodenticides and captures for the cagebird trade. As a result, the distribution map (Fig. 2C) predicts the species to be present only in lowland regions of southwestern Taiwan (Group 3).

Tawny Fish-Owl: This species is found along low- to mid-elevation rivers surrounded by natural forests (AT) and has been recorded in 38 grids scattered across all mountainous regions of Taiwan (Table 1). The distribution map predicts the species to be present in such mountainous regions with higher probabilities along river systems (Fig. 2D) (Group 1).

Brown Wood-Owl: This species is found mostly in low- to mid-altitude natural old-growth forests between 200 and 2300 m altitude all across Taiwan (AT) and has been recorded in 16 grids (Table 1) with two notable concentrations in the north of central Taiwan and scattered along the southern Central Mountain Range. The distribution map predicts the species to be present exclusively within these mountainous regions, with higher probabilities in Miaoli, Taichung and Nanto counties (Fig. 2E) (Group 1).

Tawny Owl: This species is found in mid- to high-altitude forests with scattered records across southern Taiwan (AT) and has been recorded in 13 grids (Table 1). There are approximately 10 northern locations shown in AT which are not in our database, but our modeled distribution (Fig. 2F) predicts the species to be present in mid- to high-altitude mountainous regions along the Central Mountain Range and includes most of these 10 localities (Group 1).

Northern Boobook: This species is mainly found in secondary forests below 1000 m altitude, albeit occasionally in lowlands, wetlands and seaside habitats (AT) and has been recorded in 31 grids (Table 1) scattered all across Taiwan. The distribution map predicts the species to be present in such low-altitudinal forest regions with higher probabilities in the north-east, northern central and southern Taiwan (Fig. 2G) (Group 4).

Fairy Pitta: The distribution of this species was first mapped by Severinghaus et al. (1991) and then mapped and modeled in detail by Ko et al. (2009a) who showed that the Fairy Pitta occurs mostly in low-altitude and relatively undisturbed evergreen broad-leaved forests below 1000 m altitude in western Taiwan. The data collected for the Ko et al. (2009a) study was not available to Wu et al. (in press) but was included in this study. This species has been recorded in 806 grids (Table 1), and the distribution map predicts the species to be present in appropriate foothill regions (Fig. 2H) (Group 1).

Large Cuckoo-shrike: This species is found almost exclusively in low- to mid-altitude mountainous forests all across Taiwan (AT) and has been recorded in 37 grids (Table 1). The distribution map predicts the species to be present in such mountainous regions with higher probabilities in central and southern Taiwan (Fig. 2I). The main threats to this species are logging, fragmentation and compositional change of its forest habitat, and it is therefore considered a rare and valuable species within Taiwan (AT) (Group 4).

Black-naped Oriole: This species was once abundant according to Swinhoe (1863), arriving at the end of March "in large numbers" and distributed "itself over the flat country of the island, being rare in the hilly regions near Tamsuy, but especially abundant in the bamboo-groves of the south-west." Recently, however, this species has only been recorded in 17 grids (Table 1) in several separate lowland habitats all across Taiwan. The distribution map (Fig. 3A) predicts the species to be present across all lowland areas, with higher probabilities around Hualien county and New Taipei county. Given that this species requires tall trees within lowland forests for breeding and prefers areas with a moderately open forest structure (Walther and Jones, 2008), the distribution map likely represents the historic distribution when such habitats covered much of lowland Taiwan (Group 4).

White-throated Laughingthrush: This species is found in mid-altitude mountainous forests between 900 and 2100 m altitude (AT) and has been recorded in 67 grids (Table 1) scattered across Taiwan. The distribution map predicts the species to be present in such mountainous regions (Fig. 3B) (Group 1).

Golden Parrotbill: This species is found in mid- to high-altitude bamboo thickets and scrub bordering evergreen forests with two recorded concentrations just north and just south of central Taiwan (AT) and has been recorded in 22 grids (Table 1). The distribution map predicts the species to be present only along high-altitude mountain ridges in central Taiwan (Fig. 3C) (Group 1).

Island Thrush: This species is found in mid- to high-altitude mountainous forests (AT) and has been recorded in 61 grids (Table 1) scattered across Taiwan. The distribution map predicts the species to be present in such mountainous regions (Fig. 3D) (Group 1).

Plain Flowerpecker: This species has been recorded in a variety of habitats up to 1000 m altitude, such as undisturbed primary forests as well as disturbed secondary forests, and also other cultivated habitats such as orchards, tea gardens, and even bushes (AT; Brazil, 2009) and has been recorded in 81 grids scattered across Taiwan (Table 1). The distribution map predicts the species to be present in such low-altitudinal mountainous and foothill regions with higher probabilities in northern and western Taiwan (Fig. 3E). Given the species' special food preferences, especially mistletoes, our distribution map may overpredict the current distribution if mistletoes are not spread evenly across our predicted distribution (Group 4).

Russet Sparrow: This species is found in and around mid-altitude villages and tribal settlements surrounded by forests (AT) and has been recorded in 46 grids (Table 1) with two notable concentrations north and south of central Taiwan. The distribution map predicts the species to be present in such regions (Fig. 3F). In recent decades, the Eurasian Tree Sparrow (*Passer montanus*) has been expanding its altitudinal range into the mountains. This expansion may have negatively impacted populations of the Russet Sparrow whose populations have been decreasing over recent decades so that it is now considered an endangered species within Taiwan (AT) (Group 4).

Chestnut Munia: This species is found in low-altitude plains and hills, mostly in and around cultivated fields, grasslands or open forests (AT) and has been recorded in 45 grids (Table 1) with notable concentrations in eastern Taiwan. The distribution map predicts the species to be present in such regions with higher probabilities in Yilan and Hualien county (Fig. 3G). However, it is almost impossible to visually distinguish the native breeding subspecies and the introduced invasive subspecies, and consequently, our database is certainly of mixture of both subspecies (Group 4).

Alpine Accentor: This species is found exclusively in high-altitude habitats with two recorded concentrations just north and south of central Taiwan (AT) where it has been recorded in 16 grids (Table 1). The distribution map predicts the species to be present only on the highest mountain ridges in central Taiwan (Fig. 3H) (Group 1).

White Wagtail: This species is found in various low- to high-altitude habitats in urban areas, villages, wetlands and along roads and banks of rivers and ponds all across Taiwan, but mostly in the lowlands (AT) and has been recorded in 256 grids (Table 1). The distribution map predicts the species to be present all over Taiwan with higher probabilities in lowland areas (Fig. 3I) (Group 4).

DISCUSSION

To our best knowledge, the presented distribution models are the first for 21 out of the 27 modeled species (see Introduction) and therefore represent an important advance in our knowledge of the macroecology and conservation of these species, many of which are considered rare and threatened within Taiwan.

Given that species can be 'rare' for different reasons (Rabinowitz, 1981; Kunin and Gaston, 1997), distribution models of rare species need to be interpreted with care (Pearson et al., 2007; Wisz et al., 2008; Costa et al., 2010; Marini et al., 2010). Therefore, we below place our 27 modeled species into five groups based on our knowledge of their habitat requirements, the intactness and fragmentation of their habitat, the general detectability of the species and the problem of wintering, migrant or historical records (historical records refer to old records where the species used to be present but is certainly not present anymore based on recent monitoring).

Group 1: For 9 of the 27 modeled species (Mikado Pheasant, Mandarin Duck, Tawny Fish-Owl, Brown Wood-Owl, Tawny Owl, White-throated Laughingthrush, Golden Parrotbill, Island Thrush, Alpine Accentor), our modeled distributions should adequately approximate their true distributions because (1) the underlying database did not contain wintering, migrant or historical records and (2) the species occurs predominantly in regions of Taiwan with mostly undisturbed habitats. Mean elevation and ecoregion are the most important variables for most of these species' models. Correspondingly, most of these species occur in mountainous regions of Taiwan which are difficult to access. Therefore, our distributions maps should be useful to locate additional undiscovered populations.

Despite occurring in nowadays fragmented lowland rainforest habitats, the modeled distribution of the Fairy Pitta should also approximate the true distribution very well because it is based on a recent comprehensive monitoring study. Until recently, this species was considered to be rare in Taiwan; for example, in a previous study (Wu et al., in press; in review), the Fairy Pitta was only recorded in 21 grid pixels because data originated from general monitoring studies which did not specifically target the Fairy Pitta. However, Lin et al. (2007) found that using playback is very effective in locating breeding Fairy Pittas. Using this novel censusing technique, it was possible to increase the database to 806 grid pixels. Therefore, the case of the Fairy Pitta is a good example of a species which used to be considered rare and cryptic but has now been shown to be relatively common within the study area due to improved censusing techniques and increased monitoring efforts. Given that model performance increases with sample size, this species' distribution model should be very reliable.

Group 2: We suggest that there are three species which would likewise benefit from improved censusing. Specifically, the Slaty-legged Crake, Slaty-breasted Rail, and Watercock are cryptic lowland wetland species which are difficult to monitor. For this reason, they were recorded in only 44, 36 and 12 grid pixels, respectively. Given the difficulty of recording them, they could conceivably be much more widespread. On the other hand, given their specific habitat requirements, they could indeed be rare and threatened. Our distribution models should therefore be seen as a first attempt to approximate their true distributions and be used to design more effective monitoring programs (see, for example, Guisan et al., 2006; Singh et al., 2009).

The three aforementioned species are similar to the two species (Small Buttonquail, Water Rail) which we could not model at all because of insufficient data. Again, we recommend more sustained monitoring efforts for these cryptic species.

Group 3: Our study contains three lowland species (Blue-breasted Quail, Black Kite, Australasian Grass-Owl) for which our database should contain a relatively good representation of their current distribution, and therefore our models should approximate their true distributions appropriately. However, these three species were historically much more widespread but habitat destruction and fragmentation have reduced their historical distributions considerably. We recommend a sustained effort to collect more historical data to model the historical distributions of these and other historically widespread species (e.g., Formosan Magpie *Urocissa caerulea*; Yuan-Hsun Sun, personal communication 2012). For these reasons, reintroduction of these species may also be possible outside our predicted distributions.

Group 4: The modeled distributions of nine species are possibly overpredicted for three different reasons. First, for two species (Pheasant-tailed Jacana, Russet Sparrow) we included historical localities where we know that the species used to be present but is now almost certainly absent. We included these historical records because we wanted to highlight areas where the species could be reintroduced. Especially in the case of the Pheasant-tailed Jacana, reintroduction is rather straightforward given that it requires ponds with floating vegetation which are easily created, as recent conservation efforts have shown (Chang, 2005; Ueng and Yang, 2008). The situation of the Russet Sparrow is much less well understood. Lu (2004) showed that during the breeding season, the Eurasian Tree Sparrow prefers more cultivated areas than the Russet Sparrow, but could not pinpoint reasons for the latter's increasing rarity. Given that so little is known about the Russet Sparrow, our distribution model could help with finding and studying this elusive species.

Second, for five species, we have good reason to assume that some records are from migrants (Striated Heron, Northern Boobook, Black-naped Oriole), from introduced populations (Chestnut Munia), or from overwintering individuals (White Wagtail). If these records are spatially biased (e.g., mostly coastal records for migrating Striated Herons, or mostly introduced populations of Chestnut Munia found in western plains of Taiwan), then our distribution models would overpredict their true breeding distributions. However, if the records are not spatially biased (e.g., probably for White Wagtail), then our distribution models are likely a good approximation of the true breeding distribution.

Third, for three species (as well as the Black-naped Oriole) we have some reason to believe that the species may be absent in parts of its predicted distribution because of biological reasons. The Mountain Hawk-Eagle, Large Cuckoo-shrike and Black-naped Oriole are probably absent wherever their respective habitats have been severely altered or destroyed, and the Plain Flowerpecker may be absent wherever mistletoes are rare or absent. Therefore, these three species would make interesting study species for modeling studies at smaller spatial scales. Our distribution models are based on large-scale variables of climate, habitat, topography and human activity, and can therefore not be explicit for biologically significant variables which may act at much smaller scales, such as the presence or absence of a required food source such as mistletoes.

Group 5: We can reasonably assume that the Black-shouldered Kite has not reached its equilibrium distribution, or, in other words, has not completely filled its fundamental niche. We know that the Black-shouldered Kite has been spreading since its first recorded breeding attempt in 2001 and will most likely to continue spreading beyond its current distribution until it occupies all suitable habitats. Recently, additional breeding records have been certified in lowland areas in Miaoli, Taoyuan, Hualien, Taidong and Pingtung counties (Da-Ching Chou, in litt. 2012). We suggest that a model derived from its East Asian distribution would probably be a much better estimation of the regions of Taiwan into which the Black-shouldered Kite will expand into in the coming decades.

This study highlights the usefulness of using large electronic databases and modern analytical methods to help with the monitoring and assessment of Taiwan's bird species. Recent efforts by the Endemic Species Research Institute (ESRI) in collaboration with the Chinese Wild Bird Federation and the Institute of Ecology and Evolutionary Biology at National Taiwan University to expand citizen participation in the Taiwan Breeding Bird Survey (BBS Taiwan) (Lee et al., 2010) and the Monitoring Avian Productivity and Survivorship in Taiwan (MAPS Taiwan) project (Lin, 2012) should therefore be welcomed and supported as they supply the important baseline data for distribution modeling studies like the present one.

ACKNOWLEDGEMENTS

We thank Yung-Fu Chang, Wei-Kai Chao, Chieh-Peng Chen, Ya-Hui Chen, Yi-Feng Chen, Cheng-Ching Cheng, Ko Cheng, Wen-Jay Chih, Ming-Shui Chiu, Da-Ching Chou, Chao-Sheng Chuang, Tsan-Jung Chuang, Chang-Sheng Ding, Ruey-Yuan Gu, Chia-Hsin Ho, Yi-Shen Ho, Ko-Tai Hsia, Shih-Hui Hsiao, Wei-Chin Hsu, Yu-Cheng Hsu, Chi-Lien Hsueh, Lin-Chih Hu, Teng-Hsiung Hu, Mei-Yu Kao, Chie-Jen Ko, Wen-Yuan Lai, Chao-Hsien Li, Chun-Yuan Li, Yueh-Hsia Li, Chin-Shan Liao, Hsi-Chin Liao, Fang-Tse Lin, Hui-Chu Lin, Ming-Chieh Lin, Su-Lien Lin, Wen-Lung Lin, Chien-Cheng Liu, Mei-Chu Lu, Chun-Yi Peng, Chao-Ju Su, Yuan-Hsun Sun, Yun-Chen Sung, Chiao-Mu Tsai, Chih-Yuan Tsai, Mu-Chi Tsai, Cheng-Han Wu, Chia-Ping Wu, Chung-Hsiang Wu, Liang-Tzu Wu, Li-Lan Wu, Chen-Sung Yeh, Ming-Wei Yu, Kuo-Chu Yueh for providing distributional data, Jung-Hsuan Weng for providing information of Pheasant-tailed Jacana, Tzung-Su Ding, Steve Dudley, Joslin Moore and Shui-Yan Tang for providing references, and Morgane Barbet-Massin, Frédéric Jiguet, Joslin Moore and two anonymous reviewers for helpful comments. The study was supported by National Science Council of Taiwan.

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臺灣稀有或隱蔽性鳥種之模式預測

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（收稿日期：2012年5月29日；接受日期：2012年8月14日）

摘要：為了由巨觀生態學的角度增進對臺灣鳥類的瞭解，並提供保育資訊，建構未曾被研究過之物種的分布預測模式為當務之急。本研究以在樣本數偏低時仍被認為能產生可信賴預測結果之最大熵（maximum entropy, maxent）模式方法建構27種稀有或隱蔽性繁殖鳥類之分布預測模式。我們整合生物分布調查研究報告、逐一聯絡中華鳥會資料庫中的稀有種紀錄者、搜尋網路公開資料庫以及文獻報告，建構高品質的物種分布資料庫，得到本研究27個目標物種的「出現紀錄」資料共涵蓋2022個1 × 1 公里網格；將此資料與預先篩選的10個環境因子建構各物種的分布預測機率模式，並以「最小出現機率值」（lowest presence threshold）為閾值，保留大於閾值的分布預測機率值，但將小於閾值的分布預測機率值轉換為零，作為預測結果。我們逐一探討各物種的分布預測結果，如棲地需求、棲地完整性或破碎化程度、物種偵測度，以及資料可信度，並提出應用建議。本研究屬於利用大尺度電子資料庫與近代分析技術協助臺灣鳥類監測與評估系列研究之一。

關鍵詞：生物地理學、保育等級、地理資訊系統、稀有度、臺灣鳥類相。

Table 1. The 29 Taiwanese breeding bird species which were selected for this study (see Methods). Latin and English names were taken from the Chinese Wild Bird Federation (2010) as well as their endemic species status: endemic = full endemic species status; name of subspecies' trinomial = recognized as endemic subspecies; all other species are listed as non-endemic. Alternative names were taken from AT, Brazil (2009), and Wang et al. (1991). The fifth column gives the number of 1 × 1 km grid pixels in which the respective species was recorded to be breeding ≥ 1 times during the months March to July. The sixth column gives the number of grid pixels in which the respective species was predicted to be present using our distribution models (see Methods). The seventh column gives the percentage coverage of the study area which is the number of predicted pixels (fifth column) divided by the total number of grid pixels of the study area (36022) and multiplied by 100. The eighth column gives the mean AUC and standard deviation calculated from five model runs based on data splitting (see Methods). The ninth column gives the recorded rarity scored by the Chinese Wild Bird Federation (2010) as follows: R = rare (the respective bird species was recorded in < 20% of suitable habitats); UC = uncommon (the respective bird species was recorded 20–70% of suitable habitats); C = common (the respective bird species was recorded in > 70% of suitable habitats). The tenth column gives the Taiwanese conservation status scored by the Council of Agriculture of Executive Yuan (2009) as follows: EN = endangered; RV = rare and valuable; CD = other conservation-dependent species; all other species are non-threatened.

Latin name	Endemic species status	English name	Alternative names	Number of grid pixels recorded	Number of grid pixels predicted	% coverage of study area	mean AUC ± SD	Recorded rarity	Taiwanese conservation status
Coturnix chinensis		Blue-breasted Quail	Painted Quail, King Quail, Indian Blue Quail *Excalfactoria chinensis*	7	5732	15.9%	0.918 ± 0.100	R	RV
Syrmaticus mikado	endemic	Mikado Pheasant		39	18125	50.3%	0.945 ± 0.016	R	RV
Aix galericulata		Mandarin Duck		23	1842	5.1%	0.884 ± 0.127	UC	RV
Butorides striata		Striated Heron	Little Green Heron, Green-backed Heron, striatus	60	26536	73.7%	0.812 ± 0.024	UC	-
Elanus caeruleus		Black-shouldered Kite	Black-winged Kite	105	3003	8.3%	0.980 ± 0.004	R	RV
Milvus migrans		Black Kite	Black-eared Kite *Milvus lineatus*	73	10498	29.1%	0.918 ± 0.014	R	RV
Nisaetus nipalensis		Mountain Hawk-Eagle	Hodgson's Hawk Eagle, *Spizaetus*	44	9418	26.1%	0.854 ± 0.020	R	EN
Rallina eurizonoides	*formosana*	Slaty-legged Crake	Banded Crake	44	25409	70.5%	0.752 ± 0.071	UC	-
Gallirallus striatus	*taiwanus*	Slaty-breasted Rail	Blue-breasted Banded Rail, Blue-breasted Banded Rail *Rallus striatus*	36	5792	16.1%	0.961 ± 0.023	UC	-
Rallus aquaticus		Water Rail	Eastern Water Rail *Rallus indicus*	0	-	-	-	R	-
Gallicrex cinerea		Watercock	Water Cock	12	10160	28.2%	0.823 ± 0.048	R	-
Turnix sylvaticus		Small Buttonquail	Andalusian Hemipode, Little Button Quail *Turnix sylvatica*, Common Buttonquail	1	-	-	-	R	-
Hydrophasianus chirurgus		Pheasant-tailed Jacana		22	7321	20.3%	0.911 ± 0.029	R	RV
Tyto longimembris	*pithecops*	Australasian Grass-Owl	Eastern Grass Owl, Grass Owl *Tyto capensis*	5	2976	8.3%	0.907 ± 0.047	R	EN
Ketupa flavipes		Tawny Fish-Owl	*Bubo flavipes*	38	16744	46.5%	0.864 ± 0.075	R	RV
Strix leptogrammica		Brown Wood-Owl		16	4424	12.3%	0.887 ± 0.064	R	RV
Strix aluco	*yamadae*	Tawny Owl	Chinese Tawny Owl *Strix nivicola*, Himalayan Wood Owl	13	3874	10.8%	0.947 ± 0.035	R	RV
Ninox japonica		Northern Boobook	Brown Hawk Owl *Ninox scutulata*	31	19425	53.9%	0.702 ± 0.157	UC	RV
Pitta nympha		Fairy Pitta	Indian Pitta *Pitta brachyura*	806	18492	51.3%	0.893 ± 0.005	UC	RV
Coracina macei		Large Cuckoo-shrike	*Coracina novaehollandiae*	37	19972	55.4%	0.902 ± 0.033	R	RV
Oriolus chinensis		Black-naped Oriole		17	25340	70.3%	0.750 ± 0.064	R	EN

Latin name	Endemic species status	English name	Alternative names	Number of grid pixels recorded	Number of grid pixels predicted	% coverage of study area	mean AUC ± SD	Recorded rarity	Taiwanese conservation status
Garrulax albogularis	*ruficeps*	White-throated Laughingthrush	Rufous-crowned Laughingthrush *Garrulax ruficeps*	67	8770	24.3%	0.951 ± 0.015	R	RV
Paradoxornis verreauxi	*morrisonianus*	Golden Parrotbill	Blyth's Parrotbill *Paradoxornis nipalensis*	22	1692	4.7%	0.976 ± 0.024	R	-
Turdus poliocephalus	*niveiceps*	Island Thrush	Turdus niveiceps	61	7739	21.5%	0.948 ± 0.019	R	RV
Dicaeum concolor	*uchidai*	Plain Flowerpecker		81	15360	42.6%	0.876 ± 0.030	UC	-
Passer rutilans		Russet Sparrow	Cinnamon Sparrow	46	9376	26.0%	0.961 ± 0.025	R	EN
Lonchura atricapilla		Chestnut Munia	Black-headed Munia Lonchura malacca	45	4836	13.4%	0.951 ± 0.045	R	-
Prunella collaris	*fennelli*	Alpine Accentor	Himalayan Accentor	16	3094	8.6%	0.985 ± 0.011	C	-
Motacilla alba		White Wagtail		256	31128	86.4%	0.806 ± 0.031	C	-

Table 2. Estimates of relative contributions of the environmental variables to the Maxent model of each species. The two values in each cell are percent contribution and permutation importance, respectively (for details, see Results). Empty cells represent variables not included into the final models (for details, see Methods).

English name	Distance to river	Distance to sea	Mean elevation	Forest density	Ecoregion	Mean NDVI	Annual precipitation	Road density	Mean slope	Human population
Blue-breasted Quail	-	-	38.7, 68.3	0.3, 1.2	54.5, 28.8	0, 0	0.1, 0.4	0, 0.1	0, 0	6.4, 1.2
Mikado Pheasant	-	-	57.9, 76.2	0.2, 5.3	20.8, 10.3	0, 0	0.6, 0.9	20, 6.8	0.1, 0.5	0.4, 0
Mandarin Duck	7.4, 1.1	-	8.7, 14.7	6.8, 9.5	72.2, 68.7	0.1, 0	0.6, 0.5	-	2.3, 4	1.9, 1.5
Striated Heron	12, 7.1	-	7.5, 25.2	20.6, 20.1	38.2, 30.4	6, 5.2	-	-	8.6, 7.7	7.2, 4.4
Black-shouldered Kite	-	1.2, 6.1	28.9, 9.3	5.1, 16.8	-	1.2, 1.8	50.8, 52.2	4.8, 7.5	3.4, 1.2	4.5, 5.3
Black Kite	-	2.9, 2.7	10.2, 19	7.1, 14.3	56.3, 30.8	0.4, 0	17, 23.6	-	1.9, 7.5	4.1, 2.2
Mountain Hawk-Eagle	-	-	25.7, 17.5	0.8, 1	44.5, 42.9	5.8, 1.2	2.5, 2.3	6.4, 18.1	6, 4.6	8.4, 12.3
Slaty-legged Crake	-	-	50.3, 47.9	20.2, 25.9	-	6, 8.1	7.1, 9.8	-	16.3, 8.3	-
Slaty-breasted Rail	-	-	16.6, 7.7	1, 0.4	25.2, 10.4	0.3, 0.8	-	-	51, 77.8	5.8, 2.9
Watercock	-	-	5, 14.8	11.7, 0	20.6, 20.8	0, 0	0, 0	-	62.7, 64.5	-
Pheasant-tailed Jacana	-	-	26.4, 66.8	12.8, 3.8	35.7, 17.9	0.9, 0.3	-	-	3.5, 3.7	20.8, 7.5
Australasian Grass-Owl	-	-	4.6, 26.8	0, 0.1	61.7, 53.1	0, 0	-	-	33.7, 20	-
Tawny Fish-Owl	13.2, 1.1	-	27.9, 30.4	11.4, 13.2	31.5, 23.2	0.4, 1.9	0.3, 1.6	-	0.2, 0.9	15.1, 27.6
Brown Wood-Owl	-	-	8.8, 4.5	20.8, 8.7	69.4, 83.6	1, 3.1	-	-	0, 0.1	0, 0
Tawny Owl	-	-	69.8, 44.2	5.5, 31.5	20, 10.7	1.5, 2.5	0.7, 0	2.3, 10.9	0.2, 0.1	0, 0
Northern Boobook	-	-	10.5, 12.9	11.2, 12.2	57, 53.9	0.4, 2.9	5, 6.1	13.5, 4.4	-	2.5, 7.5
Fairy Pitta	-	-	41.8, 42.1	0.2, 0.9	11.8, 14.6	1.3, 3.5	1.7, 1.3	8.8, 3.4	27, 27.7	7.5, 6.4
Large Cuckoo-shrike	-	-	43, 57.8	4, 6.9	39.5, 18.1	1.4, 8.1	0.2, 0.8	5.3, 1.9	4.8, 5	1.7, 1.4
Black-naped Oriole	-	-	1.9, 3.7	-	38.5, 36.1	0, 0	0.2, 0	1.8, 4.3	54.4, 52.3	2.6, 1.1
White-throated Laughingthrush	-	-	60.4, 71.7	0.8, 4.1	19.2, 9.9	0.2, 0.6	2.7, 7.1	10.3, 3.2	4.2, 2.6	2.1, 0.8
Golden Parrotbill	-	-	69.1, 92.5	1.2, 0.8	11, 1.5	0.1, 0	0, 0	12.8, 3.8	0.2, 0.3	5.7, 0.9
Island Thrush	-	-	53, 66.7	0.3, 0.3	22.1, 10.3	0.1, 0.5	3.7, 8.9	16.4, 6	2.1, 5.5	2.2, 1.8
Plain Flowerpecker	-	-	9.5, 22.5	5.4, 7.2	41.9, 31.3	0.7, 6.7	-	-	32.5, 28.9	9.9, 3.6
Russet Sparrow	-	-	38.1, 68.6	5.7, 1.3	29.9, 13	1.7, 1.8	-	21.7, 7.2	2.8, 8.2	-
Chestnut Munia	-	-	30.7, 26.7	6.4, 2.3	54.7, 48.2	0.3, 2.2	-	-	2.6, 11.8	5.3, 8.8
Alpine Accentor	-	-	95.8, 96.9	0.8, 0.2	-	0.2, 0.1	0.2, 0	2.9, 2.7	0, 0.1	0, 0
White Wagtail	-	-	31.6, 32.3	15.9, 20.9	32.9, 18.3	0.2, 0.5	6.1, 10.1	-	3.3, 7.9	9.9, 10

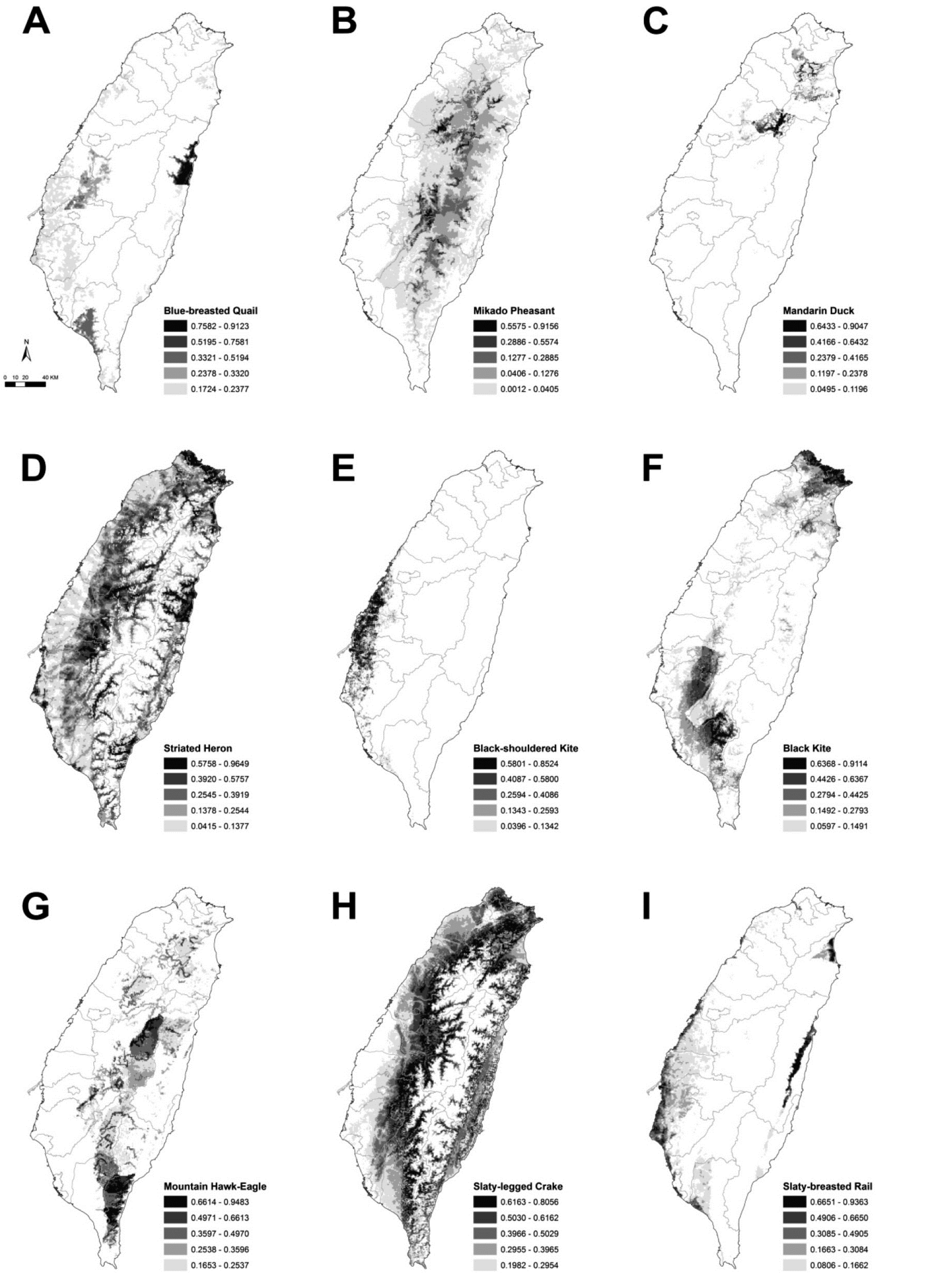

Fig. 1. Predicted probability maps of the following species: (A) Blue-breasted Quail. (B) Mikado Pheasant. (C) Mandarin Duck. (D) Striated Heron. (E) Black-shouldered Kite. (F) Black Kite. (G) Mountain Hawk-Eagle. (H) Slaty-legged Crake. (I) Slaty-breasted Rail.

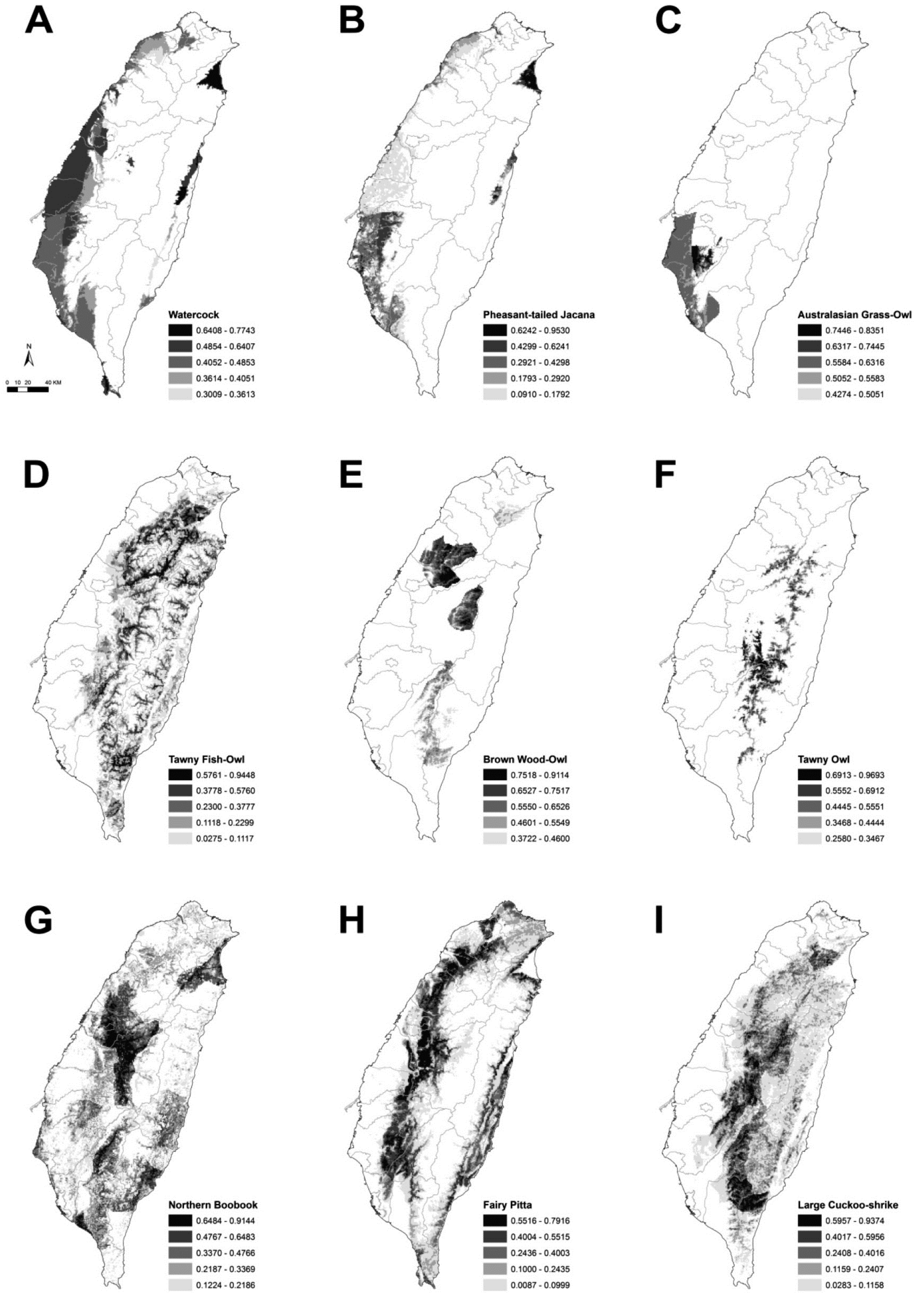

Fig. 2. Predicted probability maps of the following species: (A) Watercock. (B) Pheasant-tailed Jacana. (C) Australasian Grass-Owl. (D) Tawny Fish-Owl. (E) Brown Wood-Owl. (F) Tawny Owl. (G) Northern Boobook. (H) Fairy Pitta. (I) Large Cuckoo-shrike.

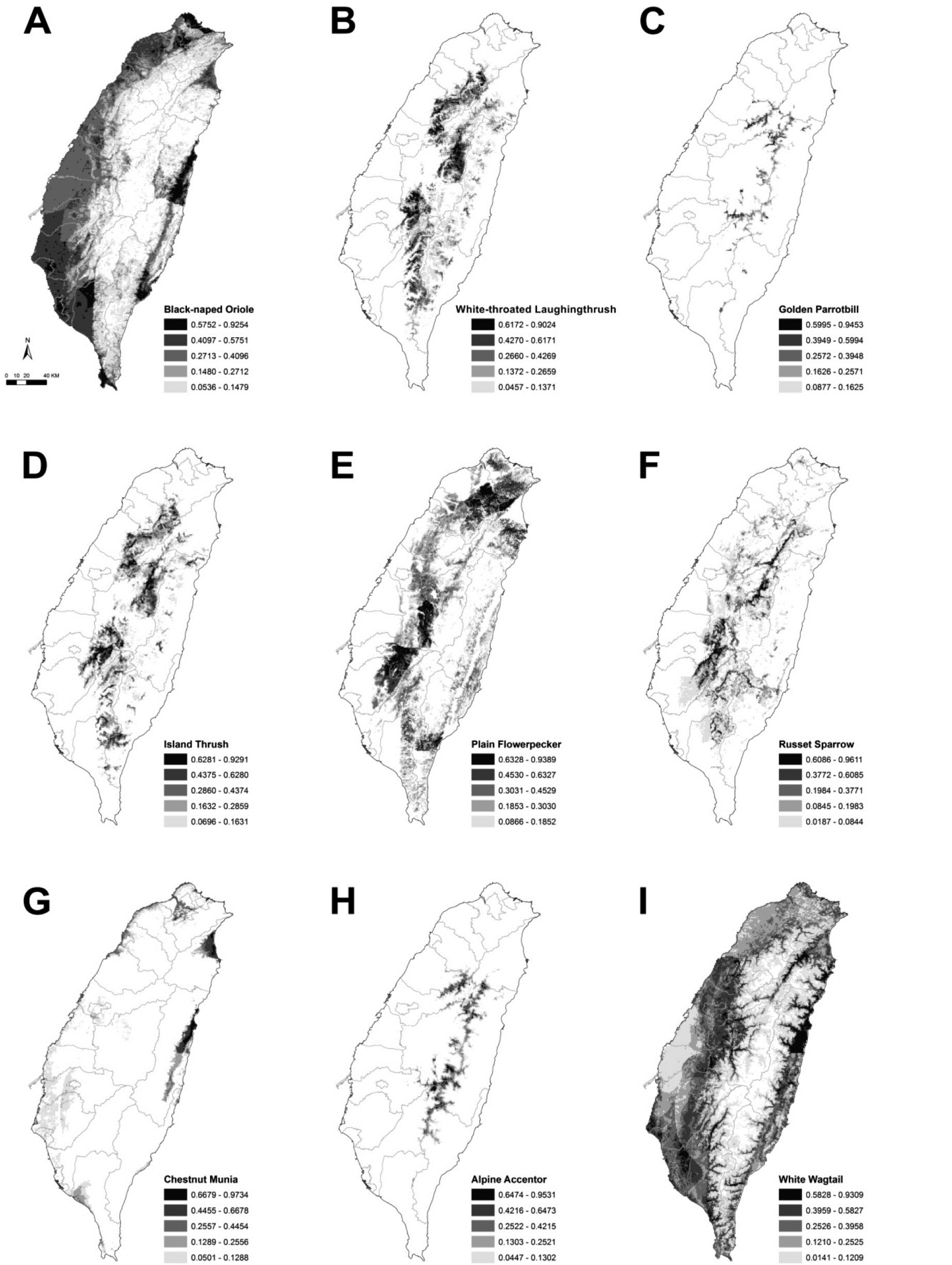

Fig. 3. Predicted probability maps of the following species: (A) Black-naped Oriole. (B) White-throated Laughingthrush. (C) Golden Parrotbill. (D) Island Thrush. (E) Plain Flowerpecker. (F) Russet Sparrow. (G) Chestnut Munia. (H) Alpine Accentor. (I) White Wagtail.