LETTER

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Incorporating biotic interactions reveals potential climate tolerance of giant pandas

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Abstract

Many studies have overestimated species' range shifts under climate change because they treat climate as the only determinant while ignoring biotic factors. To assess the response of giant pandas to climate change, we incorporated spatial effects in modeling bamboo distributions, which in turn was incorporated to represent giant panda–bamboo biotic interactions in predicting giant panda distribution. Our study revealed potential tolerance of giant pandas to climate change. We found significant residual spatial correlation in the bamboo models. The biotic interactions with bamboo understories and anthropogenic activities had large effects on panda distribution, which lowered the relative importance of climatic variables. Our results are fundamentally different from previous studies that used climate-only and nonspatial approaches, which may have overestimated the effects of climate change on panda and lead to inappropriate conservation recommendations. We strongly advocate that giant panda conservation planning continues to focus on protecting bamboo forest and reducing anthropogenic interferences.

KEYWORDS
bamboo, biotic interaction, China, climate change, conservation planning, giant panda, spatial autocorrelation, species distribution model, wildlife conservation

1 | INTRODUCTION

Climate change is challenging the conservation planning of governments and natural resource organizations (Bernazzani, Bradley, & Opperman, 2012). However, forecasts based on species distribution models (SDMs) are often criticized for being too simplistic if they assume that climate and few abiotic factors are the only determinants of a species' geographical range (Harris et al., 2014). Biotic interactions such as resource–consumer interactions and interspecific competition are also essential factors that drive species' distributions, and incorporating these factors can improve forecasts of the eco-logical consequences of climate change on species (Wisz et al., 2013). However, most studies have adopted a climate-only modeling approach and ignored important biotic factors, even when such information was available (Dormann, 2007; Pacifici et al., 2015).

Another critical but often-ignored issue is spatial autocorrelation (SAC). SAC can derive from biotic interactions, biotic traits such as dispersal limits and narrow ecophysical niche (e.g., certain soil type), and other specialized habitat use (Merckx, Steyaert, Vanreusel, Vincx, & Vanaverbeke, 2011). While incorporating biotic traits such as slow migration can improve the performance of SDMs in mapping species'

realized niche spaces (Botkin et al., 2007), data representing biotic interactions and biotic traits may not always be available, and residual SAC needs to be accounted for. Failure to account for SAC can lead to overstated predictions of species' habitat loss when extrapolated to future conditions (Crase, Liedloff, Vesk, Fukuda, & Wintle, 2014; Zhao, Boomer, Silverman, & Fleming, 2017).

Because the giant panda (*Ailuropoda melanoleuca*) is specialized to feed on bamboo, it is important to consider its biotic interaction with bamboo for conservation planning. Recent studies that directly connected giant panda distributions with climatic metrics predicted a severe habitat loss of 37–62% (Fan et al., 2014), 60% (Songer, Delion, Biggs, & Huang, 2012), or 53–71% (Li et al., 2015). However, ingoring giant panda's interaction with bamboo as well as other habitat preferences may result in overrated importance of climatic variables. Some studies have included biotic interactions (e.g., bamboo distributions) in their models, but did not consider bamboo's dispersal limit caused by its unique clustered distribution pattern and/or ignored the effect of critical anthropogenic variables. The recommendations from most of these studies is to establish new nature reserves outside of the current network to mitigate the threats of climate change (Fan et al., 2014; Songer et al., 2012; Tuanmu et al., 2013). These recommendations can be costly and risky, however, if the models used in these studies overestimated shifts in giant panda or bamboo distributions under climate change.

The goal of our study is to evaluate the response of giant pandas to future climate change. Our objectives are to: (1) examine the effects of climate on bamboo distributions while accounting for residual SAC; (2) identify the relative contributions of biotic interactions, anthropogenic disturbances, and climate in driving giant panda distributions; (3) predict future distributions of bamboos and giant panda under climate change, and (4) provide recommendations for conservation strategies. This study has strong implications to the conservation of giant panda, as well as other species that are predicted to experience a significant shift in their critical resources as a result of climate change.

2 | METHODS

2.1 | Study area

We used the distribution of giant pandas in the Qinling Mountains (hereafter referred to as Qinling) with a 10 km buffer zone as our study area. Two species, wood bamboo (*Bashania fargesii*) and arrow bamboo (*Fargesia qinlingensis*), are the main diet of giant pandas in Qinling. Both bamboo species have long flowering intervals and, between flowering events, they use asexual reproduction to spread outward along rhizomes at a rate of approximately <10 m per year (Sun, 2011).

2.2 | Species data

For giant pandas, we obtained distribution information from the Shaanxi Forestry Department (SFD). The SFD recorded giant panda signs along 424 transects (approximately 1,360 km total length) distributed across both protected and unprotected habitat in Shaanxi Province during 2010–2012 (SFD, 2017). The study area covered all existing or potential habitat for giant pandas and included forests inside and outside of eighteen nature reserves (Figure 1). Giant pandas were labeled "present" if giant panda signs (e.g., fecal and foraging site) were recorded.

For arrow and wood bamboo, 5,998 vegetation plots were surveyed across the Qinling. The plot locations were along the giant panda transects and regularly spaced across the entire potential range of giant pandas (Figure 1). Field staff recorded a bamboo species as present when it occupied an area larger than $10\,m \times 10\,m$ (SFD, 2017).

Because both the giant panda and bamboo surveys yielded presence-only data, in order to use statistical algorithms requiring both presence and absence values, we generated random pseudo-absent locations (Iturbide et al., 2015). Pseudo-absent locations for giant panda were randomly generated at 2 km from the presence points according to its home range size (approximately $5\,km^2$; Pan et al., 2014). Due to the relatively low dispersal ability of bamboos, pseudo-absence sites for bamboos were randomly selected without distance limitation from presence sites. We acknowledge that such presence–absence data represent indices of giant panda or bamboo distributions rather than true occupancy status.

2.3 | Climate data

We constructed models using current climatic conditions (average for 1950–2000, Supporting Information Table S1) and projected to the future (given by WorldClim for the range 2061–2080, hereafter referred to as future). We selected two widely used Representative Concentration Pathways (RCP) scenarios for our study: RCP4.5, an optimistic scenario where carbon emissions peak around 2040, resulting in 4.5 W/m^2 radiative forcing by 2100; and RCP8.5, a pessimistic scenario, which reflects high carbon, resulting in 8.5 W/m^2 radiative forcing by 2100 (Moss et al., 2010). We used three global climate models (hereafter referred to as GCM) for future climatic conditions: ACCESS1.0, CCSM4, and HadGEM2-AO (hereafter referred to as AC, CC, and HD, respectively) (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005).

2.4 | Environment data

We reviewed previous studies for the giant panda and the two bamboo species (Hull et al., 2014; Pan et al. 2014; Wang et al., 2014; Zhang et al., 2011, 2017), and identified abiotic
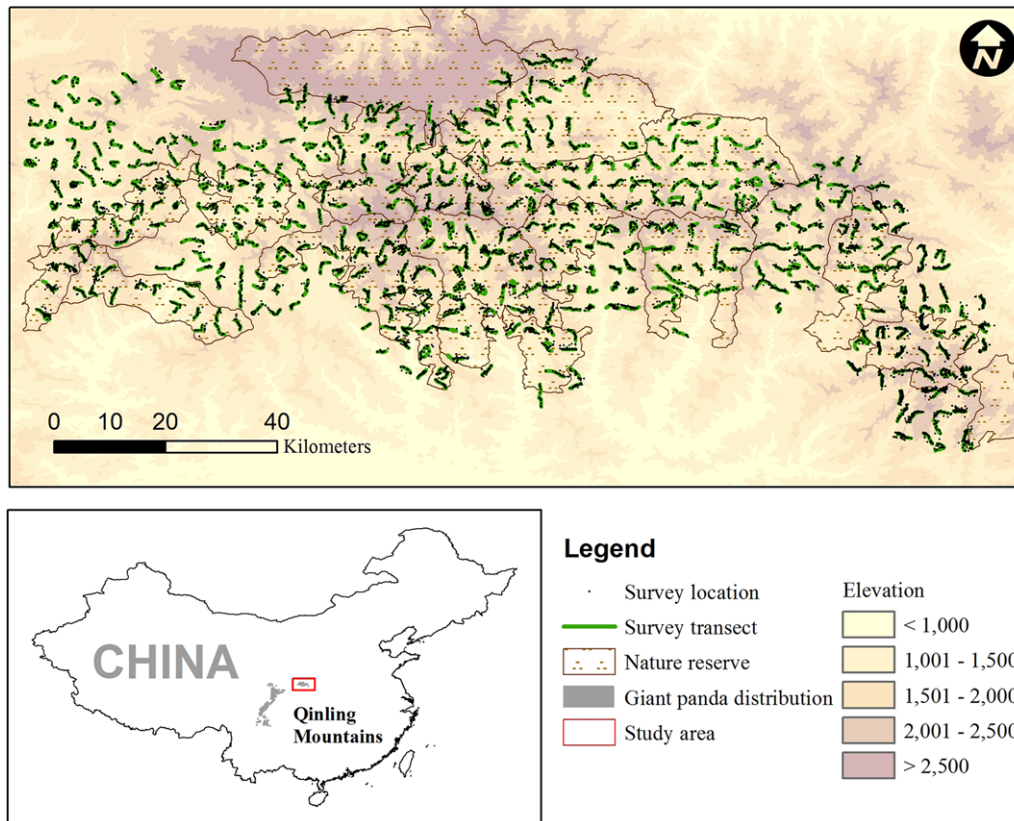
FIGURE 1 Sampling design for giant panda and bamboo species distribution in the Qinling Mountains. Government staff conducted 424 line transects across 18 nature reserves across the Qinling Mountains, covering the known giant panda distribution area with an approximate 10 km buffer. See methods for transect details. Known distribution of giant pandas is indicated in insert map

(e.g., elevation and slope), biotic (e.g., bamboo presence for giant panda), and anthropogenic (e.g., road transportation and construction for giant panda) variables that have been shown to affect their occupancy (Supporting Information Table S2). We used a 30-m resolution digital elevation model (Global ASTER, 2009) to delineate the slope, aspect, and terrain ruggedness using ArcToolbox in ArcGIS 10.2 (ESRI, 2011). Georeferenced data of nature reserves, human residences roads, and mining locations were obtained from the SFD. All the layers (Table S2) were finally standardized to 500 m × 500 m spatial resolution using ArcToolbox in ArcGIS 10.2.

2.5 | Modeling current and future bamboo distributions

Prior to modeling bamboo and giant panda distribution, we conducted a four-step variable selection to reduce the multicollinearity of remaining climatic and nonclimatic candidate variables (see details in Supporting Information 1) using a Variance Inflation Factor (VIF) method (García, García, López Martín, & Salmerón, 2015). We excluded any variable that had a VIF value greater than 5 from further analyses (Shiu, 2006).

To model the current bamboo distribution, we first compared the discriminative performance of an environmental-only model (hereafter ENV) that do not account for residual SAC, and a residual autocovariated model (hereafter RAC), which included an autocovariate term derived from the residuals of the ENV model (Crase et al., 2014). We used an ensemble modeling approach (Pliscoff, Luebert, Hilger, & Guisan, 2014), in which six modeling algorithms were used: artificial neural network (ANN), generalized linear model (GLM), boosted regression tree (BRT), maximum entropy modeling (MAXENT), multivariate adaptive regression splines (MARS), and random forest (RF). Discriminative performance was assessed under a 10-fold process using two cross-validated performance metrics, the AUC (area under curve of the receiver operating characteristic [ROC]; Fawcett, 2006) and the TSS (true skill statistic; de Oliveira, Rangel, Lima-Ribeiro, Terribile, & Diniz-Filho, 2014). We plotted Moran's I correlogram (Legendre & Legendre, 2012) to further quantify the remaining spatial autocorrelation in model residuals and validate the model performance.

To forecast future bamboo distributions, we modeled bamboo distributions using three GCMs and two RCPs (IPCC, 2012). Since the asexual reproductive dispersal for our focal bamboo species was relatively low, we used the current

autocovariate in the predictive functions for RAC models. To better demonstrate the species' distribution change, we used a threshold that maximized the sum of modeling sensitivity and specificity to transform the species occurrence probabilities to binary presences/absences predictions (Cantor, Sun, Tortolero-Luna, Richards-Kortum, & Follen, 1999).

2.6 | Modeling current and future giant panda distributions

With the bamboo model outputs, we used the same ensemble modeling method, and constructed three modeling approaches to predict current giant panda habitat: climate-only models that connect giant panda distribution with only climatic variables; bamboo-ENV model that incorporates ENV bamboo model output as well as other critical habitat preferences; and bamboo-RAC model in which RAC bamboo model output and other habitat preferences were added. To predict future giant panda distributions, we used the same three GCMs and two RCPs.

3 | RESULTS

3.1 | Bamboo–environment relationship

Five climate variables and three nonclimate environmental variables were included in bamboo models after the collinearity test (Supporting Information Table S1). The correlogram and map of model residuals revealed a significant nonrandom pattern for arrow and wood bamboo ENV models (Supporting Information Figure S1). The Moran's I ($p < 0.01$) indicated higher similarities among survey locations within 20 km for arrow bamboo and 25 km for wooden bamboo (Supporting Information Figure S2). Incorporating the RAC term significantly improved the model's discriminative ability (Figure 2), and reduced residual SAC (Supporting Information Figure S2).

For both arrow and wood bamboo, BIO13 (precipitation of the wettest month) had the highest contribution in modeling species distribution (Table 1), followed by BIO1 (annual mean temperature) and BIO6 (min temperature of coldest month) for arrow bamboo and BIO6 and BIO15 (precipitation seasonality) for wood bamboo. Though the species–climate associations were similar between the ENV and RAC models, including RAC reduced the importance of climatic variables for both bamboo species (Table 1).

3.2 | Current and future bamboo distribution

Both modeling approaches estimated a similar expected number of occupied cells for current bamboo distributions (Figure 3). However, the occurrence probability under climate change scenarios diverged (Figure 3). For the wood bamboo, the ENV model predicted a 36–85% loss (RCP4.5: 36–85%, RCP8.5: 46–88%) in its distribution under climate change, while the RAC model predicted less decrease (RCP4.5: 0%; RCP8.5: 0–31%) than the ENV model. For the arrow bamboo, the ENV model predicted more habitat loss under both climate change scenarios (RCP4.5: 52–70% and RCP8.5: 62–85%) than the RAC model (RCP4.5: 0–39% and RCP8.5: 24–51%). According to RAC models, bamboo coverage in the central Qinling where the four most important nature reserves are located remains primarily bamboo covered (>85%).

3.3 | Biotic interactions in giant panda models

Seven nonclimatic variables, five climatic variables, and a bamboo layer were included in giant panda models (Supporting Information Table S2). The biotic interactions introduced into the giant panda models significantly improved the model's discriminative ability ($p < 0.01$; Figure 2).

According to both biotic models, four predictors besides climatic variables (i.e., bamboo distribution, distance to road, distance to large residences, and distance to nature reserves) had a model weight higher than 0.1 (Table 1). The occupancy probabilities of giant pandas were higher in areas with bamboo understory in or adjacent to nature reserves. Being close to residential areas and major roads significantly reduced the occupancy probabilities of giant pandas, which suggested the negative associations between giant panda and human infrastructure. Including bamboo distributions and other nonclimate variables lowered the importance of climate variables in explaining giant panda distributions, despite that these nonclimate variables are not highly correlated to climate variables (Table S1 and S2).

3.4 | Future giant panda distribution

Climate-only models of giant panda distribution predicted results similar to previous studies that giant pandas would lose 49–85% of their current habitat under a range of climate change scenarios (Figure 4). By contrast, the biotic models predicted less habitat loss (bamboo-ENV model: mean 42%, range 33–65%; bamboo-RAC model: mean 16%, range 12–34%). Though the results diverged, all three modeling approaches predicted major habitat loss in eastern Qinling Mountains.

4 | DISCUSSION

Our study revealed potential tolerance of giant pandas to future climate change. . Previous studies either used climate-only models (Fan et al., 2014; Songer et al., 2012) or nonspatially modeled bamboo distributions and climate variables
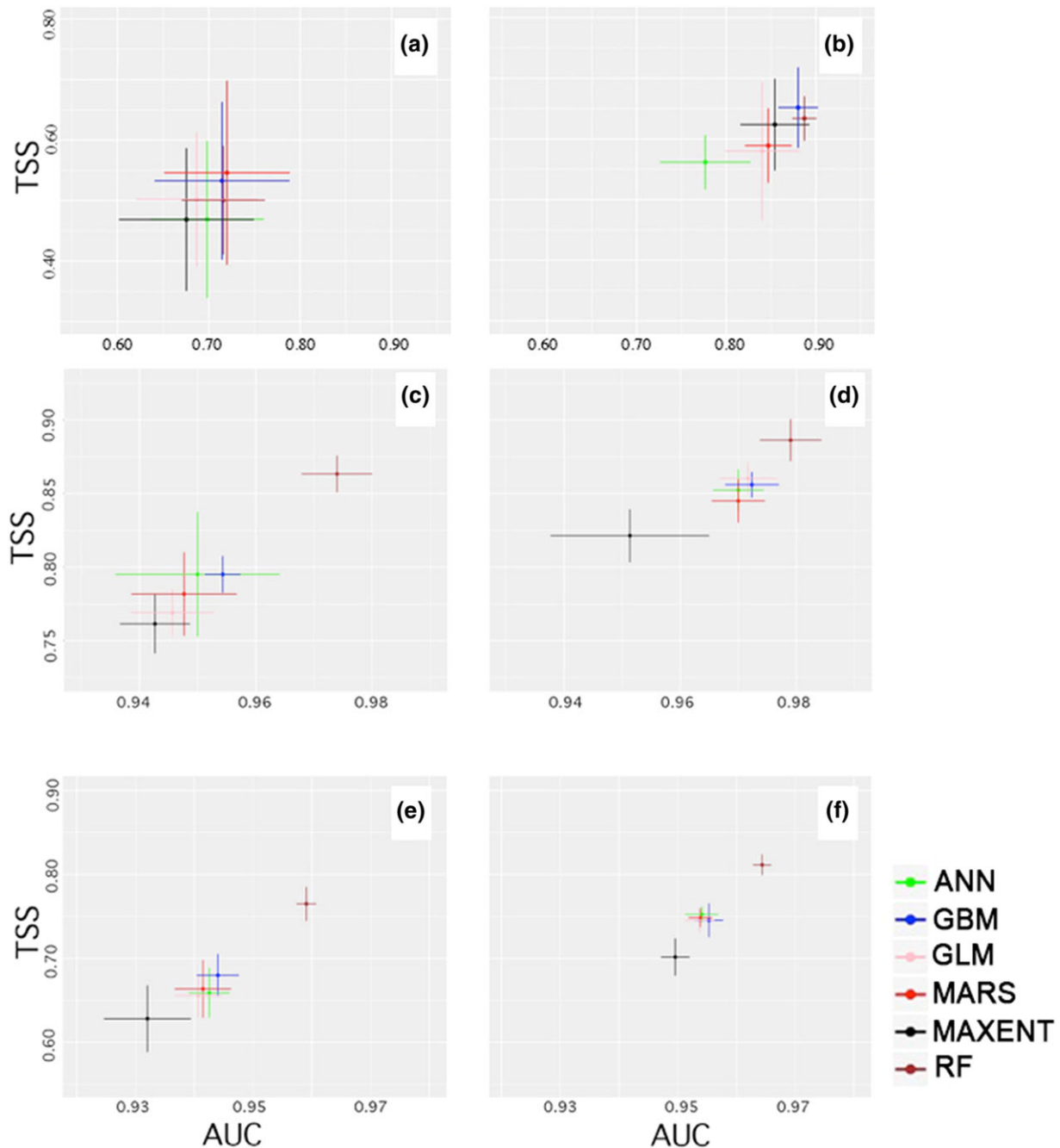
FIGURE 2 The cross-validation results using AUC and TSS to compare the performance of different modeling approaches. Each cross indicates the mean and *SD* of AUC and TSS tests for giant panda (A: climate-only model; B: bamboo-ENV and bamboo-RAC models), arrow bamboo (C: ENV model; D: RAC model), and wood bamboo (E: ENV model; F: RAC model) bamboo modeling. Higher values for both tests represent improved model performance when biological traits and a spatial term was incorporated in the modeling

(Li et al., 2015; Tuanmu et al., 2013) to model giant panda distributions. Both these methods produced dire forecasts and emphasized the effects of climate. Our climate-only giant panda models and ENV bamboo models predicted similar species' distribution changes to these previous studies. However, given their relatively poor discriminative performance and ignorance of important biotic interactions and residual SAC, we believe that they have overemphasized the effects

of climate change on giant panda distribution, and may lead to inappropriate recommendations for conservation actions.

We found that accounting for consumer–resource biotic interactions and residual SAC improved model performance and changed the forecasts. We acknowledge that our results are fundamentally different from previous studies (Fan et al., 2014; Li et al., 2015; Tuanmu et al., 2013), including some of the present authors (Songer et al., 2012). We found that

TABLE 1 The relative importance of the climatic and nonclimatic variables in modeling bamboo and giant panda distribution. Bold numbers indicate variables had a relative importance >0.1

Variable type	Variable	Arrow bamboo ENV	Arrow bamboo RAC	Wood bamboo ENV	Wood bamboo RAC	Giant panda Climate-only	Bamboo-ENV	Bamboo-RAC
Climate	Bio1	**0.21**	**0.15**	0.06	0.04	**0.26**	0.05	0.04
	Bio6	**0.14**	**0.10**	**0.19**	**0.10**	0.05	0.01	0.01
	Bio11	**0.11**	0.09	**0.14**	0.06	0.03	0.03	0.03
	Bio13	**0.32**	**0.25**	**0.39**	**0.19**	**0.36**	0.05	0.04
	Bio15	**0.11**	0.08	**0.16**	0.08	**0.32**	0.09	0.08
Land feature	Aspect	0.02	0.01	0.03	0.02	–	0.00	0.00
	Slope	0.06	0.04	0.02	0.02	–	0.01	0.01
	Ruggedness	0.01	0.00	0.00	0.00	–	0.00	0.00
Biotic	Bamboo	–	–	–	–	–	**0.36**	**0.38**
Anthropogenic	Residential area	–	–	–	–	–	**0.11**	**0.11**
	Road	–	–	–	–	–	**0.14**	**0.15**
	Mining site	–	–	–	–	–	0.02	0.01
	Nature reserve	–	–	–	–	–	**0.15**	**0.15**
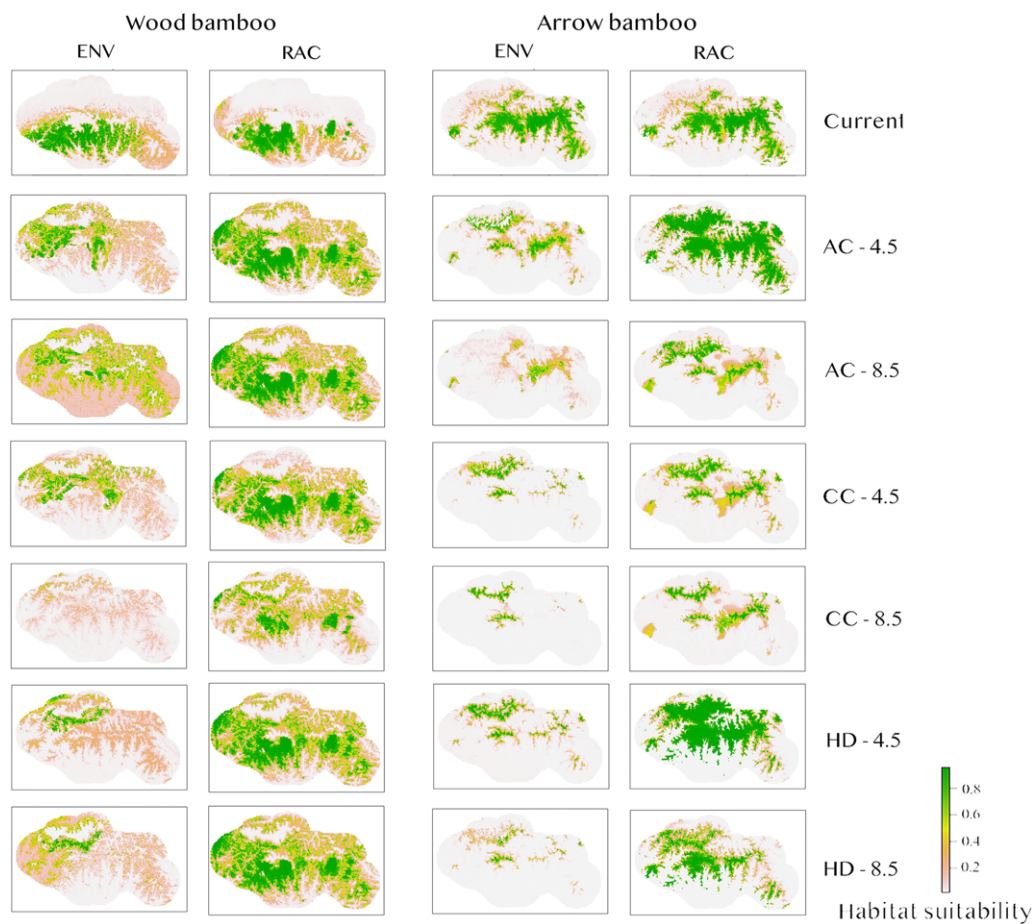
FIGURE 3 The occurrence probability for the arrow and wood bamboo under climate change scenarios. The ENV model forecasts a major decrease in both arrow and wood bamboo distribution under different GCMs and RCPs (indicated in right; see Methods for details). Combining the wood and arrow bamboo, the RAC model forecasts a more stable distribution
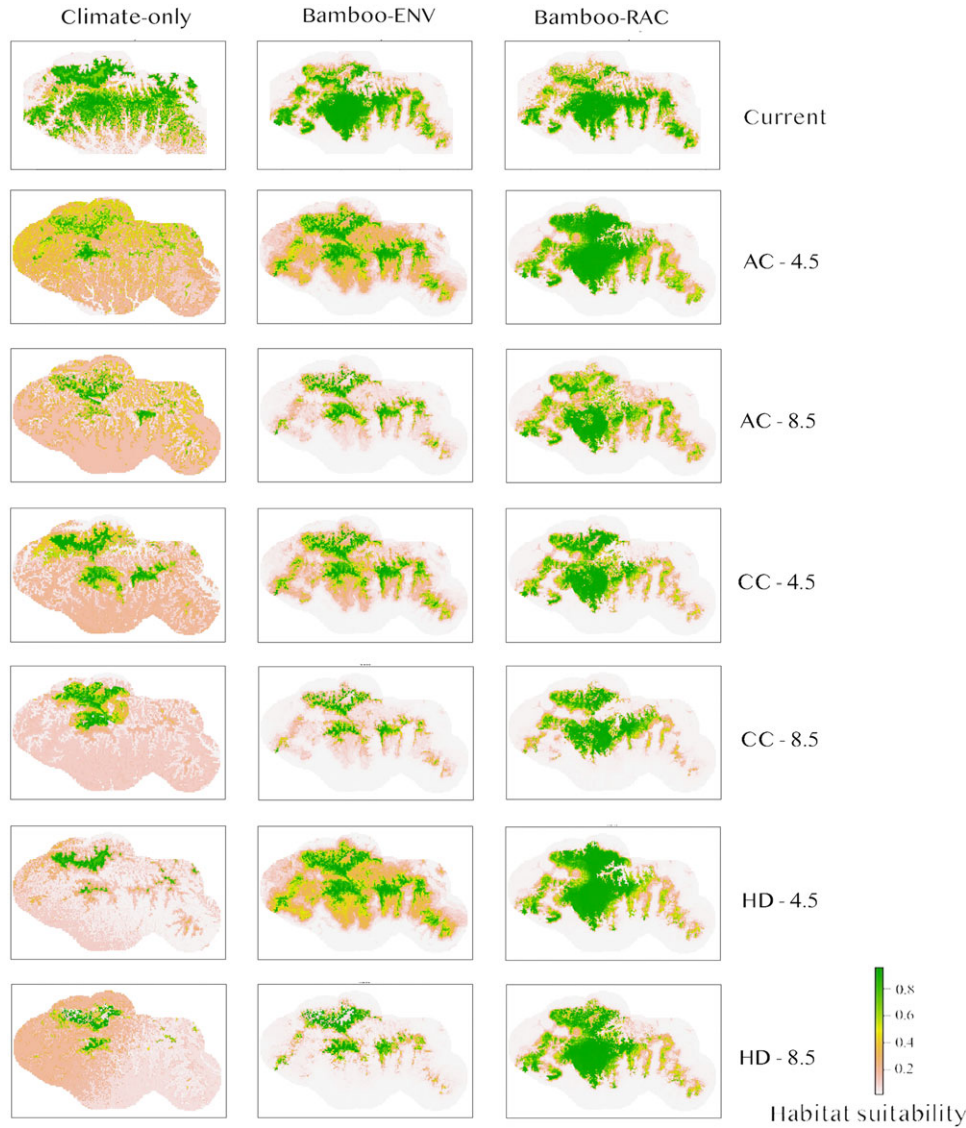
FIGURE 4 The occurrence probability of giant pandas under climate change predicted by climate-only, bamboo-ENV, and bamboo-RAC modeling approach. Climate-only models predicted similar results to previous studies under different three GCMs (AC, CC, and HD) and two RCPs (RCP 4.5 and 8.5), with giant pandas losing 49–85% of its current habitat under various climate change scenarios. The bamboo-ENV model predicted a mean habitat loss of 44% (33–65%), and the bamboo-RAC model predicted a habitat loss of 16% (12–34%), with new habitat patches located in northern Qinling Mountains

species environmental envelop (niche breadth) to be wider than the projected temperature/precipitation changes, so the species can potentially persist under the projected climatic conditions.

An advantage of our RAC approach is that the RAC term is calculated from the residuals of nonspatial models, and thus represents factors other than the covariates already included in the models such as land facet (Brost & Beier 2012; Wessels, Freitag, & Van Jaarsveld, 1999), tourism, and species interactions (e.g., livestock grazing) (Wang, McShea, Wang, & Li, 2015; Zhang et al., 2017), for which data are not available for the current study. In addition, the underground rhizome system of bamboos (He et al., 2000) may also cause residual

SAC in the models, but such effects are difficult to quantify and need to be accounted for using the RAC term. In contrast to the stems and leaves that might be more vulnerable to temperature change, the rhizome system is belowground, enabling the lateral buds to produce either canes or new rhizomes with less impact from aboveground temperatures. The asexual dispersal characteristics of bamboos may provide resilience of these species against unsuitable climatic conditions, a pattern that is consistent with the forecast of our RAC models. Due to the complex characteristics of the RAC term, future studies that focus on the effects of anthropogenic factors such as agriculture, livestock grazing and tourism on bamboo and giant panda distributions are warranted.

One of the most important principals in climate change mitigation is that the decision-making process should be based on the most comprehensive data and robust models (Nicholson & Possingham 2007). Other than proposing new nature reserves and planting bamboos in areas without current giant panda distributions, we suggest that the future conservation plans focus on reinforcing current strategy, with special emphasize on the adaptive management of fast developing tourism and other anthropogenic activities (e.g., farming and livestock grazing) in bamboo forest. For example, though the current habitats at lower elevations may remain suitable for giant panda if bamboo and forests remain, farmland moves up under warmer environment could be an emerging threat which warrants further attention. A great opportunity to better target our results in conservation practices lies in the Overall Plan of Ecological Civilization Systems Reform recently announced by Chinese government. This plan introduced major changes in the way natural resources are managed, including nationwide transfer payment for ecosystem service (PES), key ecological function regions zoning, and the establishment of three huge giant panda national parks (Ouyang et al., 2016). We strongly advocate that the newly proposed national parks as well as existing national reserves establish a comprehensive, adaptive framework of monitoring, modeling, and managing natural resources and human activities (including proposed tourism projects) (Xu et al., 2017). In addition, areas that are predicted suitable for giant panda and bamboo species, for example, the northern Qinling Mountains, should be identified as key ecological function regions with higher PES rates (Yang et al., 2018). We feel that these efforts would bear more positive results for climate change mitigation, for vulnerable giant pandas and beyond.

Despite the fast development of SDMs, many scientists and conservation practitioners still estimate species' range shifts based on the assumption that climate and few abiotic factors are the only determinants. We believe that this study has strong implications to establish a better understanding of climate-mediated range shifts for many other species around the world. Armed with such knowledge, scientists and conservation practitioners may be able to better identify conservation priorities to ensure the long-term survival of wildlife species.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.