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Expanding ensembles of species present-day and future climatic suitability to consider the limitations of species occurrence data

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A B S T R A C T

Outputs of species distribution models (SDMs) are widely used as indicators of climate conditions favorable for species occurrence. When using these outputs to inform planning and decision making, it is essential that the uncertainties associated with the projections of present-day and future climatic suitability are carefully considered. Climate change assessments routinely consider the uncertainty introduced into SDM outputs by differences in future climate projections, and other uncertainty sources, such as the choice of the threshold to convert simulated probabilities to binary climatically suitable areas, are also oftentimes considered. However, the uncertainty introduced by the limitations of the species occurrence data used in the SDM calibration is rarely evaluated. These limitations, which include location error, sampling bias, and species misidentification, may reduce the utility of SDM outputs in conservation research and practice. Using understory bamboo species in southwest China as examples, here we demonstrate that species occurrences obtained using remote sensing offer an additional dataset for calibrating SDMs that, in conjunction with conventional observations and employing an ensemble approach of outputs from multiple models, provide an estimate of the uncertainty introduced by the species occurrence data. A biweekly time series of the satellite-based Wide Dynamic Range Vegetation Index (WDRI) was employed to estimate bamboo occurrence based on phenological signatures of the bamboo species and their overstory canopies. Using Maxent, a popular modeling framework, present-day and projected future climatic suitability were assessed separately for conventional species presence observations from the Fourth National Giant Panda Survey and for the remotely-sensed presence estimates. The ensemble of model outputs suggests that the uncertainty introduced by the species occurrence data, along with the interaction with other sources of uncertainty, may be as substantial as the uncertainty introduced by the use of different climate scenarios or by the threshold used to estimate binary climatically suitable areas. Ignoring the uncertainty introduced by the limitations of the species occurrences may compromise the interpretation of SDM outputs and reduce their usefulness for conservation planning. Remote sensing is a largely untapped resource for assessing uncertainty in SDM simulations.

1. Introduction

Species distribution models (SDMs) are popular tools for developing indicators of suitable climate conditions for species occurrence. They are based on correlative relationships established using current climate conditions in observed occurrence locations (Elith et al., 2011). Model outputs provide a useful baseline of the location and extent of present-day favorable climate conditions. These correlative relationships can then be applied to projected future climate conditions to assess potential changes in species distributions due to changes in the location and extent of climatically suitable areas (e.g., Ovalle-Rivera et al., 2015).

When using projections of future conditions to inform planning and

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decision making, it is essential that the uncertainties associated with the projections are considered (Winkler, 2016). Uncertainty is often simply defined as a state of incomplete knowledge (IPCC, 2014). Although various methods have been used to evaluate uncertainty, a popular approach is the use of multi-model ensembles, where the spread of the model outputs provides an estimate of the uncertainty (Wallach et al., 2015). Ensembles have been widely used when projecting future species occurrence. These ensembles often include projections obtained from different techniques (e.g., logistic regression, maximum entropy, boosted regression trees) used to model species distributions (e.g., García-Callejas and Araújo, 2016), differences in model parameterizations (Cobos et al., 2019), alternative sources of climate observations as environmental predictors (e.g., Tang et al., 2018), multiple thresholds to covert likelihood of occurrence to binary predictions of species presence (e.g., Nenzén and Araújo, 2011), or future climate conditions acquired from numerous global climate models (GCMs) driven by several greenhouse gas concentration pathways (e.g., Tuanmu et al., 2013).

One uncertainty source that is rarely considered is the limitations of the species occurrences used to calibrate a SDM. Barry and Elith (2006) concluded that one type of modeling error arises from data deficiencies. Common deficiencies for species occurrence data include small sample sizes, bias in sampling, location error, and misidentification of species (Barry and Elith, 2006; Ensing et al., 2012; Costa et al., 2015). While an underlying assumption of SDMs is that the study area is well sampled (Phillips et al., 2009), in practice, this is rarely the case because data on species occurrences are usually obtained from museums/herbaria or from field surveys (Guillera-Arroita et al., 2015). Under these circumstances, the size of the presence dataset is often small. Also, these data typically are biased towards more accessible areas (e.g., close to roads) or towards geographic areas where more intensive sampling was conducted (Glon et al., 2017). Species misidentification is another rarely reported source of error. Studies that compared available datasets and taxonomically “reliable” records in species distribution modeling found that climatic suitability obtained using the two sets of presence data differed substantially (Ensing et al., 2012; Molinari-Jobin et al., 2012). These limitations of species occurrence data, in turn, influence the projections of future climatic suitability, with potentially negative effects on conservation actions (Schmitz et al., 2015).

Previous studies have either ignored these data limitations or have attempted to correct for them by adjusting the species occurrence datasets or by changing the SDM formulation. However, as these strategies only indirectly infer the sampling process (Guillera-Arroita et al., 2015), they do not completely remove sampling bias or correct data errors. Commonly-used strategies to adjust for sampling bias include: filtering of species occurrences to reduce spatial autocorrelation (Boria et al., 2014); down-weighting occurrences from locations with higher sampling intensity (Schulman et al., 2007); manipulating the background data such that they have a similar spatial bias as the presence data (Phillips et al., 2009); inclusion of an autocovariate (“contagion”) term within the SDM to account for spatial autocorrelation (Segurado et al., 2006); and explicitly modeling observer bias (Warton et al., 2013). While some studies reported that these adjustments improved the outputs of SDMs (e.g., Boria et al., 2014; Kiedrzyński et al., 2017), others noted substantial limitations. For example, a disadvantage of spatial filtering is that it reduces the sample size, potentially decreasing the SDM’s predictive performance (Araújo et al., 2005). Background manipulations, such as defining a target group background by using the occurrence locations of other species (Phillips et al., 2009), run the risk of substituting underestimation bias with overestimation bias in poorly sampled areas (Ranc et al., 2017). Contagion terms can conflate sampling bias with the spatial autocorrelation of environmental (e.g., climate) covariates (Segurado et al., 2006). Model-based bias corrections require relevant predictors that are independent of species occurrences (Guillera-Arroita et al., 2015). In addition to these limitations, the effectiveness of bias correction strategies has been shown to vary with the nature of the spatial clustering, the degree or intensity of the bias, and species characteristics such as geographic range sizes (Kramer-Schadt et al., 2013; Fourcade et al., 2014; Ranc et al., 2017). Thus, bias corrected models do not necessarily constitute an improvement over biased models. Furthermore, sampling data manipulations do not provide solutions to issues such as species misidentification.

New approaches are needed for assessing the influence of limitations in the species occurrence data on projections of present-day and future climatic suitability. One possible tactic is the use of the aforementioned ensemble approach for estimating uncertainty. However, multiple sources of species occurrence observations are rarely available for incorporation into an ensemble, in contrast to other uncertainty sources such as that associated with future climate projections for which a large number of climate model simulations is accessible. Even if repeated samples of species occurrence exist, such as for ongoing censuses, they likely employed similar sampling designs and share many of the same limitations. A possible approach to addressing this dilemma is the use of remote sensing to develop an additional source of species occurrences that, together with conventional species information, can provide conservation planners and managers with an estimate of the uncertainty introduced by the limitations of the species occurrence data. Although remotely sensed observations are commonly used in SDMs as environmental covariates (Rocchini et al., 2015), they have rarely been used as estimates of species occurrence (although see Andrew and Ustin (2009) for an exception). Hence, remote sensing is an untapped resource to help understand the contribution of limitations in species occurrence information to the uncertainty of the outcomes from species distribution modeling.

Here we explore the potential usefulness of an ensemble of model outputs derived from two sources of species occurrence data – conventional field survey observations and remotely-sensed estimates – to assess the uncertainty introduced by the deficiencies of species occurrence data into projections of future species distributions. As our intent is to demonstrate an approach that is transferable to a wide range of plant species and locations, we employ freely-accessible remotely sensed observations and the popular Maxent modeling framework to model species occurrence and climatic suitability. We use bamboo species in southwest China as a demonstration. These species and their geographic location are important for several reasons. As understory species, bamboo can be challenging to detect using remote sensing procedures, and thus provide a crucial test of the usefulness of the proposed ensemble approach. Although detailed field sampling of bamboo has occurred within portions of the current geographical range of the giant panda, as part of the Fourth National Giant Panda Survey (State Forestry Administration, 2015) and earlier similar surveys, inaccessible areas and areas outside of the panda’s current geographic range were not sampled, reflecting the non-uniform coverage of field observations most researchers encounter. Moreover, the bamboo species evaluated constitute the main food source of the giant panda, making up 99% of their diet (Schaller, 1985). As a global icon of biodiversity conservation (Shen et al., 2015), the giant panda constitutes a gauge for measuring the success or failure of current conservation actions (Xu et al., 2017), and projected future changes in the distribution of bamboo species, along with estimates of the uncertainty associated with these projections, are essential to maintain the long-term viability of panda populations and to support the design of successful panda reintroduction projects (Swaisgood et al., 2018).

2. Methods

2.1. Study region

The study region encompasses the current geographic range of the giant panda (Yang et al., 2017) and surrounding areas (Fig. 1). This region is characterized by steep environmental gradients, a complex vegetation mosaic (Kong et al., 2017), and a large number of understory

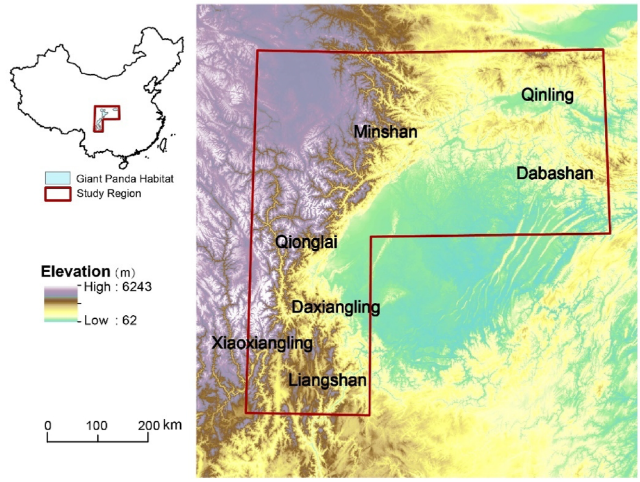

Fig. 1. Map of the study area (outlined in red) showing elevation with major topographic features and current habitat of the giant panda (light blue shading in the inset map).

bamboo species (Li, 1997; Hu and Wei, 2004). As mentioned above, this region is ideal for the study objectives, as a portion was sampled for bamboo occurrences during giant panda censuses organized by China's State Forestry Administration, with the remaining area not sampled. The latter includes areas of high elevation where bamboo is not expected to occur, but also large areas where giant pandas are not reported to occur but where bamboo species consumed by the pandas are present (Wu et al., 1994; Viña et al., 2010).

2.2. Bamboo species occurrence locations

Observed occurrence locations of understory bamboo species were obtained from the Fourth (2011–2014) National Giant Panda Survey (hereafter 4S) (State Forestry Administration, 2015). Occurrence locations were carefully checked for errors in the reported locations (e.g., geographic coordinates located away from the surveyed areas, locations exhibiting the same or inverted latitude and longitude coordinates) and in the translation of vernacular to scientific names. Locations with vernacular names that corresponded with more than one scientific name were removed. In addition, the species names were compared to those listed in the *4th National Survey Report on Giant Panda* (State Forestry Administration, 2015) to ensure that each species included in the analysis constitutes a food source for giant pandas. Only species with 15 or more occurrence locations, after removing erroneous entries, were retained for further analysis, for a total of 28 species (Table S1).

2.3. Climate observations and future projections

Baseline (i.e., present-day) climate conditions were obtained from remotely sensed estimates provided by Deblauwe et al. (2016) of long-term monthly means of temperature and precipitation for 2001–2013 and 1981–2013, respectively. In this database, temperature estimates were obtained from MODIS MOD11C3 v. 6.0, while precipitation estimates were obtained from Climate Hazards Group InfraRed Precipitation with Station data version 2 (CHIRPS v. 2.0). This dataset was selected because of its finer (0.05 degree, about 6 km) inherent spatial resolution compared to the much coarser, non-uniform resolution of conventional climate observation networks. We downloaded 19 standard bioclimatic variables derived from the monthly temperature and precipitation means (available from https://vdeblauwe.wordpress.com) and resampled the gridded fields using bilinear interpolation to a 1 km^2 resolution, a commonly used grid cell size for modeling climatic suitability of species distributions (e.g., Hijmans et al., 2005). This choice maintains a focus on mesoscale climate processes (e.g., changes in temperature with elevation) rather than on microclimate processes (e.g., aspect, local land cover) that cannot be easily inferred using spatial interpolation.

Climate projections were derived for a future (2061–2080) time slice using the popular delta downscaling method and simulations for the RCP8.5 greenhouse gas concentration trajectory obtained from 17 global climate models (GCMs) in the Coupled Model Intercomparison Project Phase 5 (CMIP5) archive (https://cmip.llnl.gov/cmip5/) (Table S2). The deltas, defined as grid point differences between GCM simulations for future and historical periods, were applied to the baseline temperature and precipitation fields, and bioclimatic variables were calculated for each of the downscaled future projections (see Tang et al. (2018) for more detail).

2.4. Estimation of bamboo species occurrence using remote sensing

Bamboo species are challenging to detect using optical remote sensing techniques given that they occur in the understory of trees. However, due to the mismatch between the phenological signatures of the overstory canopies with and without an understory of bamboo (Viña et al., 2008; Tuanmu et al., 2010), it is possible to estimate their occurrence using remotely sensed observations acquired with a high temporal resolution. A time series (2008–2010) of bi-weekly Wide Dynamic Range Vegetation Index (WDRVI; Gitelson, 2004) imagery, calculated from surface reflectance values in the red and near infrared spectral bands of the Moderate Resolution Imaging Spectroadiometer (MOD09Q1 product available from https://lpdaac.usgs.gov/), was used to estimate the bamboo occurrences. The WDRVI was preferred over the more commonly used Normalized Difference Vegetation Index (NDVI), which has been extensively used as a surrogate of vegetation biophysical characteristics, since it does not lose sensitivity at the moderate-to-high green biomass conditions characteristic of the forests in the study area with a dense understory (Viña et al., 2008). Following the procedures described by Viña et al. (2010), a principal components analysis was applied to the WDRVI image time series, and 10 principal components were retained for further analysis. These components, along with the Shuttle Radar Topography Mission (SRTM) digital elevation model (https://www2.jpl.nasa.gov/srtm/), served as explanatory variables. The 90 m digital elevation model was resampled to the resolution of MODIS-WDRVI (250 m) using bilinear interpolation.

Given species misidentification problems, together with the fact that time series of WDRVI capture not only phenological signatures of the understory bamboo but also of the overstory canopy, rather than modeling the climatic suitability of individual species we modeled the climatic suitability of phenologically-defined bamboo species groups. Such grouping of bamboo species by their phenological similarity, as defined using time series of WDRVI, not only reduces potential biases due to species misidentification, but also due to the effects of the overstory canopy, since it has been shown that floristically similar areas (i.e., composed of similar overstory and understory species) will also be phenologically similar (Viña et al., 2012, 2016). Such grouping has the additional advantage that it can be applied to datasets composed of a large number of species in a guild, each with a small sample size of occurrence locations. To obtain phenologically-driven groups of bamboo species, we used k-means cluster analysis to group the species based on the 10 principal component scores along with elevation. The resulting 11 groups (Table 1) are composed either of a single species (groups 1, 2, and 6), solely or almost entirely of species from the same genus (groups 3, 5, 9, and 10), or of species from multiple genera that exhibit similar phenological characteristics (groups 3, 4, 7, and 11).

We then used Maxent, a maximum entropy modeling algorithm (Phillips and Dudik, 2008) to obtain bamboo occurrence probability using the 11 independent input variables, together with the 4S occurrence locations of each of the 11 bamboo species groups. Although best known for its use in species distribution modeling, recent studies have

Table 1
The 11 phenologically-driven groups of bamboo species, the area under the receiver operating characteristic curve (AUC) for the models used to estimate the remotely sensed presence locations, and the number of presence locations from the Fourth National Giant Panda Survey (4S) after thinning to 1 km^2 raster cells.

Groups	Bamboo Species	AUC	Number of 4S locations (after thinning)
Group 1	*Q. opienensis*	0.971	99
Group 2	*Y. dafengdingensis*	0.965	23
Group 3	*B. faberi, F. ferax, Y. ailuropodine, Y. brevipaniculata, Y. glauca, Y. lineolate, Y. mabianensis*	0.901	987
Group 4	*C. szechuanensis, F. angustissima, Q. tumidinoda*	0.960	308
Group 5	*P. nidularia, P. nigra*	0.952	113
Group 6	*F. qinlingensis*	0.889	1476
Group 7	*B. fargesii, P. sulphurea*	0.913	948
Group 8	*F. dracocephala, I. tessellatus*	0.954	362
Group 9	*F. denudate, F. nitida, F. obliqua*	0.904	877
Group 10	*F. robusta , F. rufa, F. scabrida*	0.924	575
Group 11	*B. spanostachya, F. jiulongensis, Y. maculata*	0.927	164

found that Maxent also performs well as a one-class classifier of species presence when applied to remotely sensed data (Stenzel et al., 2014; Skowronek et al., 2017). As background data, we selected 10,000 randomly distributed pixels throughout the study region. To evaluate the accuracy of the modeling algorithm for each bamboo species group, we performed a cross-validation approach in which five replications were obtained using the "subsample" run type. To this effect, the occurrence points were split iteratively five times into random training and testing subsets, and the area under the receiver operating characteristic curve (AUC; Hanley and McNeil, 1982) was calculated. Average AUC values for the different bamboo groups ranged from 0.889 to 0.971 (Table 1).

The resulting probability maps were then resampled to the 1 km^2 resolution of the climate variables using a minimum value filter which emphasizes large bamboo patches. For each bamboo group, the resampled probability values were ranked from largest to smallest, and the locations with the largest probabilities were selected as the remotely sensed (hereafter RS) occurrence locations. For each bamboo group, the number of RS locations was kept equal to the number of 4S locations (also thinned to a 1 km^2 resolution) to remove the influence of sample size (van Proosdij et al., 2016) on the climatic suitability modeling. The steps used to estimate the RS occurrence locations are summarized in Fig. S1.

2.5. Climatic suitability modeling

Maxent was also used for climatic suitability modeling. Two climatic suitability models were calibrated for each of the 11 bamboo groups using the 4S and RS species locations. Following the procedures described in Tang et al. (2018), climatic predictor variables were selected using principal components analysis (PCA) applied to the fields of 19 commonly-used bioclimatic variables that were calculated from long-term averages of temperature and precipitation (Deblauwe et al., 2016). For each rotated component with an eigenvalue greater than one, the bioclimatic variable with the highest loading was retained for the analysis to avoid the high correlation among bioclimatic variables. Five bioclimatic variables served as predictors for the baseline climate: annual mean temperature; temperature seasonality; annual precipitation; precipitation seasonality; and annual temperature range. The simulated probabilities were converted to binary climatically suitable areas using all the thresholding procedures available within Maxent. AUC values obtained from a similar cross-validation procedure applied to evaluate the accuracy of these models as that applied to evaluate the remote sensing models described above ranged from 0.926 to 0.996 (Tables S4 and S5). In addition to the AUC, we also calculated true skill statistics (TSS) (Allouche et al., 2006) to assess the accuracy of the binary climatic suitability obtained using the equal test sensitivity and specificity threshold. TSS values ranged from 0.724 to 0.955. The models derived from the present-day climate conditions were then applied to the projected future (2061–2080) values of the bioclimatic variables for the 17 GCMs, to obtain projections of future climatic suitability for each bamboo group. The procedures for the climatic suitability modeling are summarized in Fig. S1.

3. Results

3.1. Remotely sensed occurrence locations

The RS estimates produced a similar spatial distribution for the majority of the bamboo groups as compared to surveyed data, while revealing possible occurrence locations in unsurveyed areas (Fig. 2). Beginning in the southwestern portion of the study area, considerable spatial congruence is observed for two single species groups, groups 1 and 2, with the exception of a few RS locations that are not found in the 4S datasets. Multi-species groups 3, 4, and 5 are located in the central and southwestern portions of the study region. Agreement between the RS and 4S datasets is strong for these groups, except that for groups 3 and 4 the RS estimated locations extend farther north into the western Qinling and the (unsurveyed) Dabashan Mountains. The RS locations for the three bamboo groups found mainly in the northeastern portion of the study area (groups 6, 7, and 8) suggest these species also occur in the unsurveyed Dabashan Mountains. The fewer RS locations for these three groups in areas sampled during the national survey are in large part due to constraining the number of RS locations to that of the 4S observations. Differences between the RS and 4S locations are more substantial for the remaining three groups. For groups 9 and 10, the RS estimates placed locations farther north into the Minshan Mountains and farther south into the Daxiangling, Xioxingling, and Liangshan Mountains. The RS estimates for group 10 also indicate occurrence of these species in the Qinling and Dabashan Mountains. For group 11, the RS estimates extend farther north as compared to the survey locations.

3.2. Present-day climatic suitability

For the majority of the bamboo groupings, the climatically suitable area obtained from the RS locations is larger than that obtained from the 4S locations (Fig. 3). For groups 6, 7, and 8, the greatest differences are found in the Dabashan Mountains. Whereas the models developed using the 4S locations suggest that a limited area within the Dabashan Mountains currently is suitable for these bamboo species, the use of the RS estimated locations results in a substantially expanded area of climatically suitable conditions. Additionally, the RS models suggest a larger suitable area for groups 1, 2, and 3, which is in line with the larger spatial extent of the RS locations as compared to the 4S locations. As noted above, the spatial extent of the RS locations for groups 9, 10, and 11 is larger than that for the 4S locations, and, as expected, climatically suitable area is larger for the RS models. In contrast, differences in climatically suitable areas obtained from the RS and 4S locations for groups 4 and 5 are small.

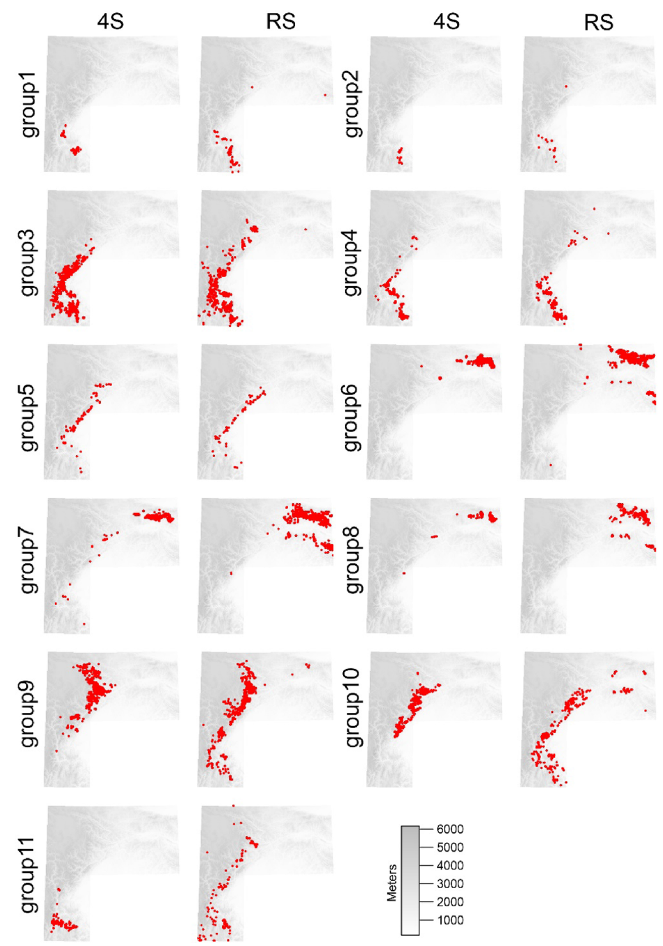

Fig. 2. Bamboo presence locations from the Fourth National Giant Panda Survey (4S) and estimated using remotely sensed data (RS) for the 11 bamboo groups. The presence locations from both sources were thinned to 1 km^2 raster cells. See Table 1 for the names of the bamboo species in each group and for the number of 4S presence locations for each bamboo group. The number of RS locations was constrained to equal that of the 4S locations. The gray shading represents elevation in meters.

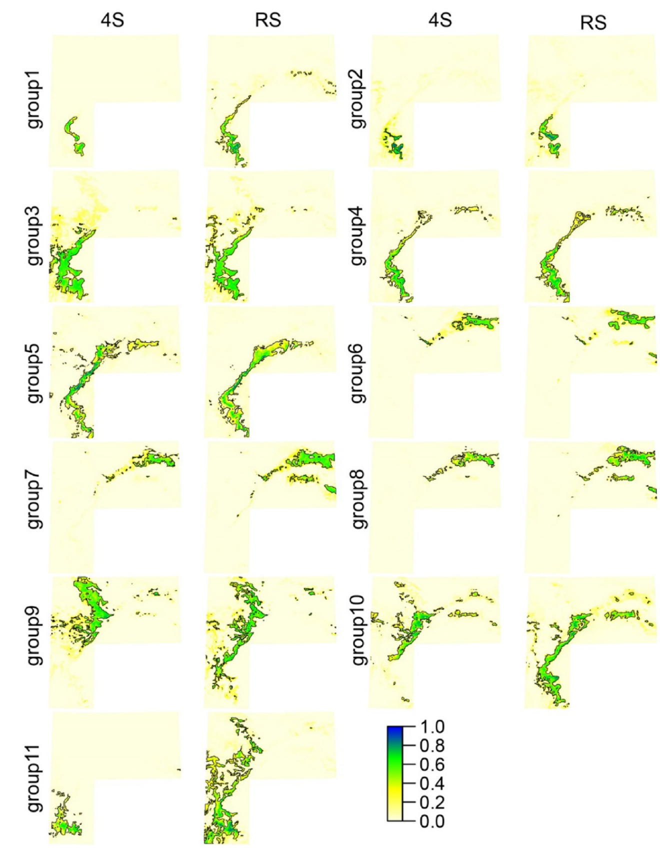

Fig. 3. Climatically suitable area under the baseline climate conditions for the 11 bamboo groups obtained from Maxent models derived using species locations from the Fourth National Giant Panda Survey (4S) and from the remotely sensed species locations (RS). The shading indicates the probability of species presence, and the boundaries delineate the climatically suitable area for each bamboo group based on the equal test sensitivity and specificity threshold.

3.3. Future climatic suitability

Focusing on the climatically suitable area obtained using the equal test sensitivity and specificity threshold to convert probabilities to binary values, we observe that for some of the bamboo groups the sign of the projected changes for 2061–2080 differs depending on the source of the occurrence data used for SDM calibration, whereas for other groups the projected changes are in the same direction but of different magnitude (Fig. 4).

Differences in the sign of the projected future changes are largest for groups 1 and 2. For group 1, the 4S derived projections, regardless of the GCM from which the future climate conditions were obtained, suggest that the climatically suitable area will decrease, with several of the projections indicating little or no remaining suitable area by 2061–2080 (Fig. S2). In contrast, all but five of the RS derived projections suggest that climatically suitable conditions will expand northward along the eastern mountain slopes to at least the southern Minshan Mountains and, for some GCMs, to the northern Minshan Mountains. For group 2, the majority of the 4S derived projections suggest that the climatically suitable area will expand northward into areas that the RS model predicts as currently suitable, but that will become less suitable in the future (Fig. S3).

Differences among GCM projections are particularly pronounced for group 3. Future climate conditions from 10 of the 17 GCMs, when input into the 4S model, and from 12 of the GCMs, when input into the RS model, suggest that the climatically suitable area will increase in the future, with the greatest increases occurring along the eastern slopes of the Minshan Mountains and the northern Qionglai Mountains (Fig. S4). This expansion is not observed in the projections obtained from the remaining GCMs. In contrast, the majority of the 4S derived projections and all of the RS derived projections for groups 4 and 5 suggest that the climatically suitable area will decrease in the future, although the location of the largest changes varies substantially among GCMs (Figs. S5 and S6). Regardless of GCM or the source of presence locations, the climatically suitable area is projected to decrease in the future for groups 6, 7, and 8. The Dabashan Mountains, for which the RS models, and to a lesser extent the 4S models, predicted areas of present-day suitable climate conditions, are projected to no longer be suitable in the future. Large decreases are also projected for the Qinling Mountains (Figs. S7–S9).

Interpretation of the differences in future changes obtained from RS and 4S models is more difficult for the remaining three groups (groups 9, 10, and 11) because of the larger number of RS locations that differ from the 4S locations. Nevertheless, the projected changes obtained for the 4S and RS models are quite similar in the geographic areas where the occurrence locations overlap. For groups 9 and 10, the projections agree that climatically suitable areas within the Minshan Mountains will decrease in extent (Figs. S10 and S11). Climatically suitable conditions are projected to expand northward for group 11, although substantial differences among GCMs are observed (Fig. S12).

The projections obtained from the two sources of species occurrence locations, the 17 GCMs, and all of the conversion thresholds available in

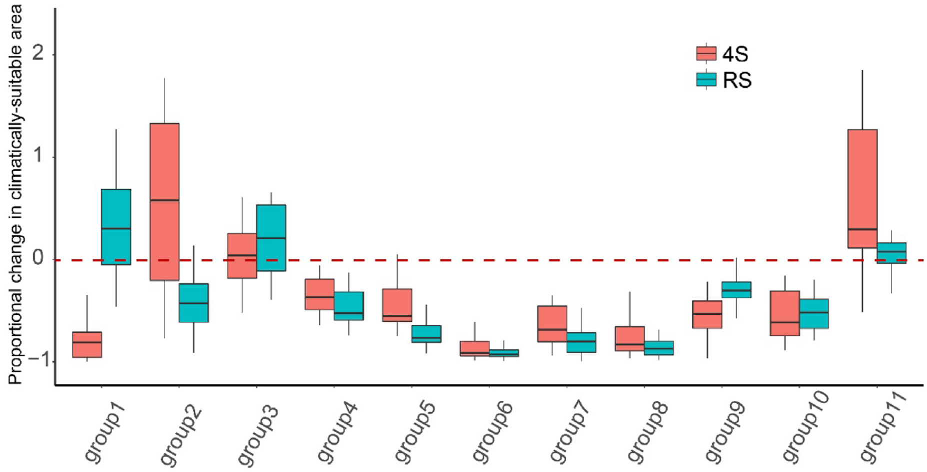

Fig. 4. Proportional change in climatically-suitable area for the 11 bamboo groups based on the species locations from the Fourth National Giant Panda Survey (4S) and the remote sensing estimated locations (RS). The projected change is expressed as the ratio of the difference in climatically-suitable area between the future (2061–2080) and present-day climate conditions to the climatically suitable area for the present-day conditions (the values can be multiplied by 100 to obtain a percentage change). Each box and whisker plot includes projections obtained from 17 global climate models (GCMs). Probabilities of species presence were converted to binary climatically suitable areas using the equal test sensitivity and specificity threshold.

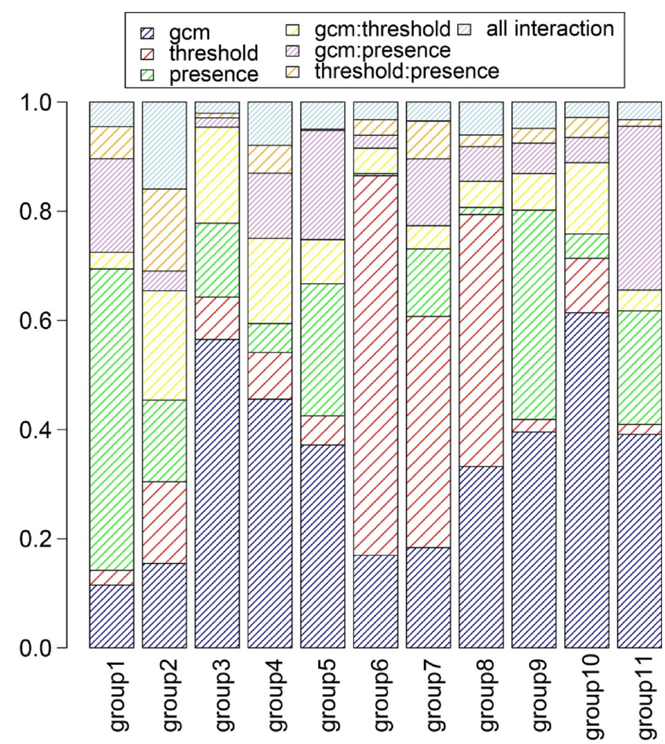

Fig. 5. Proportion of the sum of squares for each main effect and interaction term to the total sum of squares obtained from a three-way analysis of variance (ANOVA) of the projected percentage change in climatically suitable area between the future and baseline periods for each of the 11 bamboo groups. The analysis includes two sources of presence locations (Fourth National Giant Panda Survey and remote sensing estimated locations), 17 global climate models (GCMs), and 11 conversion thresholds. The main effect and interaction terms are shown in different colors and hatchings (see legend at the top of the figure), and the length of each color segment represents the variance contributed by that term to the total variance of the projections of future climatically suitable area.

Maxent were included in an analysis of variance (ANOVA) to evaluate the relative magnitudes of the uncertainty sources. Results indicate that the magnitudes of the three main effect terms differ markedly by bamboo group (Fig. 5). Ignoring groups 9, 10, and 11 for which the RS locations need to be interpreted cautiously, the uncertainty introduced by the distribution of the occurrence locations is particularly large for group 1, considerably exceeding the values of the other two uncertainty terms. For groups 2, 3, and 5, the uncertainty introduced by the occurrence locations is smaller than that of the choice of GCM but larger, or similar in magnitude, to the choice of conversion threshold. On the other hand, the main effect of the source of the occurrence data is small for groups 4, 6, 7, and 8. For most of the bamboo groups, the interactions between presence data source, choice of GCM, and conversion threshold are substantial.

4. Discussion

4.1. Implications for planning and decision making

Peterson et al. (2018) recently cautioned that uncertainty in the outputs of SDMs “may bias and limit confidence” (p. 66) in projections of the impact of climate change on species distributional potential and distributional shifts. If the outputs of SDMs are to be useful for conservation planning and research, this uncertainty must be communicated to stakeholders. Stakeholders require this information to make decisions that are robust to a range of future conditions and also to prevent against maladaptation which could lead to more, rather than less, risk and vulnerability to climate change (Perdinan and Winkler, 2014; Winkler, 2016). Deficiencies in the species presence information used to calibrate a SDM, including sampling bias, location error, and species misidentification, are a fundamental source of uncertainty. We investigated whether remote sensing can be useful in estimating this uncertainty. Based on the analyses presented above, we argue that the answer is a definite “yes”, although with some caveats but also with avenues for modification and improvement, along with customization for different species, data availability, and geographic regions. We emphasize that our intent was not to replace conventional species occurrence data from field surveys and/or museums/herbaria with remotely sensed estimates of species presence, but rather to develop SDMs using both sources of species presence information and evaluate uncertainty from the ensemble of model outputs.

Our example analyses for bamboo species in southwest China demonstrate that the uncertainty introduced by species presence information may be large. In general, the SDMs derived using the RS estimates of species presence predicted considerably larger present-day climatically suitable areas for the phenologically-derived bamboo groupings compared to the models derived using the field survey observations. This expansion occurred primarily in the portions of the study area without field observations, suggesting that the field survey observations captured only a portion of the fundamental niche of the bamboo species. When the SDMs were applied to future climate conditions obtained from global climate models, projections of future climatically suitable area differed considerably depending on the source of species occurrence data, and for some of the bamboo groups the variability in the model outputs attributed to the species presence data was as large as that attributed to the choice of future climate scenario or the conversion threshold used to estimate binary climatically suitable areas. Thus, the uncertainty contributed by the species occurrence data used to calibrate a SDM cannot be ignored, as has been the case in most previous studies.

The ensemble approach advocated for here is only appropriate if the remotely sensed estimates of species presence are plausible. Bamboo species are challenging to detect using remote sensing given that they occur in the understory and are covered by a tree overstory, but even for these species our findings suggest that widely-available remote sensing datasets along with a popular modeling tool (i.e., Maxent) can provide a plausible dataset of species presence for uncertainty estimation. The high AUC scores, obtained in a cross-validation procedure over five replications, indicate that bamboo species presence was well estimated using remote sensing. In addition, comparisons with atlases and other secondary sources provide confidence in the remotely sensed presence estimates outside of the areas sampled during the field survey. For instance, the northward extension of the RS presence locations compared to the 4S locations for groups 4 and 5 is supported by maps published in the *Atlas of Woody Plants in China* (Fang et al., 2011) of the individual species included in these two groups. The RS locations in the unsurveyed Dabashan Mountains for groups 6, 7, and 8 are supported by several secondary sources (Tang and Wei, 1983; Wu et al., 1994; Wang et al., 2005; Fang et al., 2011). Similarly, secondary sources (Ohrnberger, 1999; Royal Botanical Gardens, 2017) support the northeastward extension of the RS-estimated presence locations compared to the 4S locations for groups 9 and 10. Unfortunately, we were unable to identify secondary sources to support the southward extension of the RS-estimated presence locations into the Daxiangling, Xioxingling, and Liangshan Mountains for groups 9 and 10, or the northward extension of the RS estimates for group 11. Although we cannot rule out that these species occur in these areas but were not sampled during the field survey, especially given the large model AUC values, an alternative explanation for these differences is that the RS estimation may conflate bamboo species within a group with other species with similar phenological characteristics. For instance, the species within group 11 occur at high elevations (>3000 m) (Ohrnberger, 1999) and may be conflated with species with similar phenologies located at lower elevations but higher latitudes. These differences between the 4S and RS locations highlight that evaluating the plausibility of both the conventional and remotely sensed species presence information is an essential initial step when using an ensemble approach to estimate the uncertainty contributed by the species occurrence data to future projections of climatic suitability.

In addition to outlining an approach for assessing uncertainty, this research, along with the companion paper by Tang et al. (2018), also provides additional insights on potential future changes in bamboo distribution in southwest China. The impact of climate change on the distribution of the bamboo food staples of the giant panda within the panda's current geographic range has been the focus of a number of previous studies (e.g., Tuanmu et al., 2013; Li et al., 2015a,b; Zhang et al., 2018). However, when calibrating species distribution models, these studies employed a single source of species presence data and a single source of present-day climate data, thus ignoring the contributions of these uncertainty sources to the projected future climatic suitability and bamboo distributions. Direct comparison of the results of this study and Tang et al. (2018) with those of previous studies is difficult because the number and type of bamboo species and climate models included in the analysis vary considerably between the different studies. However, Fig. 5 from this analysis and Fig. 8 from Tang et al. (2018) provide a reference that can be used to infer for which bamboo species the projected future climatic suitability is more likely to have been impacted by the choice of data used in the SDM calibration. This allows stakeholders to place more confidence in the results for those species for which the uncertainty introduced by the calibration datasets is small and less confidence for species for which the uncertainty is large, increasing the utility of the larger body of research for conservation planning and decision making. In addition, our analysis extends beyond previous research to also consider future climatic suitability and bamboo distribution in areas outside, but nearby, the current panda range that may be options for panda reintroduction.

4.2. Limitations and opportunities

Just as conventional species presence data have limitations, so do the remotely-sensed estimates, as mapping species distributions using remote sensing is imperfect (Bradley, 2014). Such limitations need to be fully acknowledged. One limitation is the resolution of the remotely sensed data, with users often trading a finer temporal resolution for a finer spatial resolution. Moreover, remotely sensed data with finer spatial resolutions, such as those obtained from aircraft or unmanned aerial vehicles, are usually available for only limited spatial extents and/or at higher costs (Andrew et al., 2014). To demonstrate the potential wide applicability of the proposed approach, we constrained our analyses to a freely available global dataset, although the choice of remotely sensed data, including those obtained from the fusion of data acquired by different platforms (e.g., Viña et al., 2016), should be customized to the species under consideration and to the resources available for each particular study. In addition, numerous authors have noted the difficulty distinguishing among species with similar characteristics (e.g., Dronova et al., 2017). This is a concern for our analysis as well, as many bamboo species have overlapping phenologies and habitat requirements. We attempted to address this concern by grouping bamboo species with similar phenological characteristics and estimating occurrence by group rather than by individual species. However, a confounding factor is that a number of bamboo species have large latitudinal ranges and hence their phenological characteristics may vary quite substantially across space, making occurrence estimations more challenging. Another challenging factor related to the spatial extent of understory species is latitudinal and elevation variability in the associated overstory canopy (Du et al., 2011).

The limitations of an ensemble approach for estimating uncertainty also need to be acknowledged. In particular, ensemble members are rarely independent of each other. For example, the GCMs used to assess the uncertainty introduced by the source of future climate projections share many of the same computational procedures and parametrizations (Pennell and Reichler, 2011). Similarly, the 4S observations were used in the estimation of the RS locations, and thus the climatically suitable area obtained from the RS estimated occurrences is not fully independent of that obtained from the 4S observed locations. In addition, RS locations were estimated from differences in phenological characteristics, but phenology, in and of itself, is influenced by climate. Furthermore, the uncertainty estimates obtained from ensembles must be carefully interpreted, keeping in mind that the full uncertainty is unknown. Rather, ensembles provide an estimate of the 'calibrated range of uncertainty' (Jones, 2000) or the 'lower bound on the maximum range of uncertainty' (Stainforth et al., 2007).

In spite of these limitations, the combined use of the 4S and RS presence locations provided insights on the uncertainty of future species distributions contributed by the species occurrence data. Moreover, the RS occurrence locations have a number of useful features that can be capitalized upon. For instance, we limited the number of RS locations to that of the 4S locations for comparison purposes, but a less stringent threshold would provide a broader spatial coverage and a larger sample size for SDM calibration. Also, our ensemble approach does not need to be limited to only conventional species occurrences and occurrences estimated from a single RS dataset, but can be expanded to include estimates obtained from multiple remote sensing platforms/sensors. For example, previous researchers have used 30 m Landsat Thermatic Mapper data (Linderman et al., 2004) and 2 m WorldView-2 data (Tang et al., 2016) to estimate bamboo occurrence in the Qionglai Mountains. Furthermore, as remotely sensed observations useful for species distribution modeling will continue to be available through time and from different platforms and sensor systems (He et al., 2015), they will allow re-assessing model uncertainty through ensemble approaches developed using newly obtained field data acquired concurrently with the remotely sensed data.

5. Conclusions

We proposed that an ensemble of projections of future climatically suitable area obtained from SDMs calibrated using conventional species occurrence locations and from SDMs calibrated using remotely sensed estimates of species presence can provide an estimate of the contribution of the species occurrence data to the uncertainty of future projections. Using bamboo species in southwest China as an example, we obtained valuable insights on the uncertainty introduced by the limitations of species occurrence data, which can help inform planning and decision making. Our analysis is, to the best of our knowledge, the first study to employ an ensemble approach to estimate the relative magnitude of the uncertainty associated with the species occurrence data used to calibrate SDMs. We found that, depending on the bamboo group, this uncertainty can approach, and sometimes even exceed, the uncertainty introduced by the choice of future climate scenarios and conversion thresholds used to convert the modeled probabilities into binary climatically suitable areas. Furthermore, the uncertainty related to occurrence datasets interacts with other sources of uncertainty, thus complicating the interpretation of projected future changes. Integration of the findings of this study with those from a companion study (Tang et al., 2018), which investigated the uncertainty introduced by the choice of baseline climate information, emphasizes that users need to pay as much attention to the input datasets used to calibrate the SDM as to the uncertainty of the future climate scenarios. While it is now de rigueur to include multiple sources of future climate projections, most studies calibrate SDMs using a single source of species occurrences and baseline climate data. These two studies, in combination, illustrate that ignoring the uncertainty in both occurrence data and explanatory variables may compromise the interpretation of SDM outputs and limit their usefulness for conservation planning. Moreover, the usefulness of remote sensing in assessing both of these uncertainties was demonstrated.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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