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Hotspot analysis of Taiwanese breeding birds to determine gaps in the protected area network

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Abstract

Background: Although Taiwan is an important hotspot of avian endemism, efforts to use available distributional information for conservation analyses are so far incomplete. For the first time, we present a hotspot analysis of Taiwanese breeding birds with sufficient sampling coverage for distribution modeling. Furthermore, we improved previous modeling efforts by combining several of the most reliable modeling techniques to build an ensemble model for each species. These species maps were added together to generate hotspot maps using the following criteria: total species richness, endemic species richness, threatened species richness, and rare species richness. We then proceeded to use these hotspot maps to determine the 5% most species-rich grid cells (1) within the entire island of Taiwan and (2) within the entire island of Taiwan but outside of protected areas.

Results: Almost all of the species richness and hotspot analyses revealed that mountainous regions of Taiwan hold most of Taiwan's avian biodiversity. The only substantial unprotected region which was consistently highlighted as an important avian hotspot is a large area of unprotected mountains in Taiwan's northeast (mountain regions around Nan-ao) which should become a high priority for future fieldwork and conservation efforts. In contrast, other unprotected areas of high conservation value were just spatial extensions of areas already protected in the central and southern mountains. To combine the results of our four hotspot criteria, we assessed which grid cells were the most valuable according to all four criteria. Again, we found the Nan-ao mountain regions to be important. We also showed that different hotspot criteria only partially overlapped and sometimes barely at all.

Conclusions: Therefore, to protect areas based on only one hotspot criterion (total species richness) would not protect areas based on other hotspot criteria (endemic species richness, threatened species richness, or rare species richness) in Taiwan.

Keywords: Hotspots; Biodiversity; Conservation priorities; GIS; Distribution modeling

Background

The conservation of biodiversity has gained increasing attention from both the public and decision-makers because biodiversity is the basis for functioning ecosystems and the life-support system of the earth (Millennium Ecosystem Assessment 2005; Walther et al. 2011a). At the same time, all levels of biodiversity are rapidly eroding (Butchart et al. 2010).

In response to these challenges, one important concern of conservation biology is to locate biodiversity hotspots because it is an effective way to protect a large number of species within functional landscapes (Myers et al. 2000). The concept of ‘biodiversity hotspots’ was first developed by Myers (1988) and has since blossomed into a large body of local, regional, and global analyses (Myers et al. 2000; Ceballos and Ehrlich 2006; Garcia 2006; Grenyer et al. 2006; Callicott et al. 2007; Schouten et al. 2010).

The definition of a hotspot has been intensely debated; for example, hotspots could be defined as those areas with the highest species richness including all species (Samson and Knopf 1993; Williams et al. 1996; Kerr 1997; Myers et al. 2000; Orme et al. 2005; Grenyer et al. 2006) or only endemic species (Kerr 1997; Orme et al. 2005), rare species (Prendergast et al. 1993; Grenyer et al. 2006; Williams et al. 1996), or threatened species (Dobson et al. 1997; Orme et al. 2005; Grenyer et al. 2006). Many of these hotspot analyses used birds (Williams et al. 1996; Ho 2005; Orme et al.

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2005; Chen 2007; Jenkins et al. 2010) because they are relatively easy to monitor over large areas. Therefore, avian datasets are often the most comprehensive in terms of both spatial and temporal coverages.

Taiwan is an important hotspot of endemism for many different taxa, including birds (Shao et al. 2008). More than 570 bird species have been recorded throughout Taiwan, including several outlying islands (Chinese Wild Bird Federation 2010). On the island of Taiwan proper, 145 species were reported as breeding birds (Fang 2008), among which, at least 17 species (12%) are considered endemic to Taiwan (Chinese Wild Bird Federation 2010). Over the last two decades, basic information on avian distributions and ecology has increased through records by both amateur and professional observers. Using this newly available information, Severinghaus (1994) published the first study of avian zoogeography and the first comprehensive avifauna for Taiwan (Severinghaus et al. 2010). Lee et al. (1998) created the first 2 × 2-km distributional database to analyze the relationship between environmental factors and avian distributions (Nieh 1999; Huang 2001; Koh et al. 2006a,b). Further studies focused on species richness patterns in local regions (Hsu et al. 2004; Ko 2004; Peng 2008), Taiwan's mountains (Shiu and Lee 2003), or all of Taiwan (Lee et al. 2004) but without using distribution modeling. Early modeling techniques were used to study bird distributions in local regions (Huang 2001; Koh et al. 2006a,b) or of a single species or subfamily (Liao 1997; Ko et al. 2009a). Ho (2005) and Ding et al. (2006) selected avian biodiversity hotspots and studied bird species richness patterns in East Asia but did not focus on Taiwan. So far, the only hotspot analysis using Taiwan's birds was restricted to 14 endemic bird species (Ko et al. 2009b).

Therefore, we herein present the first hotspot analysis of all of the Taiwanese breeding birds with sufficient sampling coverage for distribution modeling, using these models to generate hotspot maps of total, endemic, threatened, and rare species richness.

Methods

Study area

Our study area is the island of Taiwan which spans latitudes 22° to 25°18′N and longitudes 120° to 122°27′E (with a maximum elevation of 3,952 m) which can be roughly divided into an almost flat western plain, which has been highly modified by humans, and mountainous areas of 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 an island-wide mean annual temperature of 18°C and average annual precipitation of 2,510 mm). The natural vegetation is almost exclusively forest, except at high elevations and on river floodplains. We divided this study area into a total of 36,022 grid pixels of 1 × 1 km in size.

Species data

We selected the 145 breeding bird species listed for the island of Taiwan (Fang 2008) and determined each species' endemic and conservation status (Wu et al. 2013). We collated spatiotemporal data from various field studies, including Taiwan's Breeding Bird Survey and studies conducted within the national parks to build the first comprehensive distributional dataset of Taiwan's 145 breeding bird species (more details given in Walther et al. 2011b). We then restricted records to the months of March to July, which is the main breeding season of most species. We also *a priori* excluded the White Wagtail *Motacilla alba* from all analyses because it is not possible to visually distinguish breeding individuals from wintering visitors.

For each species, we then coded each 1 × 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 (Hernandez et al. 2006; Wisz et al. 2008) which left us with 116 species (Wu et al. 2013).

Environmental data layers

A much more detailed account of the building of each species' distribution model is given in the studies of Walther et al. (2011b) and Wu et al. (2013). The distribution models were used in the latter paper to reassess each species' conservation status; in this study, we used the same distribution models to determine species richness hotspots. To briefly summarize, we built distributional models for each of the selected 116 bird species using 120 environmental gridded data layers compiled by the Spatial Ecology Lab of National Taiwan University (for details, see Lee et al. 1997). All layers covered the entire island of Taiwan with 36,022 grid pixels at 1 × 1 km. For our analysis of hotspots outside of protected areas (Figure 1), we used shape files of each of Taiwan's protected areas which were created by the same lab in December 2010 (which were categorized into high, medium-to-high, and low-to-high protection depending on the severity of protection; see Wu et al. 2013 for details).

We then used three steps to reduce the layers and build each species' distribution model from the original 120 layers. First, we chose a relevant subset of layers for each bird species based on their habitat choices (Fang 2008). We then used a two-tailed t test for each of the selected layers to test for a significant association with the presence or absence of the species using a significance level $p < 0.05$ and

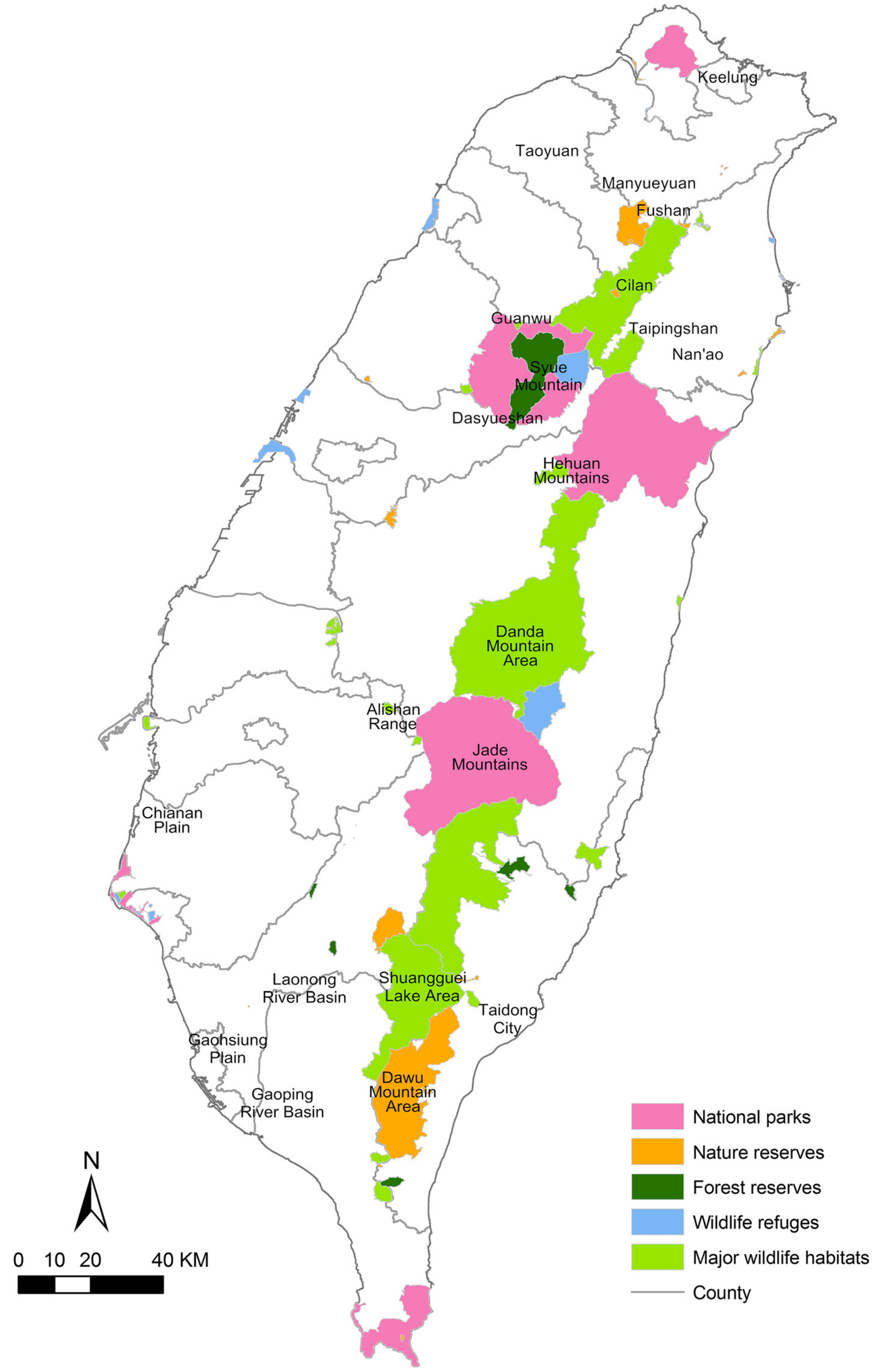

Figure 1 Map of Taiwan's protected areas. All location names mentioned in this study are English transcriptions of the original Mandarin names.

retained only significantly associated variables. We finally eliminated correlated variables using the unweighted pair group method with arithmetic mean tree in the ecological niche factor analysis (ENFA) program (Hirzel et al. 2002).

Building distribution models

We briefly describe below the four steps used to build the presence-absence distribution for each species (for more details, see Walther et al. 2011b; Wu et al. 2013).

First, we produced five probabilistic distribution models using the following methods: multiple discriminant analysis (Johnson and Wichern 2007), logistic regression (Austin 2002), genetic algorithm for rule-set production (Stockwell et al. 2006), an ENFA (Hirzel et al. 2002), and maximum entropy (Phillips et al. 2006). Each method was used to model each species' distribution using 50% of all presence and 50% of all absence records (training data) and then evaluated the remaining 50% of presence and absence records (test data). Dividing the data randomly into training and testing data is a prerequisite for calculating evaluation metrics such as MaxKappa and the area under the operating characteristic curve (AUC) score (Fielding and Bell 1997). Second, we ranked the performance of the five models for each species using the AUC score. Third, we produced an ensemble model for each species using a variant of the frequency histogram method (Figure one in Araújo and New 2007) by summing up the three best performing models for each species based on their respective AUC scores. 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 for each species coded 0, 1, 2, or 3). We then re-coded codes 0 and 1 into absence and codes 2 and 3 into presence. Fourth, we deleted overpredictions for 11 of the 116 species by comparing the modeled distributions with published distribution maps (Severinghaus et al. 2010). Overprediction occurs when a distribution model extends a species' range into areas where the species has never been observed (Walther et al. 2007; 2010). Any region of Taiwan where the species had never been observed was converted into absence using a variety of appropriate shape files (elevation, ecoregions, counties).

The final presence-absence map for each species is shown in Wu et al. (2013). Using these final maps, we subdivided species into four quartile categories whereby first, second, third, and fourth quartile species corresponded to the modeled distribution of respective species covering 0%-25%, 25%-50%, 50%-75%, and 75%-100% of all pixels in our study area.

Mapping hotspots

We generated hotspot maps using the following 'hotspot criteria': total species richness (all species included), endemic species richness (only species with full endemic species status included), threatened species richness (only endangered, rare and valuable, and other conservation-dependent species included), and rare species richness (only first quartile species included). The four hotspot criteria were equally weighted in all of our overlapping analyses. We did not map hotspots for the seven Taiwanese breeding species which are globally threatened according to the IUCN criteria (Fairy Pitta *Pitta nympha* and Taiwan Bulbul *Pycnonotus taivanus* listed as 'Vulnerable' and five species as 'Near Threatened,' see IUCN 2011) because they are all included in the species listed as threatened within Taiwan. Therefore, they were just a small subset of all threatened bird species within Taiwan. Given that this is a country-specific analysis, we decided to include all threatened birds as defined for Taiwan.

Results and discussion

Results

Hotspot analyses

We generated one presence-absence 'final map' for each species which we then combined to generate one species richness map and two types of hotspot maps for each of the four hotspot criteria as follows:

1. A species richness map for each hotspot criterion was created by simply adding up the final maps of all species which were included in the hotspot criterion.
2. The first type of hotspot analysis was generated by turning the species richness maps into hotspot maps by categorizing grid cells into either hotspot (most species rich) or not, whereby we selected the top 5%, 10%, 15%, 20%, and 25% most species-rich grid cells. However, each grid cell has a fixed species richness which is an integer value. Therefore, there were usually a lot of grid cells with the same values, making it impossible to select the exact percentage (e.g., 5%) of grid cells. Instead, we selected a threshold for species richness which was just below the given percentage to ensure that all of the depicted grid cells conformed to our hotspot definition (for more details, see Table 1).
3. The second type of hotspot analysis was generated in essentially the same way, but this time, we excluded all grid cells which fell inside protected areas of Taiwan. Thus, we were able to determine those grid cells which would add the most valuable grid cells to the already established protected areas. In this case, we decided to deal with the same values by choosing a threshold for species richness which was just above a certain percentage (e.g., 5%) to ensure that no grid cells which were valuable for future protection were missed (for more details, see Table 1).

Total species richness

We first mapped the total species richness for all of mainland Taiwan (Figure 2a). Overall, areas with high species richness corresponded to higher elevation areas, while low-elevation areas had lower species richness.

Table 1 Number of grid cells which fulfilled various hotspot criteria

	Hotspot criteria					Hotspot criteria outside of protected areas				
	Top 5%	Top 10%	Top 15%	Top 20%	Top 25%	Top 5%	Top 10%	Top 15%	Top 20%	Top 25%
Total species richness										
Species richness threshold of selected grid cells	≥74	≥71	≥69	≥67	≥65	≥70	≥66	≥63	≥59	≥56
Selected number of grid cells	1,472	3,245	4,856	6,583	8,373	2,201	4,006	5,560	7,697	9,190
Percent of total study area	4.1%	9.0%	13.5%	18.3%	23.2%	6.1%	11.1%	15.4%	21.4%	25.5%
Endemic species richness										
Species richness threshold of selected grid cells	≥14	≥14	≥13	≥13	≥12	≥12	≥11	≥9	≥8	≥7
Selected number of grid cells	1,519	1,519	5,266	5,266	7,656	2,647	3,647	6,824	8,810	10,344
Percent of total study area	4.2%	4.2%	14.6%	14.6%	21.3%	7.4%	10.1%	18.9%	24.5%	28.7%
Threatened species richness										
Species richness threshold of selected grid cells	≥23	≥22	≥21	≥20	≥19	≥21	≥18	≥16	≥14	≥12
Selected number of grid cells	1,577	3,514	5,161	6,655	8,049	2,036	4,231	6,091	7,826	9,472
Percent of total study area	4.4%	9.8%	14.3%	18.5%	22.3%	5.7%	11.8%	16.9%	21.7%	26.3%
Rare species richness										
Species richness threshold of selected grid cells	≥15	≥13	≥12	≥10	≥9	≥9	≥8	≥7	≥6	≥5
Selected number of grid cells	229	3,398	4,826	6,459	7,905	2,855	4,566	6,060	7,766	9,684
Percent of total study area	0.6%	9.4%	13.4%	17.9%	21.9%	7.9%	12.7%	16.8%	21.6%	26.9%

For four different kinds of species richness, we counted the number of grid cells which fulfilled the criterion of being greater than or equal to a specific species richness threshold. We chose the various thresholds for species richness by selecting that species richness where the actual selected number of grid cells that respectively remained just below 5%, 10%, 15%, 20%, and 25% of the grid cells of the study area. For example, choosing all grid cells with a total species richness of ≥73 and ≥74 species would have respectively selected 5.42% and 4.09% of the grid cells in the entire study area. Therefore, we chose ≥74 as the species richness threshold. Note that the thresholds remained the same for different percentages when we dealt with very low number of species, e.g., endemic species richness for the entire study area.

The most species-rich grids were concentrated in the northeastern (northern Syue Mountain (Mt.), e.g., Manyueyuan, Fushan; northern Central Mountain Range (CMR), e.g., Nan-ao, Cilan, and Taipingshan) and south central mountains (Alishan Range, Jade Mt., southern CMR, e.g., Shuangguei Lake area and North Dawu Mt. areas) (Figure 2b). Focusing on the most species-rich grid cells outside of protected areas revealed that most of the unprotected areas were again found in the northeastern (northern Syue Mt. and the northern CMR, e.g., Nan-ao) and south central mountains (Alishan Range, southern part of Jade Mt., southern CMR) (Figure 2c).

Endemic species richness

Again, the highest concentration of endemic species was found in mountainous areas (Figure 3a). The most species-rich grids were concentrated mostly in the south central mountains (Alishan Range, Jade Mt., southern CMR, e.g., Shuangguei Lake and North Dawu Mt. areas), with scattered grids also found in the north (Guanwu, Syue Mt., Dasyue Mt., Nan-ao, Hehuan Mt., and the Danda Mt. areas) (Figure 3b). Focusing on the most species-rich grid cells outside of protected areas revealed a somewhat similar distribution to that for total species richness but with additional grid cells selected in the northwestern (northwestern Syue Mt., e.g., Guanwu) and central mountain areas (east side of the CMR) (Figure 3c).

Threatened species richness

For species threatened within Taiwan, we lumped the three threat categories (endangered, rare and valuable, and other conservation-dependent species) together because their respective richness maps were very similar (Figure 4a). The most species-rich grids were mostly concentrated in the south central mountains (Alishan Range, Jade Mt., and southern CMR), with scattered grids also found in the north (Guanwu, Syue Mt., Dasyue Mt., Nan-ao, Hehuan Mt., and Danda Mt. areas) (Figure 4b). The most species-rich grid cells outside of protected areas were almost all found in mountainous areas that are unprotected (Figure 4c).

Rare species richness

Mapping rare species displayed a more complex picture (Figure 5a); besides mountainous areas, low-lying areas in

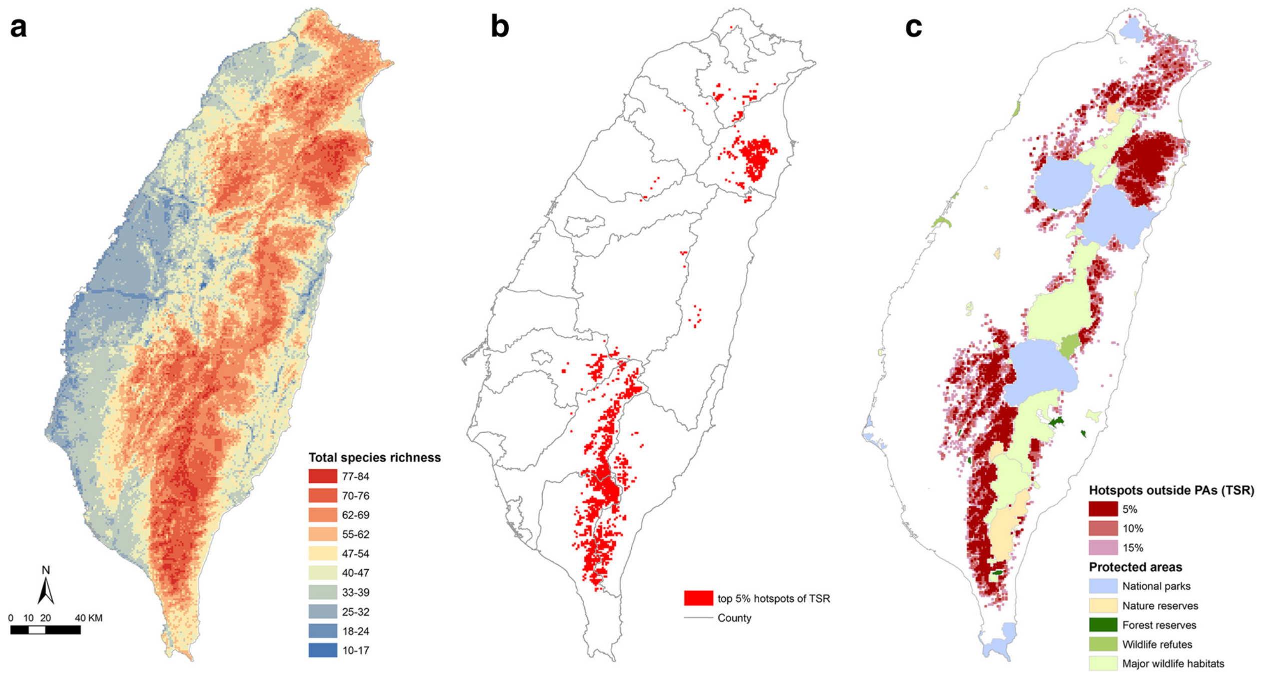

Figure 2 Total species richness and hotspots. (a) Total species richness: adding up the 116 final maps of the breeding birds of the island of Taiwan. **(b)** The top 5% hotspots show grid cells which were the 5% most species-rich using the thresholds for total species richness given in Table 1. Borders of Taiwanese counties are shown. **(c)** Hotspots outside protected areas show grid cells which were the 5%, 10%, and 15% most species-rich using the thresholds for total species richness given in Table 1.

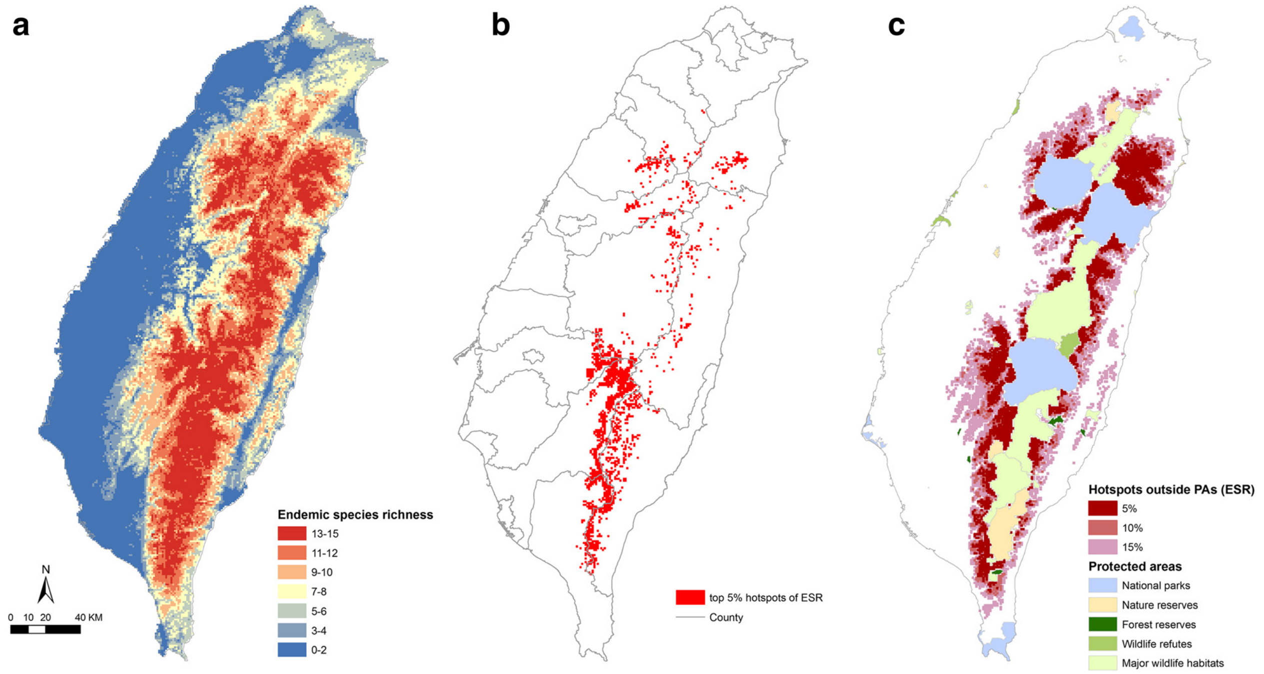

Figure 3 Endemic species richness and hotspots. (a) The endemic species richness was determined by adding up the 16 final maps out of the 17 endemic birds of the island of Taiwan. **(b)** Top 5% hotspots and **(c)** hotspots outside of protected areas (specifics as described in Figure 2).

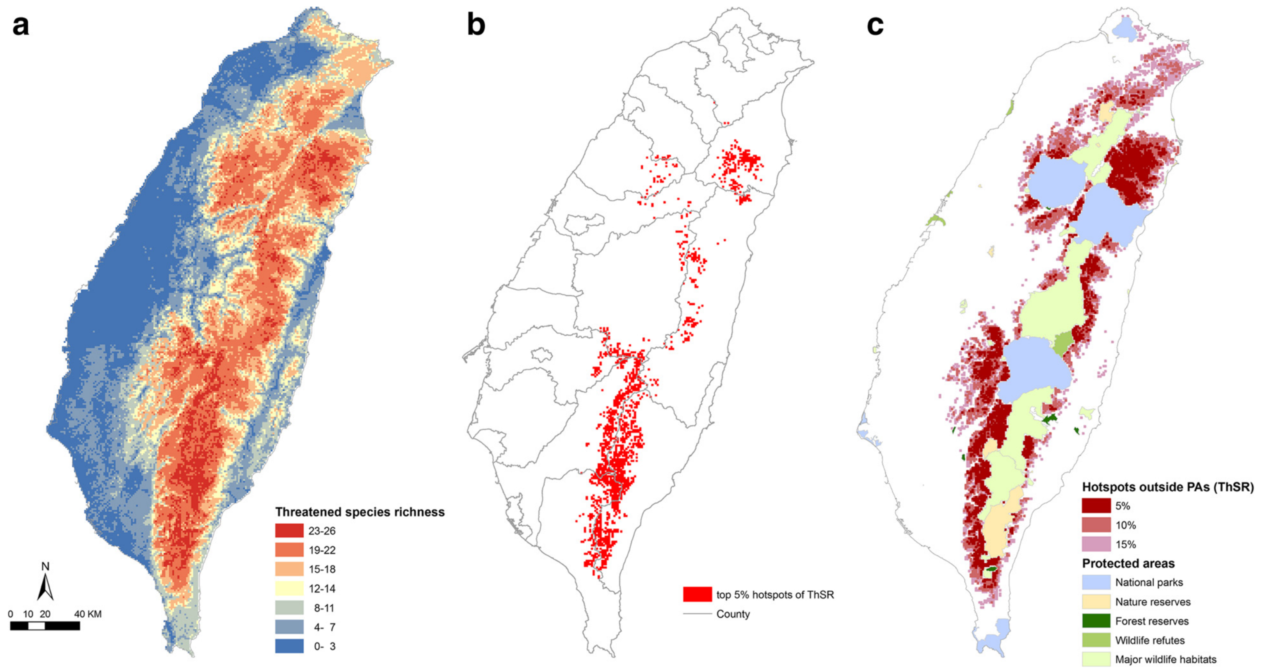

Figure 4 Threatened species richness and hotspots. (a) The threatened species richness was determined by adding up the 31 final maps of the 49 threatened birds of the island of Taiwan (see details in Wu et al. 2013). **(b)** Top 5% hotspots and **(c)** hotspots outside of protected areas (specifics as described in Figure 2).

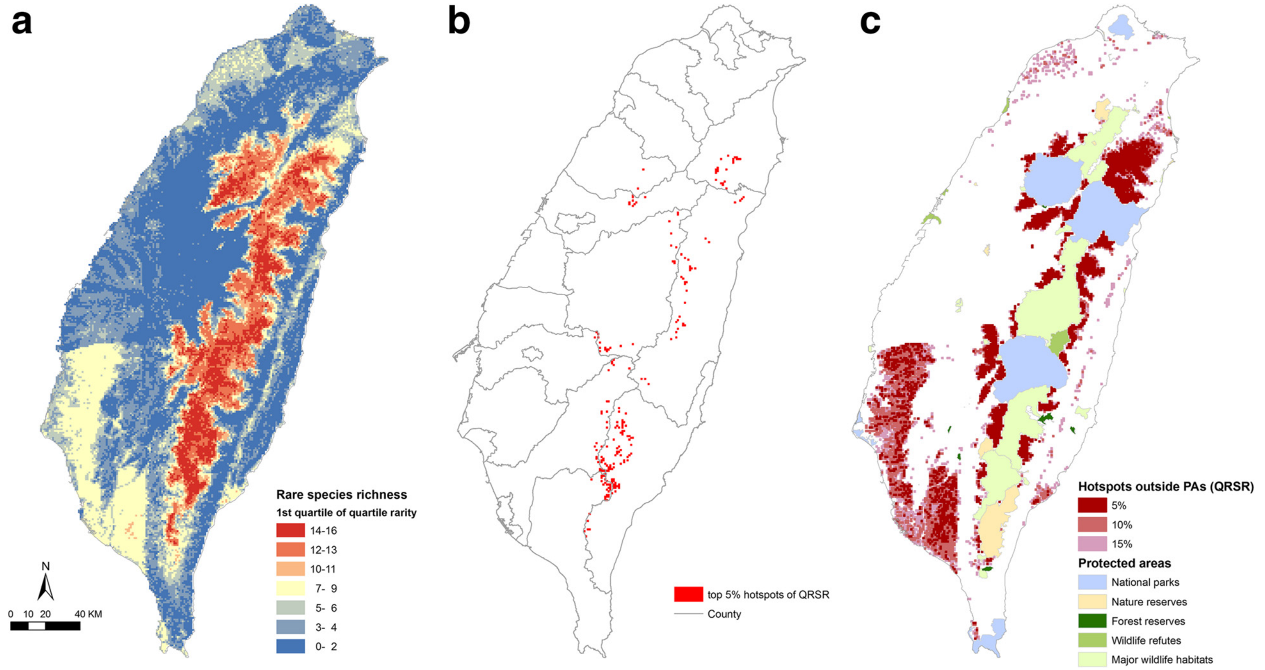

Figure 5 Rare species richness and hotspots. (a) The rare species richness was determined by adding up the 29 final maps of the first quartile birds of the island of Taiwan (see details in Wu et al. 2013). **(b)** Top 5% hotspots and **(c)** hotspots outside of protected areas (specifics as described in Figure 2).

the northeast (Keelung), northwest (Taoyuan), southwest (Chianan Plain and Gaoping River Basin) and the southern tip (Taitung City), and the longitudinal valley near the southeastern coast were also important. The most species-rich grids were scattered in various mountainous regions (Dasyue Mt., Nan-ao, Hehuan Mt., Danda Mt. area, Alishan Range, Jade Mt., Shuangguei Lake area, and North Dawu Mt.; Figure 5b). Focusing on the most species-rich grid cells highlighted a region in the southwest (Chianan Plain, Kaohsiung Plain, and Laonong River Basin) which was selected in addition to the usual mountainous regions (Figure 5c).

Combining and comparing hotspot analyses

We finally combined the results for our four hotspot criteria to assess which grid cells were the most valuable according to all four criteria.

For the first analysis, we included only those grid cells which were the 5% most species-rich (as depicted in middle panels of Figures 2, 3, 4, and 5). Simply adding up these four hotspot maps yielded Figure 6 which contains two distinct clusters of valuable grid cells in the northeastern (Nan-ao) and south central mountains (southern CMR). For the second analysis, we also

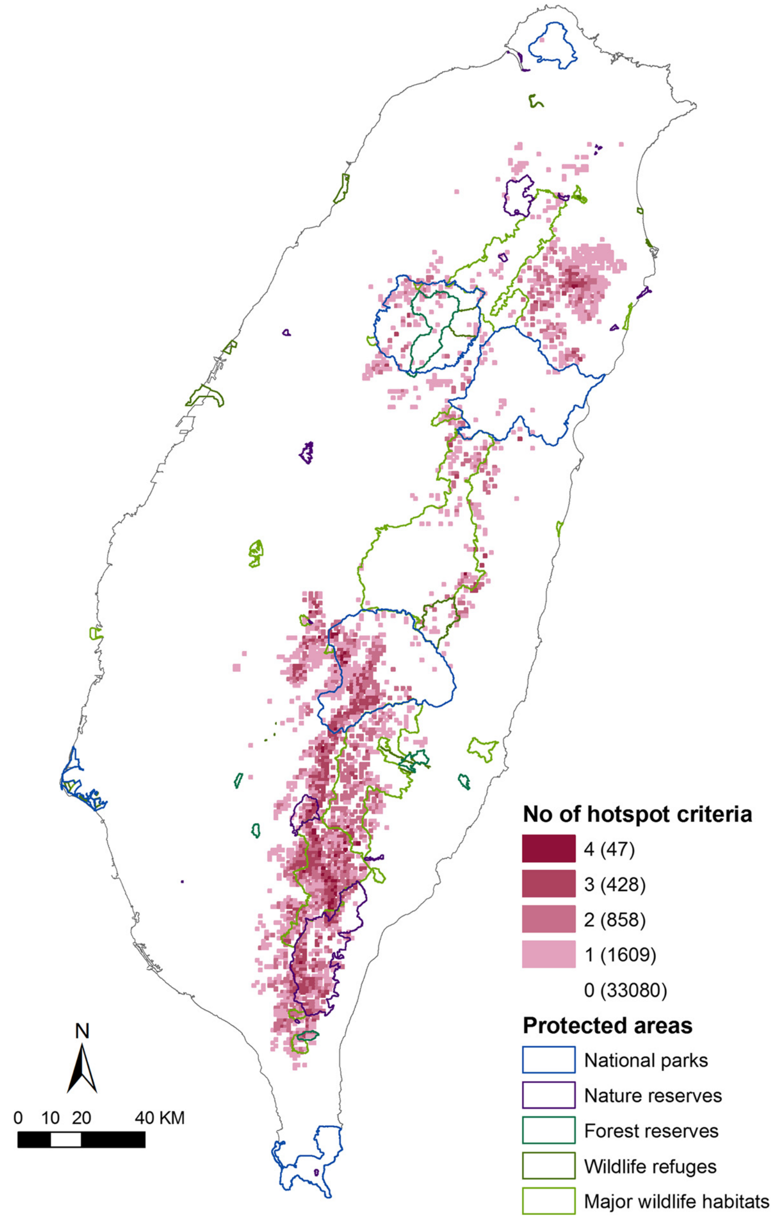

Figure 6 Map of combined four hotspot criteria (middle panels of Figures 2, 3, 4, and 5) in Taiwan. Colors range from dark red (all four hotspot criteria fulfilled) to pink (only one of four hotspot criteria fulfilled). The number of grid cells which qualify for each category of combination hotspots is given in parentheses (see also Tables 1 and 2). The outlines of Taiwan's protected areas are also shown (see Figure 1).

selected the top 5% most species-rich grid cells but *a priori* excluded those cells within protected areas (as depicted in the right panels of Figures 2, 3, 4, and 5), which yielded Figure 7; it contained the same two clusters as in the previous analysis but also included two smaller clusters in the northwestern (Syue Mt.) and central mountains (central region of the CMR, e.g., Hehuan Mt. and Danda Mt.).

We then calculated the percentage coverage of these combined hotspot criteria by the protected area network of Taiwan (Table 2). National parks covered <20% of each of the four hotspot criteria (column 3, Table 2). However, these percentages improved quite considerably to 27.0%-39.3% and 48.5%-87.2% for medium-to-high and low-to-high protection areas (columns 7 and 9 in Table 2), respectively. Therefore, a considerable percentage of the best avian hotspots were covered by protected areas, as illustrated in Figure 6.

While the above analyses showed that those grid cells where different hotspot criteria overlap were reasonably

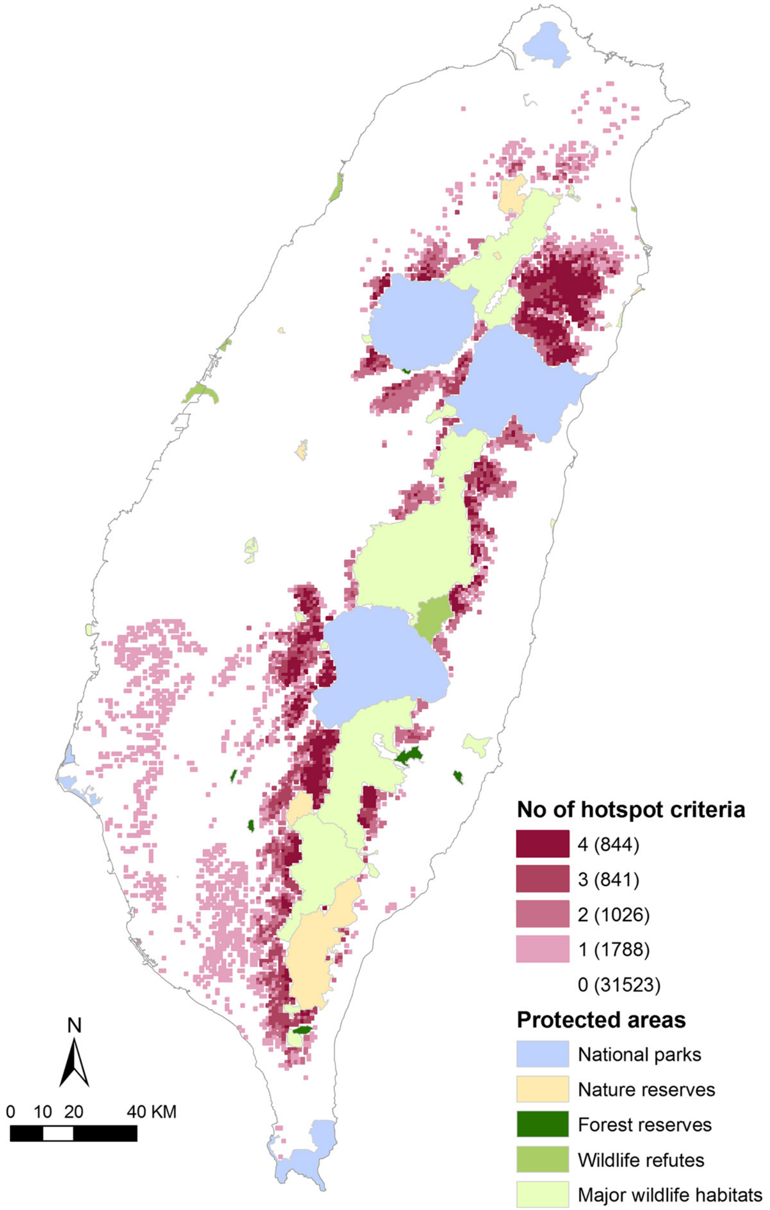

Figure 7 Map of combined four hotspot criteria (right panels of Figures 2, 3, 4, and 5) in Taiwan. These hotspot criteria are the top 5% hotspots shown in the right panels of Figures 2, 3, 4, and 5 across the island of Taiwan but outside of protected areas. Colors range from dark red (all four hotspot criteria fulfilled) to pink (only one of four hotspot criteria fulfilled). The number of grid cells which qualify for each category of combination hotspots is given in parentheses (see also Table 1). The outlines of Taiwan's protected areas are also shown (see Figure 1).

Table 2 Number of grid cells within the study area that fulfilled the four hotspot criteria

Hotspot criteria fulfilled	Grid cells within the study area	Highest protection, i.e., national parks	Nature reserves	Forest reserves	Wildlife refuges	Medium-to-high protection	Major wildlife habitats	Low-to-high protection
4	47	8 (17.0%)	6 (12.8%)	0 (0.0%)	0 (0.0%)	14 (29.8%)	28 (59.6%)	41 (87.2%)
3	428	82 (19.2%)	84 (19.6%)	2 (0.5%)	0 (0.0%)	168 (39.3%)	143 (33.4%)	306 (71.5%)
2	858	109 (12.7%)	110 (12.8%)	12 (1.4%)	5 (0.6%)	232 (27.0%)	437 (38.1%)	529 (61.7%)
1	1,609	290 (18.0%)	129 (8.0%)	22 (1.4%)	20 (1.2%)	438 (27.2%)	416 (25.9%)	781 (48.5%)
0	33,080	3,066 (9.3%)	561 (1.7%)	350 (1.1%)	389 (1.2%)	3,965 (12.0%)	3,191 (9.7%)	6,583 (19.9%)
Total	36,022	3,555	890	386	414	4,817	4,817	8,240

Columns 3 to 9 show how many of the grid cells of column 2 fell within the various protected area categories, followed by the percentages in brackets (e.g., for hotspot criterion 4, eight of a total of 47 grid cells (17.0%) were inside national parks). Note that the highest protection level (i.e., national parks) plus nature reserves, forest reserves, and wildlife refuges was defined as medium-to-high protection and that the addition of major wildlife habitats was then defined as low-to-high protection (see the 'Methods' section for details).

well protected, it is also important to establish how much these four different hotspot criteria overlapped (Table 3). For example, only 512 grid cells of the total of 36,022 grid cells for the entire study area (1.4%) were hotspots for both total and endemic species richness (upper right triangle in Table 3). These 512 grid cells accounted for 34.8% of the hotspot grid cells of total species richness (1,472, see Table 1) and for 33.7% of the hotspot grid cells of endemic species richness (1,519, see Table 1). The overlap between total, endemic, and threatened species richness was also around 50%, but the overlap with rare species richness ranged widely, from 3.9% to 82.5%. Repeating this analysis for the 5% most species-rich grid cells outside of protected areas (lower left triangle in Table 3), we found much higher overlap percentages, ranging from 33.2% to 83.1%.

To further analyze the extent of congruence between the four hotspot criteria, we calculated overlaps of all possible combinations of criteria (Table 4). Among the 2,942 grid cells which fulfilled at least one hotspot criterion, only 1.60% (47 grid cells) fulfilled all four criteria (Table 4, Figure 6). Percentage increases for increasingly fewer hotspot criteria fulfilled were 14.55%, 29.16%, and 54.69%, respectively (Table 4).

Discussion

Species distribution models have become an important tool in conservation biology because they usually allow a much better approximation of the true species distribution than the old-fashioned dot or range maps. This is especially important for hotspot analyses where false absences due to undersampling substantially bias the results. Given that some of Taiwan's most valuable habitats are almost inaccessible to humans and therefore most certainly undersampled (Wu et al. 2013), the use of distribution models should considerably improve conservation recommendations for Taiwan. For example, almost all our analyses point to an important avian hotspot in Taiwan's northeastern Nan-ao mountainous areas even though sampling efforts in that region have been relatively moderate (Wu et al. 2013).

Our analyses are a major advance for Taiwan's conservation efforts because not only were we able to produce the first almost-complete avian hotspot maps for Taiwan, but we were also able to test how well Taiwan's protected areas cover these hotspots. Almost all of our species richness and hotspot analyses revealed that mountainous regions of Taiwan hold most of Taiwan's avian biodiversity. Previous studies showed a hump-shaped relationship between avian species richness and Taiwan's elevation gradient, meaning that the highest species richness was found in mid-elevation forests (Koh and Lee 2003; Shiu and Lee 2003; Hsu et al. 2004; Lee et al. 2004; Ding et al. 2005; Koh et al. 2006b), which is unlike the species richness pattern found on Hainan Island, China in the northwestern South China Sea

Table 3 Percentage overlap between different hotspot criteria using the 5% most species-rich grid cells

	Total species richness	Endemic species richness	Threatened species richness	Rare species richness
Total species richness	-	512 (1.4%, 34.8%, 33.7%)	742 (2.1%, 50.4%, 47.1%)	58 (0.2%, 3.9%, 25.3%)
Endemic species richness	1,356 (3.8%, 51.2%, 61.6%)	-	832 (2.3%, 54.8%, 52.8%)	91 (0.3%, 6.0%, 39.8%)
Threatened species richness	1,474 (4.1%, 72.4%, 67.0%)	1,691 (4.7%, 83.1%, 63.9%)	-	189 (0.5%, 12.0%, 82.5%)
Rare species richness	948 (4.6%, 33.2%, 43.1%)	1,881 (5.2%, 65.9%, 71.1%)	1,263 (3.5%, 44.2%, 62.0%)	-

In each cell, the number of grid cells which overlapped for both hotspot criteria given in the row and column is given. In the following parentheses, we calculated the percentage for this number divided by (1) the total number of grid cells of the study area (36,022 grid cells), (2) the number of grid cells falling into the hotspot criterion in the row, and (3) the number of grid cells falling into the hotspot criterion in the column. To the upper right of the diagonal, this calculation was done for grid cells which were determined to be the 5% most species-rich grid cells within the entire study area (Table 1, Figure 6), and to the lower left of the diagonal, the calculation was done for grid cells which were determined to be the 5% most species-rich grid cells outside of protected areas (Table 1, Figure 7).

Table 4 Extent of congruence between the 4 different hotspot criteria as depicted in Figure 6

Hotspot criteria fulfilled	Hotspot criteria combination	Number of grid cells	Percentage	Total
4	T-E-Th-R	47	1.60	47 (1.60%)
3	T-E-Th	378	12.85	428 (14.55%)
	T-E-R	1	0.03	
	T-Th-R	10	0.34	
	E-Th-R	39	1.33	
2	T-E	86	2.92	858 (29.16%)
	T-Th	307	10.44	
	T-R	0	0.00	
	E-Th	368	12.51	
	E-R	4	0.14	
	Th-R	93	3.16	
1	T	643	21.86	1,609 (54.69%)
	E	596	20.26	
	Th	335	11.39	
	R	35	1.19	
Total		2,942	100.00	

The second column shows specific combinations of hotspot criteria: total species richness (T), endemic species richness (E), threatened species richness (Th), and rare species richness (R). For example, the criterion 'T-E' means that the grid cells fulfilled the total and endemic hotspot criterion but not the threatened or rare hotspot criteria. The third column gives the number of grid cells fulfilling the criteria combination given in the second column. The fourth column is the percentage in relation to all hotspot grid cells (a total of 2,942 grid cells which fulfilled at least one hotspot criterion). The fifth column gives the number of grid cells (and percentage) fulfilling the hotspot criteria (or criterion) given in the first column.

(Zou et al. 2012). Therefore, it is not surprising that our analyses confirmed that species richness and hotspots were mostly found in mountainous areas.

However, it is quite conceivable that the almost-complete transformation of Taiwan's lowland areas led to many species becoming extinct there, meaning that the hump-shaped relationship is a human-induced artifact. Previous studies demonstrated a negative relationship between the human population density and avian species richness in Taiwan (Lee et al. 2004; Koh et al. 2006a). Avian hotspots may thus have existed in the lowlands before humans transformed those areas and could possibly be reestablished if substantial lowland areas were restored to more natural conditions.

One of our hotspot analyses, namely rare species richness, pinpointed unprotected areas in the southwestern lowlands (Figures 5 and 7) which had not been emphasized by previous studies (Nieh 1999; Ko et al. 2009b) and could form the basis for such an attempt to restore lost biodiversity. However, this is unlikely to happen in the near future because of the high human population density there. Consequently, short-term conservation efforts should focus on protecting those species-rich hotspots pinpointed in Figure 7 which are still unprotected and occur in areas with relatively intact natural habitats. The reason for areas in the southwestern lowlands being selected by this analysis but not by the others is that several rare species occur in the southwestern lowlands of Taiwan (as also discussed below).

The only substantial and still relatively intact region which our analyses consistently highlighted as an important avian hotspot was a large area of unprotected and relatively intact forested habitat in Taiwan's northeast (Figures 6 and 7) which should become a high priority for future fieldwork and conservation efforts. Other unprotected areas with high conservation value are basically spatial extensions of areas already protected in the central and southern mountains, whereby different hotspot criteria pointed to somewhat different areas. Such differential prioritization should be expected because different hotspot criteria only partially overlap and sometimes hardly at all (Tables 3 and 4, Figures 6 and 7). For example, the overlap (also called 'congruence') between hotspots of total species richness and endemic species richness was only 34.8% (for total species richness) to 33.7% (for endemic species richness) (Table 3), which goes against the hypothesis that endemic hotspot richness might be a good indicator of total hotspot richness in Taiwan (Nieh 1999; Ko et al. 2009b). Therefore, to protect areas in Taiwan based on only one hotspot criterion would not necessarily result in the protection of areas deemed important using other hotspot criteria.

Since we did not test macroecological hypotheses in this paper, future studies should investigate macroecological correlates to the different species richness patterns which are documented in this study. However, such correlative studies will always suffer from the absence of historical data to test real cause-and-effect relationships: an example is the mid-elevation species hump due to a mid-domain effect (Colwell and Lees 2000) or the almost-complete anthropogenic alteration of Taiwan's lowland ecosystems (Shiu and Lee 2003; Lee et al. 2004; Koh et al. 2006a). For the purposes of conservation, however, it is sufficient to highlight important areas which should be the target of more intensive field work and conservation management.

Our study included a few more endemic species than previous studies. Specifically, we included the Taiwan Barbet *Megalaima nuchalis* and Taiwan Hwamei *Garrulax taewanus* which were not included by Nieh (1999) and Ko et al. (2009b); we further included the Taiwan Bush-Warbler *Bradypterus alishanensis* which was not included by Nieh (1999), and we also included Styan's Bulbul *Pycnonotus taivanus* which was not included by Ko et al. (2009b). Nevertheless, our results mostly confirmed those of previous studies. Our mean and standard deviation for the elevation of endemic species hotspots was 2,016 ±

463.0 m, while Nieh (1999) reported 1,941 ± 602.5 m, and Ko et al. (2009b) reported 1,917 ± 437.8 m. Furthermore, a visual comparison of our Figure 3B with figure thirty of Nieh (1999) and figure five in Ko et al. (2009b) shows a very good agreement, with the exception that our analysis highlighted more hotspots in southern Taiwan, and Nieh (1999) failed to pick out the northeastern Nan-ao mountainous areas. This could have been due to differences in the lists of endemic species, especially lowland species, as described above. Our analysis is therefore important in that it confirms some previous results and also highlights additional previously undetected areas of high species richness. Furthermore, our results are much more relevant as they are based on a much more complete set of species.

Our results are also relevant to hotspot studies globally. Most importantly, different hotspot criteria overlapped only partially and sometimes hardly at all in our analysis (see above), thereby confirming previous results of limited overlap or congruence (e.g., Prendergast et al. 1993; Moritz et al. 2001; Lund and Rahbek 2002; Moore et al. 2003; Ho 2005; Orme et al. 2005; Grenyer et al. 2006; Franco et al. 2009; van Weerd and de Haes 2010; but see Kerr 1997; Mac Nally et al. 2002). This lack of congruence was especially evident at smaller spatial scales (Lund and Rahbek 2002; Grenyer et al. 2006; Franco et al. 2009; van Weerd and de Haes 2010). Since our results were based on a very fine scale of a 1 × 1-km grid size, they are supportive of this trend. Therefore, no subset of species could be taken to be a generally good indicator for all the species within a taxon, nor could a taxon be taken as good indicator for other taxa, especially at smaller spatial scales. Rather, as many taxa and as many criteria as possible need to be analyzed to make value judgments about how to prioritize our findings (Prendergast et al. 1993; Chen 2007; Moilanen et al. 2009; see also our suggestions for further studies in Taiwan below). Unlike most other hotspot studies, we eliminated hotspots from inside protected areas in our third analysis (Figures 2, 3, 4, 5C, and 7) which highlighted areas in need of future protection. Such an analysis should be considered for hotspot studies in many other regions. Finally, we cannot overemphasize the importance of using species distribution models instead of raw locational data to achieve reliable results for undersampled regions (e.g., Franco et al. 2009).

The relatively high number of endemic species is one of Taiwan's outstanding biodiversity features. The existing protected areas network, as it is mostly found in mountainous areas should, according to our analyses, protect most endemic species rather well as they are also concentrated in the mountains (Figure 3) with a few notable exceptions (the Taiwan Barbet, Formosan Blue Magpie *Urocissa caerulea*, Taiwan Hwamei, and Styan's Bulbul). However, this could change if mountain species are forced to migrate upwards because of climate change (Ko 2010; Chien et al. 2012). Moreover, although percentages of hotspot criteria covered by 'low-to-high' protection were rather high (48.5% to 87.2%, Table 2), a large portion of those percentages come from major wildlife habitats, which are in the lowest protection category. For the highest protection category, namely national parks, percentages were much lower (12.7% to 19.2%, Table 2). Therefore, we strongly support upgrading the protection status of some of the less well-protected areas and establishing some completely new protected areas, especially in the northeastern mountains (Figures 6 and 7).

Hotspots are just one, albeit important, criterion for establishing conservation priorities. Future studies need to complement this study in a number of ways: (1) Other criteria, foremost among them would be complementarity analyses, need to be included in conservation recommendations (Lehtomäki et al. 2009; Moilanen et al. 2009; Visconti et al. 2010); such analyses would most likely highlight more of Taiwan's lowland areas as priority sites, e.g., sites occupied by threatened species such as the Fairy Pitta (Ko et al. 2009a). An obvious drawback of hotspot analyses is that they may leave out areas important to rare species, and Taiwan's lowland species are rare exactly because their habitats have already been almost completely destroyed. Therefore, complementarity analyses are required to pinpoint lowland areas of conservation importance. (2) Other taxa, such as mammals, insects, and plants, need to be incorporated in the analyses to make conclusions more relevant to all of Taiwan's biodiversity. As hotspots for different taxa frequently do not overlap (i.e., are not congruent, see Prendergast et al. 1993; Moritz et al. 2001; Lund and Rahbek 2002; Moore et al. 2003; Ho 2005; Orme et al. 2005; Grenyer et al. 2006; Franco et al. 2009; van Weerd and de Haes 2010), the more taxa that are included in the analyses, the more comprehensive the resulting recommendations will be. One obvious problem with including other taxa is that reliable distribution models need to be based on a minimum number of observation records (usually >20 to 30) which might not be available for many other taxa (e.g., cryptic mammals and undersampled beetles). Therefore, we must caution against the use of our methodology if sample sizes are too small or sample coverage too biased. In such cases, locational records themselves should be used, while the results of distribution models should only be used with great care (Wisz et al. 2008; Costa et al. 2010). Nevertheless, once a sufficient sample size and reliable sample coverage have been achieved (see summary in Wu et al. 2012), the use of distribution models should overall result in much better conservation recommendations because distribution models fill in gaps of sampling coverage; in other words, much limited time and resources can be saved by not having to determine a species' presence or absence within every possible grid cell. (3) Potential future land use and climate change effects should be investigated to safeguard elevational corridors, multiple populations, and viable ecological niches (Polasky 2008; Klein et al. 2009; Carroll et al. 2010; Kharouba and Kerr 2010; Chien et al. 2012). In Taiwan, most high-elevation species are probably endangered by climate change, but low-elevation species may also be endangered if they cannot utilize corridors to migrate upwards. Furthermore, some lowland species (e.g., Blue-breasted quail *Coturnix chinensis*, Pheasant-tailed Jacana *Hydrophasianus chirurgus*, and Australasian Grass Owl *Tyto longimembris*) are already close to extinction because of continuous land use conversion and will likely become extinct if their few remaining habitats are not urgently protected.

Distribution modeling and geographic information systems allow researchers to pinpoint areas of high species richness, but they also allow calculation of the coverage provided by the already existing protected area network. Currently, Taiwan's protected areas cover almost 30% of the distributional ranges of the 116 bird species that we modeled, which drops to 16.9% for medium-to-high and to 12.5% for the highest protection but with much variation between species (Wu et al. 2013). While this is not bad compared to many other regions of the world, it is still questionable whether most species can survive in case they are confronted with future land use and climate changes. To protect Taiwan's unique avifauna, further analyses as outlined above are needed, and conservation recommendations need to be turned into actual conservation measures.

Conclusions

We present a hotspot analysis of Taiwanese breeding birds with sufficient sampling coverage for distribution modeling. Almost all of the species richness and hotspot analyses revealed that the mountainous regions of Taiwan hold most of Taiwan's avian biodiversity. The only substantial unprotected region which was consistently highlighted as an important avian hotspot is a large area of unprotected mountains in Taiwan's northeast (mountain regions around Nan-ao) which should become a high priority for future fieldwork and conservation efforts. In contrast, other unprotected areas of high conservation value were just spatial extensions of areas already protected in the central and southern mountains. We also found that different hotspot criteria only partially overlapped and sometimes barely at all. Therefore, to protect areas based only on one hotspot criterion (e.g., total species richness) would not protect areas based on other hotspot criteria (e.g., endemic species richness, threatened species richness, or rare species richness) in Taiwan.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

PFL initiated the idea, built the bird and environment database, and participated in the writing of this paper. TYW built the avian distribution database, carried out the analysis, and drafted the manuscript. BAW carried out the analysis and completed the final draft. YHC built distribution models, and RSL provided avian data and also drafted the manuscript. All authors read and approved the final manuscript.

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