Movement distances enhance validity of predictive models

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ABSTRACT

Including the distance species are able to move in predictive models improves conservation practice. Bird inventory projects carried out from 1993 to 2004 in Taiwan provide an opportunity to investigate the relationships among species distribution, movement distance, and the environment. We compared projected distributions of 17 Taiwanese endemic bird species using what we called the Standard Method (*i.e.* movement distance is zero) and what we called the Buffer Method (*i.e.* movement distance is longer than zero) in three presence-only models (GARP, MAXENT and LIVES). The Standard Method used species original occurrence records directly while the Buffer Method expanded the occurrence of species to areas 1 km^2 around each recorded location. We first tested the efficacy of the Buffer Method using ten common species of the 17, and then applied the method to two rare species of the 17. For both the common and rare species, the distributions predicted by the two methods showed slight but important differences. The Buffer Method for all species had a higher average predictive probability, while the Standard Method had a higher maximum predictive probability. Most of the values for the area under the curve (AUC) were over 0.8 with the exceptions of Taiwan Barbet (*Megalaima nuchalis*) and Taiwan Hwamei (*Garrulax taewanus*), which have recently separated from Indochinese Barbet (*Megalaima annamensis*) and Chinese Hwamei (*Garrulax canorus*), and since 2008 and 2006 have been regarded as species endemic to the study area. Kappa values showed good performance for all species using both methods. The Buffer Method, however, resulted in significantly higher sensitivity and accuracy values for all models of species ($p < 0.05$). We conclude that when modeling species distribution including the area where the species was censused along with areas within the minimum movement areas better defines the surrounding areas that might supplement core habitat requirements. Therefore, using the Buffer Method, species surrounding distribution can be obtained which provides a better understanding of the species distributions. Given that distribution size is a key to the conservation of species, we suggest the Buffer Method can be used in conservation planning.

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1. Introduction

Numerous species of animals and plants around the globe are detecting the 0.75 °C of warming over the last century (Root et al., 2005). One way they are responding is by shifting their ranges towards the poles and to higher elevations (Root and Schneider, 2002, 2006; Root et al., 2003; Parmesan and Yohe, 2003). The Intergovernmental Panel on Climate Change (Parry et al., 2007) predicted that the average global temperature will continue to increase by 1.1–6.4 °C above 1990 levels during the 21st century. Such increases will affect the conservation and management of different species in different ways. Projections of future distributions of

species by assuming a retaining relationship between each species distribution and environment further indicated that species either with or without dispersal/movement would face a quite extinction risk under climate change (Thomas et al., 2004). However, effect of species movement on modeling is unknown yet. Estimating how species movement affects a predictive model, thus, could certainly aid in addressing the current and future species–environment relationships.

Many predictive models of species distributions have been developed and applied to various landscape scales (Guisan and Zimmermann, 2000; Cushman and McGarigal, 2002; Store and Jokimäki, 2003; Johnson et al., 2004; Guisan and Thuiller, 2005; Elith et al., 2006; Hernandez et al., 2006; De Mas et al., 2009). Additionally, the majority of modeling exercises, species data are transferred to a grid system (Vallecillo et al., 2009; Ko et al., 2009). Modeling methods traditionally have used linear algorithms and emphasized both species presence and absence data (Austin and Meyers, 1996; Jose and Fernando, 1997). Nonlinear

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algorithms and species presence-only models have been recently developed and used widely (Lek et al., 1996; Jose and Fernando, 1997; Aitkenhead et al., 2004; Stockman et al., 2006; Phillips et al., 2006). Results from these latter models have been found to better explain the relationship between species and environmental factors (Manel et al., 1999a,b; Ko et al., 2009). Species absence data are frequently unavailable or inadequate to interpret species distributional ranges/patterns because of uncertainties of those actual or undetectable absences, such as a period of species hibernation as well as inactivity (Gu and Swihart, 2004; Vaclavik and Meentemeyer, 2009). Incorrect absence data even leads to misleading model predictions of species potential distributions (Ko et al., 2009). We thus used the presence-only models in this study which often exhibit good accuracy on predicting species distributions (Elith et al., 2006; Tsoar et al., 2007; McPherson and Jetz, 2007).

Surrounding habitats, as a primary consideration for conservation as species occupancy areas (Saab, 1999), are usually been highly used by bird species as breeding and foraging habitats owing to their high vagility (Ambuel and Temple, 1983; Lees and Peres, 2009). The vagility of different forest birds and waterbirds varies from less than 1 km to more than 200 km (Shirley, 2006; Keller et al., 2009). Spatial-use patterns of species within both the species occupancy and surrounding areas differ greatly at multiple temporal and spatial scales due to varying interactions between landscape structure and species responses to that structure. The structure and pattern of the landscape, natal dispersal, mate selection behaviors, seasonal migration, temperature change, movement potential mortality, and food availability within those areas potentially influence the species' spatial-use patterns, especially movement distances of a species (Desrochers and Hannon, 1997; Norris and Stutchbury, 2001; Cooper et al., 2002). Main factors influencing a species' spatial patterns, however, are often not well understood, but Shirley (2006) found that in general focusing on species moving from one place to another, to engage in particular activities in particular places, provides a rough understanding of how species response to adjacent habitat or forest remnants. The areas where species have been recorded and the areas within the movement distance of the species are the areas most occupied by species. Cooper et al. (2002) used two movement rules to simulate population dynamics in the Brown Treecreeper in Australia, which explained that species' nearest neighbors are important for population and direction of movement affects a species distribution. Therefore, quality of surrounding habitats needs to be addressed, and the species movement patterns, such as movement distance and direction, are valuable inputs when linking species spatial-use patterns and the surrounding habitats together.

Bird surveys in Taiwan have been carried out since 1993 provide an opportunity to estimate the possibility of species movement patterns as an input variable to predictive models of species distributions. The Taiwan Island, an area of about 36,000 km², lies in the western Pacific Ocean, less than 161 km from the southeast coast of mainland China, from which it is separated by the Taiwan Strait. Though several survey sites have only been surveyed once over the 17 years, data for at least one year have been recorded over the entire island of Taiwan. Volunteer bird observers trained by Taiwanese organizations have recorded species, heard and seen, along designated transect lines. These data provide information throughout the island on species distributions. Endemic bird species in Taiwan were chosen only as sampling data in this study according to their subjects of concern, especially rare endemic species. Their low population and naturally secretive behaviors, however, increase the difficulty of observation (Ko et al., 2010) as well as predicting their distributions. Fortunately, common species can play as reference when drawing insights into rare species' conservation when they are sympatric related species

(Githiru et al., 2007). Finding a method to be used on common species and then applied to rare species will be feasible to understand rare species distributions more. Simultaneously, combining the movement ability of rare endemic species with predictive model will have even greater control and understand their possible distribution.

Using these data from the bird surveys, we addressed two questions in this study: (1) can predictive models using additional species presence based on species vagility (i.e. species movement distances) with actual species occurrence records tell us more than using actual species occurrence records alone? and (2) can we enhance the value of predictive models by adding consideration of species' spatial-use patterns (i.e. movement patterns)? In general, this study combined predictive models and species minimum movement distances to determine if the predicted distributions were more accurate than those not using species movement information. To do this, we compared traditional methods, which had emphasized species recorded presence only, referred to as the "Standard Method" in our study, with the novel method such as the "Buffer Method", which broadened species recorded presence to neighboring regions, to see how predictive models could become more effective. Three presence-only models, GARP, MAXENT and LIVES, were finally used to predict species potential distributions on the Taiwan whole island.

2. Materials and methods

2.1. Species occurrence data collection

We used two bird inventory projects in Taiwan from 1999 to 2003 (Koh et al., 2006) and 1993 to 2004 (Hsu et al., 2004) in this study. The data included a total of 4082 census locations, which covers around 10% of Taiwan when placed on a 1 km² grid system. Each location was censused at least once a year during the breeding season or seasonally during the survey period. Bird-occurrence data were recorded by geographical coordinates and transformed to a square kilometer grid. There are 17 endemic bird species currently in Taiwan and ten of these are common. We used these ten common species and two rare species of the 17 to compare different modeling methods. In addition, the two rare species were used to determine the possible conservation effectiveness of each model (Table 1).

2.2. Modeling methods

Five types of environmental factors were used in the models: topography, climate, vegetation, human disturbance, and ecological regions. The first four types were estimated using ArcGIS and ERDAS and described in detail by Lee et al. (2004) and Ko et al. (2009). We interpolated annual mean temperature and annual total precipitation through 355 stations data including weather stations and auto rain gauges offered from Central Weather Bureau of Taiwan. The last type, ecological regions, included two factors: ecoregions and eastern index. The whole of Taiwan was divided into 41 ecoregions according to township districts, geographical zones and biological boundaries (Su, 1992). The eastern index weighted the three eastern counties more than the other 13 counties. The three counties, Yilan, Hualien, and Taitung, are located on the eastern side of the Central Mountain Range and were assigned an eastern index value of 1 and distinguished from the other counties that were assigned a value of 0. All of environmental variables were estimated by univariate analysis with actual species occurrence records first. We then left the variables which had high relationships ($p < 0.01$) with the species

Table 1
12 Taiwanese endemic bird species included in the study. Ten species are common which were used to compare the Standard and Buffer methods and two species are rare which were used as further applications.

Category	Family	English common name	Scientific name
Common species	Megalaimidae	Taiwan Barbet	*Megalaima nuchalis*
	Phasianidae	Taiwan Partridge	*Arborophila crudigularis*
	Pycnonotidae	Styan's Bulbul	*Pycnonotus taivanus*
	Timaliidae	Steere's Babbler	*Liocichla steerii*
		Taiwan Hwamei	*Garrulax taewanus*
		Taiwan Yuhina	*Yuhina brunneiceps*
		White-whiskered Laughingthrush	*Garrulax morrisonianus*
		White-eared Sibia	*Heterophasia auricularis*
	Turdidae	Collared Bush-Robin	*Luscinia johnstoniae*
		Formosan Whistling-Thrush	*Myiophonus insularis*
Rare species	Phasianidae	Mikado Pheasant	*Syrmaticus mikado*
		Swinhoe's Pheasant	*Lophura swinhoii*

occurrence records, compared spatial autocorrelation among these important variables, and finally remained the most important variables as inputs to predictive models. Elevation, temperature, and precipitation were not excluded after the spatial autocorrelation analysis according to their unique ecological meanings for organisms. The relationships between each species and the environmental variables were implemented by the above procedure independently.

The movement patterns of the Taiwanese endemic bird species are not clearly known yet. We defined the minimum movement distance (*i.e.* 1 km) mentioned by Shirley in 2006 as the sizes of the grid, and assigned species occurrence to the center of the grid square overlaying the species location. We also referred to Cooper et al. (2002) and Howard (1983) to assume that species would move mostly to the nearest neighboring areas with random/all directions in a search range. Only grids with actual species presence were used in the Standard Method, where those grids along with those grid squares adjacent to an actual presence grid that squares were regarded as species-present grid squares in the Buffer Method (Fig. 1).

We utilized three presence-only models, GARP, MAXENT, and LIVES, to predict species potential distributions. These three models are widely used in conservation studies and have been shown to perform well in comparison to other algorithms (Elith et al., 2006; Hernandez et al., 2006; Jin and Hilbert, 2008). A total of 67% of all occurrence records for each species were used to determine the models (*i.e.* as a training set) and 33% were used to evaluate (*i.e.* as a testing set). The detail of each model used in our study is as follows:

GARP (Genetic Algorithm for Rule-set Production, http://www.nhm.ku.edu/desktopgarp/) models the ecological niches of species and describes the environmental conditions under which species are able to maintain populations (Stockwell and Peters, 1999). GARP creates a unique genetic algorithm using a series of rules relating to species ecological characteristics in order to predict species occurrences. The optimized parameters were set for 100 runs, a 0.01 convergence limit and 1000 maximum iterations. Four types of rules, including atomic, range, negated range, and logistic regression, were used simultaneously. The final probability of a species-possible distribution by GARP prediction was averaged over the output of 100 runs.

MAXENT (Maximum Entropy Method) is a generative approach for making predictions through statistical concepts (Phillips et al., 2006). It analyzes individually the weights of environmental factors and calculates a continuous probability value for species distribution. For all of our species, we used the default setting in MAXENT, except for the maximum number of iterations (Phillips and Dudik, 2008). A maximum of 1000 iterations was used rather than the 100 used in GARP.

LIVES (Limiting Variable and Environmental Suitability) uses limiting-factor theory and predicts that a species distribution is limited within a certain range on environmental gradients (Odum, 1997). The theory of LIVES is different from GARP and MAXENT, because it focuses on habitat not suitable for a species instead of suitable habitat used in GARP and MAXENT. It finds the potential limiting factors for "non-habitats" where they are beyond the range in which a species is known to occur. We followed the methods of Li and Hilbert (2008) and calculated the suitability of each grid square as a possible location of a species distribution.

2.3. Model evaluation

We selected the area under the curve (AUC), Kappa, sensitivity, specificity, and accuracy as measurements to evaluate predictive ability of the three presence-only models under the Standard and Buffer methods. The AUC can be used to assess the models' overall performance because measures of the area under the receiver operating characteristic (ROC) plot show which have values between 0.5 (random) and 1.0 (perfect discrimination) (Manel et al., 2001; Fawcett, 2004). Kappa, sensitivity, specificity, and accuracy values derive from a confusion matrix that cross-tabulates the actual and predictive patterns (Fielding and Bell, 1997). Kappa measures the extent to which the agreement between actual and predicted areas is higher than that expected by chance alone. Sensitivity calculates the percentage of presences that are correctly predicted as presences while specificity calculates the percentage of absences that are correctly predicted as absences. Accuracy estimates the overall percentage of presences and absences that are correctly predicted. A model has a higher predictive performance with a Kappa value greater than 0.4 and a sensitivity/specificity/accuracy value close to 1. We first used the AUC to ensure a model's availability and then calculated the other four values. In addition, we set threshold values, so that a species would be considered present with a certain predictive probability, by comparing a species' original prevalence and its AUC. If the AUC value of a species was greater than the species' prevalence, we used the AUC value as the species; threshold, otherwise we used the prevalence. This threshold-determination method is rigorous and is expected to make more accurate predictions than other approaches (Ko et al., 2009). The predictive power of all the models in predicting presence and absence was differentiated after setting thresholds.

The differences in Kappa, sensitivity, specificity, and accuracy values between the Standard and Buffer methods for each presence-only model were analyzed using paired samples Student's *t*-test. All these assessments and statistics were implemented in SPSS 17 (Anon, 2001).
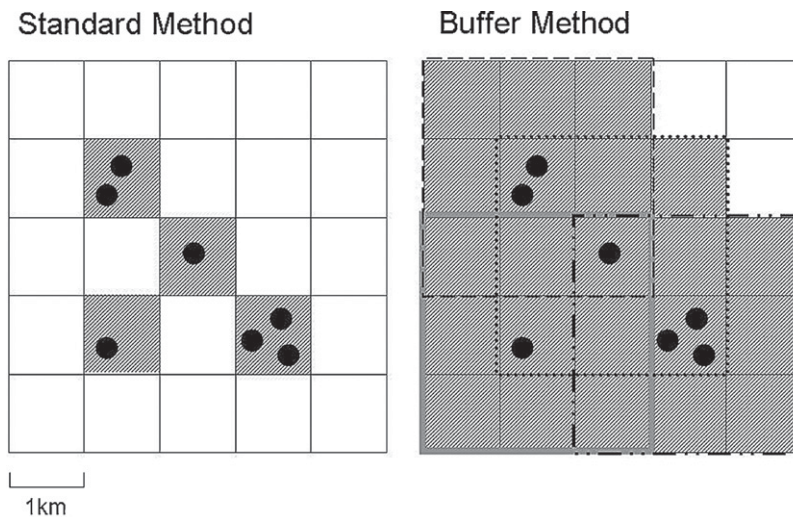
Standard Method   Buffer Method

1km

Fig. 1. Diagrams of the two interpolation/extrapolation methods used to calculate each grid system. Solid black dots represent location where species were recorded. The Standard Method only notes the areas where species were recorded as species occurrence data. The Buffer Method extends the areas where species were recorded into the neighboring 1 km regions (indicated by squares with differently dashed boundaries).

3. Results

3.1. Estimation through common species

Original data from the areas occupied by all ten common species and used in the Standard Method averaged 1.6% (0.54–4.36%) of total number of 37,552 1 km² grid squares of Taiwan. When we allowed for bird species movement distances within 1 km in any direction, data for the Buffer Method raised the average occurrence to 8% (2.50–20.52%) of the total grid squares. That is, the results of the data in the Buffer Method for all common species used to build the predictive models increased by 6.4% (Table 2).

The general patterns of predicted distributions for the whole of Taiwan for each method (*i.e.* the Standard and Buffer methods) were similar for each species (Fig. 2 top two maps); however, the Buffer Method had higher sensitivity and accuracy values (Fig. 3) and detected finer changes than the Standard Method (Fig. 2 bottom six maps). There were more areas of species potential distribution in the Buffer Method (Fig. 2). Comparing predictive probabilities showed that the Buffer Method had higher average probability values (Table 3) and lower maximum probabilities than the Standard Method for all common species.

Table 2
Environmental factors used in the three presence-only models: GARP, MAXENT, and LIVES.

Type	Description
Topography	Mean Elevation, Distance to Sea, Mean Slope, Length of Ridge
Climate	Annual Mean Temperature, Annual Total Precipitation, Total Water Deficiency, Warmth Index, Number of Month in Humid Period, Precipitation in Humid Period, Precipitation in Prehumid Period
Vegetation	NDVI, Forest Density, Vegetation, Natureness Index
Human disturbance	Road Density, Urbanization Index, Distance to Road, Distance to City
Ecological region	41 Ecoregions, Eastern Index

The distribution of AUC values for the three presence-only models (GARP, MAXENT, and LIVES) for each species were over 0.8, except for Taiwan Barbet (mean AUC = 0.62) and Taiwan Hwamei (mean AUC = 0.53) (Table 3). Consequently, we did not use these species to assess Kappa, sensitivity, specificity, and accuracy, using only the remaining eight species having AUC values over 0.8, which confirm reliability of the models. The individual values of these eight species in the two methods performed well on Kappa val-
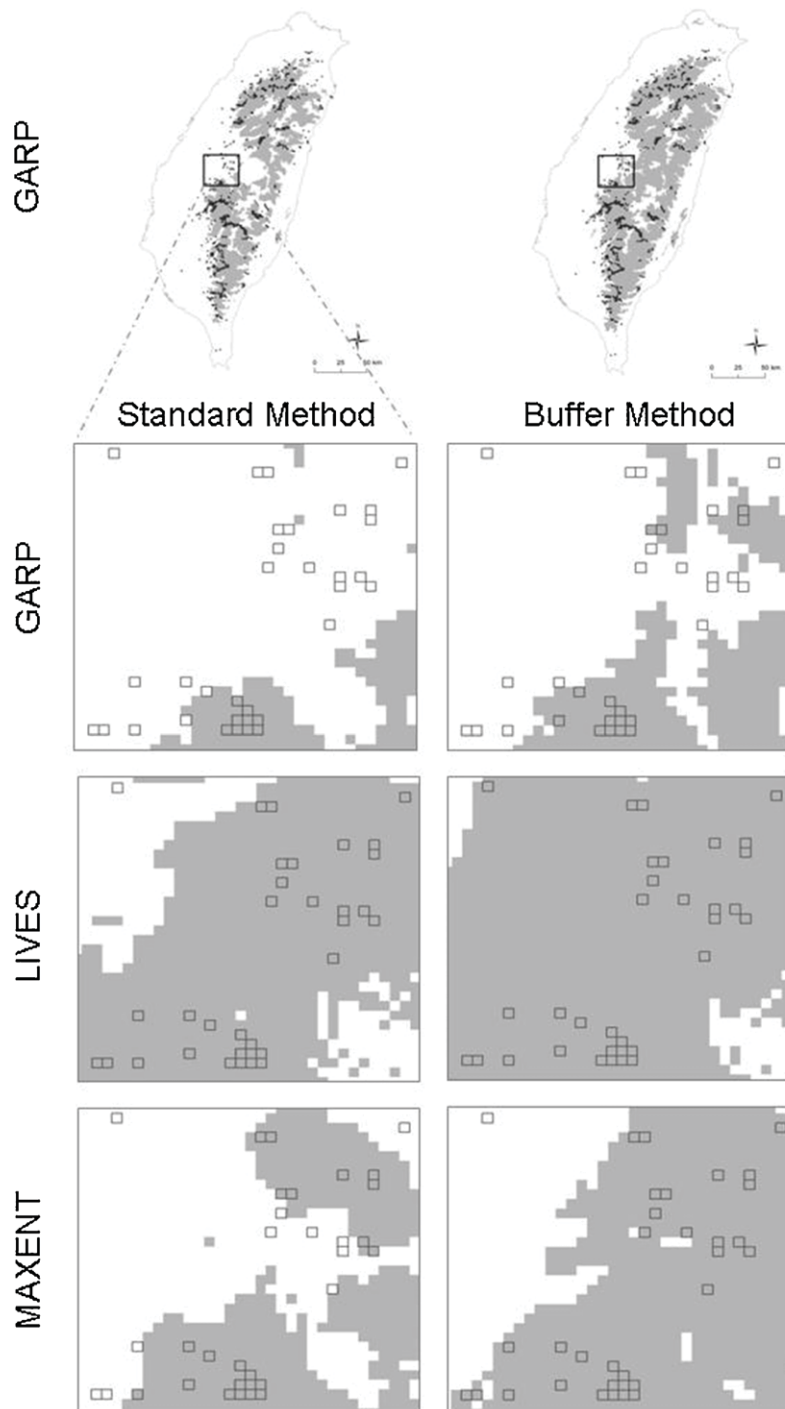
Table 3
Values of average predictive distribution probability (first values), Kappa (second value), and sensitivity (third value) for all species for the three presence-only models in the Standard and Buffer methods. AUC values were calculated to confirm reliability of the models of ten common species before comparing Kappa, sensitivity, specificity, and accuracy values. Except for Taiwan Barbet and Taiwan Hwamei, with AUC values lower than 0.8, other species were used to further comparisons on Kappa, sensitivity, specificity, and accuracy.

Category	Species	Presence-only models					
		GARP		MAXENT		LIVES	
		Standard	Buffer	Standard	Buffer	Standard	Buffer
Common species	Taiwan Barbet	0.54, 0.20, 0.67	0.45, 0.21, 0.64	0.36, 0.20, 0.79	0.40, 0.20, 0.83	0.90, 0.15, 0.71	0.94, 0.11, 0.87
	Taiwan Partridge	0.41, 0.56, 0.78	0.46, 0.56, 0.75	0.23, 0.58, 0.88	0.31, 0.61, 0.93	0.86, 0.48, 0.96	0.89, 0.50, 0.99
	Styan's Bulbul	0.23, 0.78, 0.84	0.24, 0.78, 0.84	0.06, 0.74, 0.89	0.11, 0.74, 0.87	0.56, 0.61, 0.71	0.60, 0.74, 0.87
	Steere's Babbler	0.32, 0.65, 0.76	0.36, 0.74, 0.90	0.17, 0.74, 0.91	0.26, 0.70, 0.96	0.84, 0.95, 0.99	0.88, 0.91, 0.99
	Taiwan Hwamei	0.40, 0.07, 0.39	0.46, 0.08, 0.46	0.22, 0.10, 0.38	0.31, 0.10, 0.45	0.86, 0.08, 0.56	0.89, 0.12, 0.90
	Taiwan Yuhina	0.35, 0.69, 0.76	0.40, 0.70, 0.78	0.21, 0.81, 0.94	0.27, 0.75, 0.93	0.81, 0.60, 0.68	0.85, 0.56, 0.83
	White-whiskered Laughingthrush	0.21, 0.76, 0.76	0.26, 0.93, 0.94	0.06, 0.94, 0.94	0.11, 0.98, 0.99	0.74, 0.64, 0.64	0.79, 0.87, 0.88
	White-eared Sibia	0.32, 0.61, 0.70	0.38, 0.73, 0.86	0.22, 0.80, 0.96	0.30, 0.77, 0.97	0.77, 0.41, 0.72	0.78, 0.42, 0.81
	Collared Bush-Robin	0.20, 0.61, 0.69	0.21, 0.61, 0.73	0.09, 0.76, 0.91	0.13, 0.82, 0.92	0.75, 0.71, 0.92	0.81, 0.70, 0.97
	Formosan Whistling-Thrush	0.48, 0.56, 0.70	0.51, 0.52, 0.70	0.26, 0.62, 0.77	0.33, 0.67, 0.88	0.86, 0.44, 0.87	0.89, 0.47, 0.99
Rare species	Mikado Pheasant	0.18, 0.61, 0.71	0.24, 0.74, 0.87	0.14, 0.68, 0.68	0.14, 0.77, 0.77	0.77, 0.40, 0.29	0.82, 0.50, 0.52
	Swinhoe's Pheasant	0.33, 0.43, 0.60	0.39, 0.55, 0.75	0.85, 0.58, 0.87	0.89, 0.66, 0.92	0.18, 0.86, 0.97	0.21, 0.92, 0.99

Fig. 2. Distribution of White-eared Sibia (*Heterophasia auricularis*) predicted throughout Taiwan using the Standard and Buffer methods. Top two maps show species distribution predicted by GARP in the whole of Taiwan (left: Standard Method; right: Buffer Method). Bottom six maps represent minor changes between the Standard and Buffer methods in the three presence-only models. Black points and black open squares are species occurrence grid squares records while gray areas are species potential distributions.

ues (>0.4) (Table 3). The highest Kappa value was 0.98 using the Buffer Method with MAXENT for the White-whiskered Laughingth-rush (*Garrulax morrisonianus*) (Table 3). For sensitivity and accuracy values, the Buffer Method was better than the Standard Method (Table 3; Figs. 3 and 4) with the differences in these two mea-surements for each species significantly between the Standard and Buffer methods for each model (for overall, $p < 0.01$ in sensitivity and $p < 0.05$ in accuracy; for individual models, $p < 0.05$ in GARP and MAXENT, and $p < 0.01$ in LIVES) (Figs. 3 and 4). There were no

significant differences in Kappa and specificity values between the two methods (all with $p > 0.05$) (Fig. 3).

3.2. Application to rare species

Data for two rare species could be analyzed using the Buffer Method. Original data for Swinhoe's Pheasant (*Lophura swinhoii*) covered 0.31% of the area of Taiwan and rose to 1.93% using the Buffer Method, while Mikado Pheasant (*Syrmaticus mikado*)
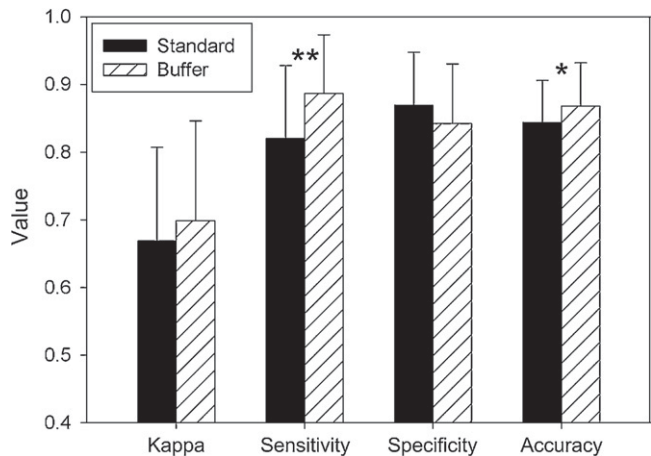
Fig. 3. Averages of four measurements for model evaluation in the Standard and Buffer methods. Eight common species with AUC values over than 0.8 were used to compare the four measurements. Sensitivity and accuracy values showed significantly differences between the two methods ($p < 0.01$ in sensitivity; $p < 0.05$ in accuracy) while Kappa and specificity values had no differences.

increased from 0.08 to 0.58%. Predictive distributions showed that there are some suitable habitats in Taiwan for these two rare species. AUC values of over 0.8 were obtained in the Standard and Buffer methods for three models found to predict these two species distributions well. The four measurements had similar patterns to the common species (Table 3). The two rare species showed no significant differences between the Standard and Buffer methods for Kappa and specificity while having significant differences for sensitivity and accuracy.

4. Discussion

Combining presence-only predictive models with species movement characteristics (e.g. movement distance and direction) to
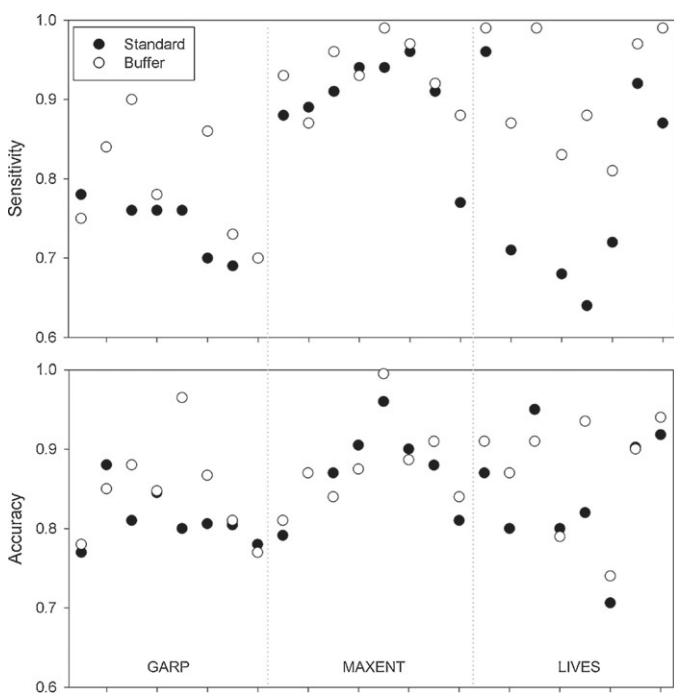

Fig. 4. Sensitivity and accuracy values of the eight common species, having AUC values over than 0.8, for each presence-only model in the Standard and Buffer methods.

predict species potential distribution provides useful insight in conservation planning. Predictive models not only use biogeographical data but also incorporate the biological aspects of the species under the study. Knowing the potential distributions of species will help to develop better conservation plans for them.

In this study, using the Buffer Method was better than the Standard Method at predicting species actual distributions much more accurately and at knowing species surrounding distributions. Especially, the sensitivity values, defined as the percentages of actual occurrence accurately predicted, were higher using the Buffer Method than the Standard Method (Table 3). Although the assumptions in this study were to increase the prevalence of twelve Taiwanese endemic bird species and to treat it as preference for species distribution, we used actual species occurrence records, not including those occurrences expanded the Buffer Method, to estimate the value of sensitivity. The assumptions here would not lead to biased sensitivity. When considering species absence data, the predictive performance of the Buffer Method was as good as that of the Standard Method. The original data for species absence, which was used to build the predictive models, however, is affected by collection of the data, such as the limitations of survey designs, and census-taken availability, which may fail to reveal species when they are actually present. This is particularly true for rare species and near the range boundaries of all species. Accordingly, the data may certain inadequacies in the records of species absence. Therefore, using sensitivity vales, which emphasizes species present data, as a prime value for assessment of predictive models is reliable in ecological and conservation studies and the Buffer Method did show a good sensitivity in our case.

However, at the sensitivity value point, the Buffer Method simultaneously faced a challenge: bigger predicted areas would always get a higher sensitivity value. We agreed this challenge and that is why we primarily used five evaluations to compare the two methods. AUC provided a basic threshold and proved the usability of these two methods first. Kappa, sensitivity, specificity, and accuracy values gave us more information on the two methods, either predicting species presence or absence. Both of the Buffer and Standard methods in the results showed a considerable ability on prediction. Although Kappa and specificity values did not have significant differences between the two methods, the Buffer Method had more high Kappa values than the Standard Method in three models (Table 3), especially when using the Buffer Method on rare species. We believed that the Buffer Method provided more species potential surrounding distribution areas, especially on rare species, which would lead further conservation management and landuse planning.

Our results showed that the maximum values of predictive probabilities for the Buffer Method for all species were lower than those of the Standard Method for all three models. That is because the Standard Method had more precise species occurrence data, which helped the models to achieve maximum predictive values.

The average probability values predicted by the Buffer Method were higher than those predicted by the Standard Method (Table 3). The resolution of species-specific buffer distance needs to be noted but is often difficult to assess in practice. Several studies using a radio tracking method have showed that certain species' daily dispersal distances were generally less than 500 m and the home range size averaged with less than 50 ha (Rothstein et al., 1984; Groombridge et al., 2006; Trejo et al., 2008). It is possible that we might have used excessive buffer distances in our study. However, a species spatial use of habitat is influenced by landscape structure, birds moving farther in fragmented landscapes, and sometimes occupying discontinuous territories comprising multiple fragments (Leonard et al., 2008). The topography in Taiwan is heterogeneous (Lee et al., 2004) and often has large variations within a grid square that may facilitate longer dispersal distances and larger territories.

Furthermore, Shirley (2006) suggested that wide habitats may provide valuable connections within forest at clear-cut and river edges, in addition to providing breeding habitat. The species occurrence records used in this study included whole year records and we assumed that it captured general patterns of species distribution during different seasons. In addition, using a one-by-one grid system provided a finer resolution to predict a wide range of species distributions. Based on the above, 1 km buffer distance was the best choice to combine our modeling methods and species dispersal distances.

Different models can provide best fit for different species. Several studies have used the three presence-only models chosen in this study (Elith et al., 2006; Tsoar et al., 2007; Phillips and Dudik, 2008; Ko et al., 2009). Moreover, these models seem to provide the best predictions so far, compared with traditional linear models, such as linear regression and multiple discriminant analysis, and some non-linear models, such as artificial neural networks (Ko et al., 2009). We found however that LIVES was not as good as the others in our case.

The theory of LIVES originated from the concept of limiting factors and tries to find unsuitable habitat of a species distribution – a totally different concept to GARP and MAXENT. Environmental factors in Taiwan vary with elevation, and adjacent grid squares sometimes have enormous differences. Due to such differences, LIVES could not easily catch the characteristics of species-unsuitable areas in our study. Moreover, if a specific environmental factor does significantly effect a species' distribution, prediction by LIVES would put weight on some areas where that specific environmental factor exits, and predict all those areas as species occurrence areas. LIVES may neglect other environmental factors contributing to a species' distribution. Using either the Standard Method or the Buffer Method, LIVES predicted much more potential distribution than GARP and MAXENT (Fig. 2). Although LIVES predicted almost all the species occurrence areas (only one area was not predicted by the Standard Method of LIVES), it also predicted many areas as being a potential species presence distribution instead of being a potential species absence distribution as predicted by GARP and MAXENT (Fig. 2). Because of this, the Kappa values of predictions of LIVES were lower than GARP and MAXENT (Table 3). Furthermore, finding species-unsuitable habitats sometimes needs more data to be certain that a species does not exist there. Rare species have higher conservation priority but due to their rarity, they can have fewer occurrence records, which can easily lead to limited information and poor prediction while using LIVES.

Choosing appropriate environmental factors to use in predictive modeling methods is important but difficult. Most species were well predicted by each model with the exception of Taiwan Barbet and Taiwan Hwamei. Both of these birds are recent endemic species in Taiwan as shown by the examination of their microsatellite DNA between subspecies (Li et al., 2006; Feinstein et al., 2008). Observers may confuse these two new endemics and other subspecies with more established species and log incorrect records, which would further compromise the results. Moreover, both of these species live more in lower elevation sites where human disturbance and noise may make them wary and harder to spot. Otherwise, the remaining eight common and the two rare species were all well recorded in the study.

Environmental data at a fine spatial resolution usually capture environmental variability better than at a lower resolution, especially in mountainous areas. Global climate data are recorded at a resolution of $30''$ ($\leq 1\,km^2$) by interpolated climate surfaces for global land areas and are used widely around the world (Hijmans et al., 2005). In this study, however, we used annual mean temperature data, with a very high resolution, interpolated by ourselves rather than global climate data. From the records of weather sta-

tions in Taiwan, we found that annual mean temperature has increased with time, particularly after 1990. The temperature data used in this study were collected from 1990 to 2000, and spanned the period of the bird census (1993–2004) more precisely than the global climate data (mostly from 1950 to 2000). The elevation bias used to adjust uncertainty in climate surfaces in our and the global climate data was the same. Therefore, even though we did not use the global climate data in this study, our results are still credible.

In this study, the occurrence records of common and rare species showed their overlapped habitats in elevation. We followed Githiru et al.'s observation (2007) that common species can play as reference when drawing insights into rare species' conservation when they are sympatric related species. Thus, we supposed common species could be a precursor for testing our methods. According the results, the Standard and Buffer methods could be used well on common species which avoided bias from small quantity of data and ensured the availability of the Buffer Method. Then using on rare species, the Buffer Method indeed provided us different and important thoughts to structure rare species needed-habitats.

For conservation purposes, we have demonstrated that the Buffer Method can clarify species potential "surrounding" distributions. The movement distances of bird species can be extensive due to feeding and reproductive needs. These movements can cover more distances than the areas where bird species are seen and heard. So the use of point data alone may not suffice because point data cannot reflect the whole distribution of a bird as it moves about. We suggest use of the Buffer Method to adjust these original point data. Forest birds are wary of crossing habitat boundaries, and conservation of a wide array of suitable habitats may provide valuable connections, for example between unlogged patches and breeding habitat. The Buffer Method examined in this study is able to take account of such matters. The Buffer Method can be made more flexible by changing the length of the buffer to suit species with different habits or movement patterns and has great potential for developing further conservation management strategies.

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