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Climate-change impacts on understorey bamboo species and giant pandas in China's Qinling Mountains

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Climate change is threatening global ecosystems through its impact on the survival of individual species and their ecological functions[1,2]. Despite the important role of understorey plants in forest ecosystems[3–5], climate impact assessments on understorey plants and their role in supporting wildlife habitat are scarce in the literature. Here we assess climate-change impacts on understorey bamboo species with an emphasis on their ecological function as a food resource for endangered giant pandas (*Ailuropoda melanoleuca*). An ensemble of bamboo distribution projections associated with multiple climate-change projections and bamboo dispersal scenarios indicates a substantial reduction in the distributional ranges of three dominant bamboo species in the Qinling Mountains, China during the twenty-first century. As these three species comprise almost the entire diet of the panda population in the region, the projected changes in bamboo distribution suggest a potential shortage of food for this population, unless alternative food sources become available. Although the projections were developed under unavoidable simplifying assumptions and uncertainties, they indicate potential challenges for panda conservation and underscore the importance of incorporating interspecific interactions into climate-change impact assessments and associated conservation planning.

Like many understorey plants[3,4], understorey bamboo species are an essential component in many forest ecosystems[6,7]. They not only influence the species composition and structural complexity of forests[6,7], but also provide essential food and shelter for wildlife species, including one of the most endangered species in the world, the giant panda[8,9]. Deforestation and forest degradation are threatening the survival of about half of all bamboo species worldwide[10], and climate change may present an additional significant threat. Many bamboo species are vulnerable to climate change because their unusual extended sexual reproduction intervals (from 10 to 120 yr; ref. 11), along with limited seed dispersal ability[12], render them less capable of adjusting their distributions to the rapidly changing climate projected to occur within this century[1]. In addition, unlike other bamboo species with rapidly growing underground stems, many understorey bamboo species in mountain ecosystems have limited vegetative dispersal ability (for example, about 0.2–0.35 m yr^{-1} for *Bashania fargesii* and *Fargesia robusta*)[13,14]. Despite the vulnerability of bamboo species to climate change, knowledge of climate-change-induced dynamics of bamboo distribution and their effects on other species is lacking. This leaves an important knowledge gap of particular significance for biodiversity conservation efforts.

Understorey bamboo is a necessary component of giant panda habitat because pandas are extreme dietary specialists who devote most of their active time to feeding on large amounts of bamboo (up to 38 kg d^{-1}; refs 8,9). The dependency of giant pandas on understorey bamboo not only affects the present panda distribution[15,16], but is also believed to have driven historical changes in panda distribution, as bamboo distributions shifted in response to climate fluctuations[8,9]. Therefore, the tight bamboo–panda relationship provides an excellent opportunity to examine the potential cascading effects of climate-change-driven shifts in plant species distributions on the distribution of trophically dependent wildlife species.

Here we report an assessment of the potential impacts of climate change on bamboo distribution, and emphasize the cascading effects on giant panda habitat in the Qinling Mountains (located in the northern part of the present panda distributional range[15] and covering approximately a quarter of the remaining panda habitat[17]; Fig. 1a). Together, three bamboo species, Qinling arrow (*Fargesia qinlingensis*), dragon-head (*F. dracocephala*) and wooden (*B. fargesii*), account for more than 90% of bamboo cover in this region[15]. They constitute the main diet of the panda population in the region (about 270 panda individuals corresponding to 17% of the entire wild panda population[15]). Although this panda population lives in a region that, at present, has arguably the best habitat conditions and receives the best protection across the entire panda distributional range[17], it is both geographically (Fig. 1a) and genetically isolated[8] from other populations.

Our assessment contains three main steps. First, using bioclimatic models to associate bamboo-presence locations recorded in the field with bioclimatic variables derived from observational climatologies[18], we characterized and mapped present suitable climate conditions for each of the three bamboo species (Fig. 1b). The predicted climatically suitable areas (CSAs) effectively captured the observed bamboo-presence locations according to model-accuracy evaluations (see Supplementary Methods). The spatial patterns of predicted CSAs were also consistent with our understanding of the present bamboo distribution[8,15] (that is, Qinling arrow and wooden bamboos are distributed from 1,800 to 3,000 m, and from 900 to 1,900 m, respectively, with the distribution of

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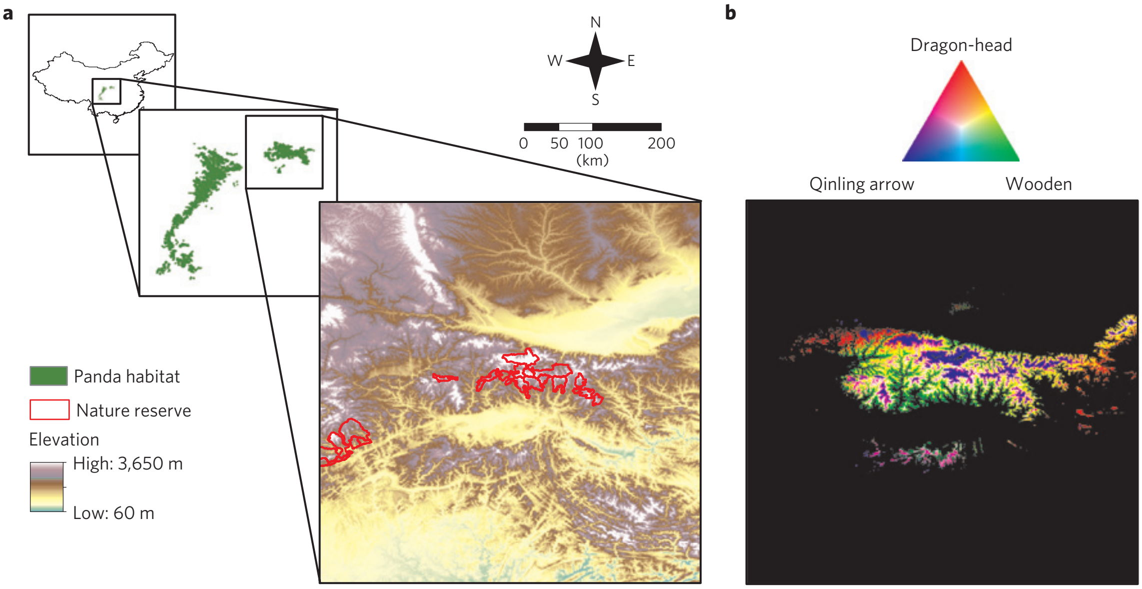

Figure 1 | Location and topography of the study area, and the baseline CSAs for the three bamboo species studied. a, The study area includes the Qinling Mountains and surrounding areas (5° × 5°). **b**, The CSAs for the Qinling arrow, dragon-head and wooden bamboos were obtained from the bioclimatic models under the baseline climate, and blue, red and green colours indicate the CSAs for the three species, respectively. The mixtures of the three colours indicate overlaps of the CSAs for individual species. The brightness of the colours shows the number of bioclimatic models (among the ten models with different presence data partitions) predicting pixels as suitable for each species, with brighter colours indicating a larger number of models.

dragon-head bamboo overlapping between 1,100 and 2,300 m; Supplementary Fig. S1).

In the second step, we applied the bioclimatic models to future climate projections for three time slices during the twenty-first century (2010–2039, 2040–2069 and 2070–2099) to evaluate potential temporal dynamics of the CSAs. We used the climate projections downscaled to about 1 km^2 resolution from four general circulation models (GCMs) for the Intergovernmental Panel on Climate Change (IPCC) third assessment report (IPCC TAR) under SRES A2 and B2 greenhouse-gas emissions scenarios (Supplementary Table S1). All four GCMs projected a warming climate within the study area over this century, but variations in diurnal temperature range and temperature and precipitation seasonality exist among the GCM projections (Supplementary Fig. S2). We also incorporated downscaled climate projections for the time slice of 2040–2069 from 15 GCMs (Supplementary Table S1) for the IPCC fourth assessment report (IPCC AR4) under the A2 greenhouse-gas emissions scenario. Although available only for a single time slice, downscaled projections from additional GCMs better capture the uncertainty associated with future climate projections, and, furthermore, allow for the differences in projections between IPCC TAR and IPCC AR4 GCMs to be assessed.

Our bioclimatic models with the climate projections from the four IPCC TAR GCMs indicate substantial changes in the CSAs during the twenty-first century with considerable variations among GCMs (Fig. 2 and Supplementary Fig. S3). Areas in the north and northwest of the Qinling Mountains become climatically suitable for the three bamboo species under the climate projections from two GCMs (that is, Commonwealth Scientific and Industrial Research Organisation (CSIRO)-Mk2 and Hadley Centre Coupled Model, version 3 (HadCM3)), especially for the lower-elevation species, that is, the wooden bamboo (Fig. 2 and Supplementary Fig. S3). However, within the Qinling Mountains region, our projections suggest that the CSAs shift to, and become restricted at, higher elevations (Supplementary Fig. S1). The projected CSAs under the climate projections from the 15 AR4 GCMs also indicate large GCM-related uncertainty about the extent and spatial distribution of CSAs of the three bamboo species (Supplementary Fig. S4). However, compared with the CSA projections associated with the TAR GCMs (Supplementary Fig. S3i–l), those associated with the newer GCMs show a higher degree of consensus as all projections indicate a reduction of CSA extent (Supplementary Fig. S4).

In the final step of the assessment, we estimated the amount of panda habitat on the basis of the projected CSAs of the three bamboo species. To capture the uncertainty of the ability of bamboo species to occupy their CSAs, we used two bamboo dispersal scenarios representing opposite and extreme situations (that is, no dispersal and unlimited dispersal). We then obtained the extent of suitable panda habitat by combining the occupied CSAs of the three bamboo species under the assumption that the occurrence of at least one species is sufficient for providing food and thus constituting habitat for the pandas. Results suggest that almost the entire panda habitat in the region may disappear by the end of the twenty-first century (80–100% projected decreases in median area) if bamboo species cannot colonize new CSAs beyond their present distributional ranges (Fig. 3b,d). With unlimited bamboo dispersal ability, a considerable amount of panda habitat is projected to persist over the entire century, but only if future climate is closer to the projections from two of the four GCMs (CSIRO-Mk2 and HadCM3), and then only with a lower greenhouse-gas emissions scenario (that is, SRES B2; Fig. 3a,c). In addition, all panda habitat projections associated with the 15 IPCC AR4 GCMs show substantial habitat losses (59–100% projected decreases in median area), with about half of the projections indicating an almost complete loss by the middle of this century under both bamboo dispersal scenarios (Fig. 4). Compared with the habitat projections derived from the IPCC TAR GCMs, those associated with the AR4 GCMs, including those obtained from newer versions of the TAR GCMs (CSIRO-Mk3.0 versus CSIRO-Mk2 and Canadian Global Climate Model (CGCM)3.1 versus CGCM2), indicate more pronounced losses of panda habitat (Fig. 4). This suggests that the projected habitat expansion associated with two of the older GCMs (CSIRO-Mk2 and HadCM3; Fig. 3) may be overly optimistic (Fig. 4a).

Potentially making the situation more difficult for the panda, no increase in CSAs for the three bamboo species within present nature

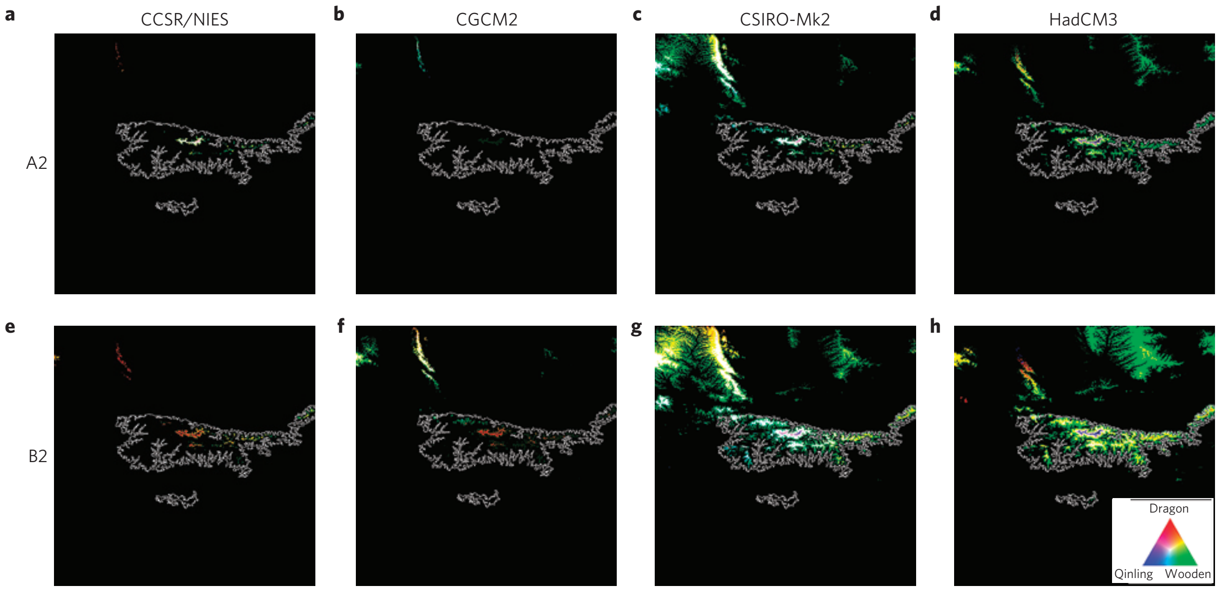

Figure 2 | Projected future distributions of CSAs in 2070–2099 for the three bamboo species studied under the climate projections from four IPCC TAR GCMs (Supplementary Table S1). a–h, The distributions were projected using bioclimatic models under the SRES A2 (**a–d**) and B2 (**e–h**) greenhouse-gas emissions scenarios. Blue, red and green colours indicate the CSAs for the Qinling arrow, dragon-head and wooden bamboos, respectively. See the legend of Fig. 1 for detailed information on the colour representation. For comparison, the outline of the CSAs for the baseline climate for all three species is shown in white. CCSR/NIES: coupled model from the Center for Climate System Research and the National Institute for Environmental Studies.

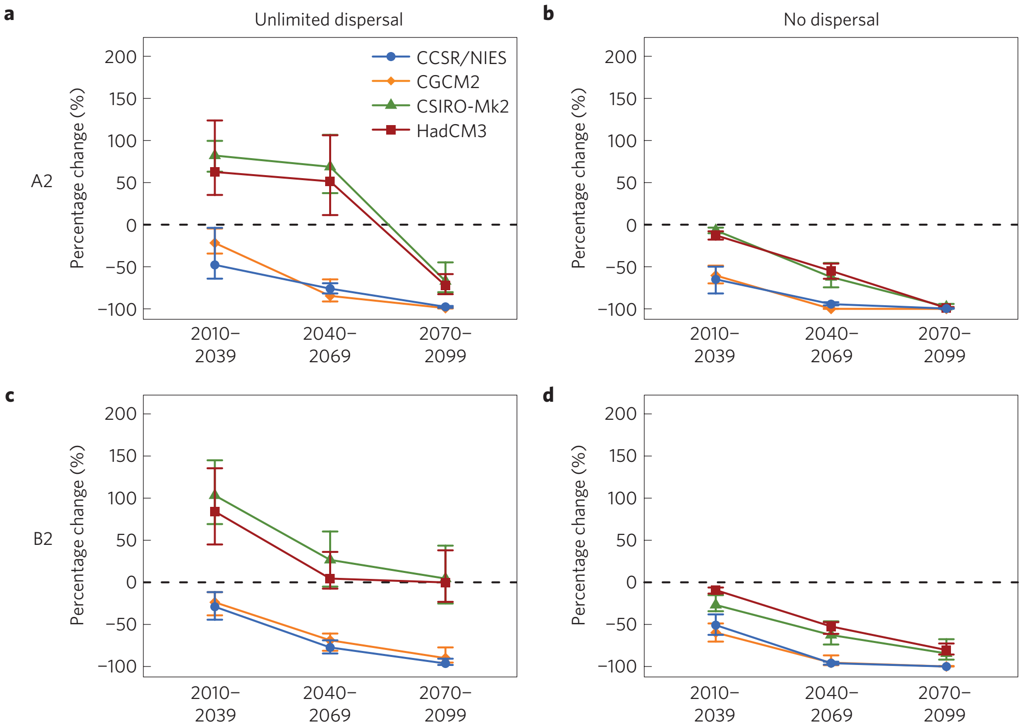

Figure 3 | Temporal dynamics of the projected changes in the area of giant panda habitat over the twenty-first century. The changes (%) are relative to the area of panda habitat (CSAs for the three bamboo species studied combined) under the baseline climate. **a–d**, Projections of panda habitat were obtained from the bioclimatic models for the three bamboo species under the unlimited- (**a**,**c**) and no- (**b**,**d**) bamboo-dispersal scenarios using multiple future climate projections for three time slices from four IPCC TAR GCMs (Supplementary Table S1), and under the SRES A2 (**a**,**b**) and B2 (**c**,**d**) greenhouse-gas emissions scenarios. Ten bioclimatic models were built for each bamboo species. The points indicate the median value and the vertical bars indicate the range of projected values obtained from the combinations of those models (that is, ten bioclimatic models for the Qinling arrow bamboo × 10 for the dragon-head bamboo × 10 for the wooden bamboo, thus 1,000 combinations).

reserves is projected under all model projections across this century (Supplementary Fig. S5). This suggests that although some areas may become climatically suitable for the bamboo species under a changed climate (Fig. 2 and Supplementary Fig. S3), most of them may lie outside the present network of nature reserves. In addition, the remaining CSAs are projected to be distant from present

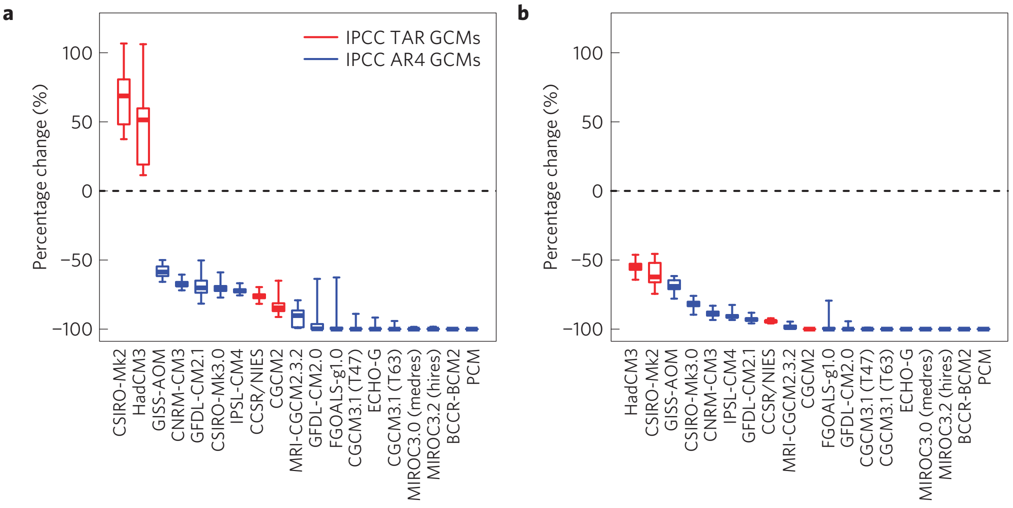

Figure 4 | GCM-related uncertainty of projected changes in giant panda habitat area for the time slice of 2040–2069 under the SRES A2 greenhouse-gas emissions scenario. The percentage changes are relative to the area of panda habitat (CSAs for the three bamboo species studied combined) under the baseline climate. **a**,**b**, The projections were obtained from bioclimatic models for the three bamboo species under the unlimited- (**a**) and no- (**b**) bamboo-dispersal scenarios and under multiple future climate projections from four IPCC TAR and 15 AR4 GCMs (Supplementary Table S1). Ten bioclimatic models were built for each bamboo species. Each boxplot shows the maximum, 75th percentile, median, 25th percentile and minimum of the projected values obtained from the combinations of those models. BCCR-BCM: Bjerknes Centre for Climate Research-Bergen Climate Model; CNRM: Centre National de Recherches Meteorologiques; ECHO-G: coupled ECHAM4 atmosphere and HOPE ocean model; FGOALS: Flexible Global Ocean-Atmosphere-Land System model; GFDL: Geophysical Fluid Dynamics Laboratory; GISS-AOM: Goddard Institute for Space Studies-Atmosphere–Ocean Model; hires: high resolution; IPSL: Institut Pierre Simon Laplace; MIROC: The Model for Interdisciplinary Research on Climate; medres: median resolution; MIR-CGCM: Meteorological Research Institute-Coupled Atmosphere–Ocean General Circulation Model; PCM: Parallel Climate Model.

bamboo distributional ranges and panda habitat (Fig. 2g,h). With a long history of intense human activities surrounding the Qinling Mountains, keeping the projected CSAs from human disturbance, and maintaining or re-establishing ecological connectivity among those areas will be difficult. This fragmented landscape may thus hinder the range shifts of bamboos and pandas in response to climate change.

As a global icon of biodiversity conservation, the giant panda has attracted unparalleled conservation efforts and resources for reducing its habitat loss and degradation due to land use/cover change. However, the projected loss and shift of CSAs for the bamboo species during the twenty-first century indicate that climate change may become an additional threat to the giant pandas, thus posing a challenge for their conservation. As the bamboo species evaluated constitute, at present, almost the entire diet of giant pandas in this region[8,15], the pandas may face a shortage of food, unless they can find alternative food resources. Although giant pandas have survived large-area die-offs of single bamboo species by shifting their home ranges and foraging on non-affected bamboo species[8,16], they may face regional extinction if climate change, as projected by this study, induces simultaneous die-offs of multiple bamboo species. Although the geographic isolation of the study area may prevent the dispersal of bamboo species from other mountain regions, other species, especially those growing at lower elevations, might have the potential to occupy the areas dominated at present by the three species evaluated. However, almost all lower-elevation species in the study area belong to the genus *Phyllostachys*[19], which the giant panda at present avoids consuming[20]. The only other species known to constitute suitable food for pandas in this region (that is, *Fargesia nitida*)[15] is distributed at present at very low densities in small patches. Long-term monitoring and further studies are needed to assess the potential of this species to substitute the three dominant bamboo species under a changed climate as an alternative food resource for the panda population in the study area.

Like all other assessments of potential climate-change impacts on species distributions, the present study is limited by a number of underlying assumptions and uncertainty in model projections[21]. The extended sexual reproduction intervals of the bamboo species evaluated (for example, 70–75 years and about 50 years for the wooden and Qinling arrow bamboos, respectively)[22] make niche conservatism[21] a reasonable assumption. In addition, our projection ensemble has captured, at least partially, the uncertainty associated with future climate projections and bamboo dispersal ability. However, the ensemble cannot address all assumptions or capture the full range of associated uncertainty. For example, our definition of giant panda habitat is based on two simplifying assumptions that may introduce additional uncertainty. We assumed that panda habitat is determined only by the presence of bamboo species and the presence of any one of the three species evaluated is sufficient to support the panda's demand for food. However, the presence of bamboo is not the only factor determining panda habitat. Many other factors, such as forest cover, human activities and pandas' climatic tolerance and dispersal ability, further limit panda distribution[8,23]. Similarly, because giant pandas forage different bamboo species in different seasons[8], a single bamboo species may not be able to support giant pandas year-round. Therefore, with these assumptions, our assessments probably overestimate the extent of panda habitat or underestimate panda habitat loss due to climate change.

In addition, our models did not account for the potential influence of overstorey tree species on bamboos' responses to a changed climate, or capture the potential benefits of the release of bamboo species from their natural enemies under a changed climate[24]. Nevertheless, although characteristics of the forest canopy may alter resource availability and microclimate for bamboo species at small spatial scales, at larger scales climate conditions are usually the dominant determinant of species distribution[25]. Furthermore, although the bamboo population may benefit from enemy release, these effects on the giant panda may be very limited because pandas do not strongly compete for bamboo with other natural enemies of bamboo species[8].

Many studies have observed or projected climate-change-induced distributional shifts or extinction of individual species[1,2,26]. However, the cascading effects of these changes through interspecific interactions, especially those across trophic levels, are usually neglected[27]. This may result in an underestimation of the ecological impacts of climate change, thus compromising the benefits obtained from present biodiversity conservation efforts. This study underscores the importance of incorporating these cascading effects not only in impact assessments but also in conservation planning in the face of climate change.

Methods

We collected bamboo-presence data in 293 field plots covering the elevational range of the distributions of three dominant bamboo species within the Qinling Mountains, which form the northern limit of the present giant panda distributional range (about 21,300 km^2). We used gridded bioclimatic variables (30 × 30 arc s), which were based on weather station records from 1950 to 2000, obtained from the WorldClim database[18] to represent the baseline climate in the study area. Using the maximum entropy algorithm[28], we generated bioclimatic models to map baseline CSAs for each bamboo species based on the presence data and seven bioclimatic variables (Supplementary Table S2) that are biologically and statistically important for characterizing the three bamboo species' CSAs (Supplementary Methods). To incorporate the uncertainty introduced by potential sampling bias, we generated 10 bioclimatic models for each species with different data partitions, each of which contained a randomly selected 70% of the bamboo presence data. The remaining 30% were used for validating the models and determining thresholds (corresponding to a 10% omission error) to convert the continuous model outputs (presence probability) into binary values (suitable or unsuitable). We then projected the spatial distribution of the CSAs over the twenty-first century by applying the bioclimatic models to future climate projections that were statistically downscaled to a 30 × 30 arc s resolution from 19 GCMs (Supplementary Table S1) based on the spatial interpolation of anomalies between 30-year averages of temperature and precipitation for future and present-day simulations[29]. We obtained the portion of CSAs occupied by each bamboo species under two dispersal scenarios. With the unlimited-dispersal scenario a bamboo species can occupy all CSAs, whereas with the no-dispersal scenario it cannot occupy the areas beyond its baseline CSAs. Although neither of these two scenarios reflects the real dispersal ability of the bamboo species, they capture the range of uncertainty in terms of bamboo dispersal ability. Finally, we combined the occupied CSAs of the three bamboo species to define suitable panda habitat and calculated the percentage change of the area from the baseline values for every combination of the CSA projections for the three bamboo species (10 × 10 × 10 bioclimatic models × 2 dispersal scenarios) under multiple future climate projections (4 (or 15) GCMs × 2 (or 1) greenhouse-gas emissions scenarios). See Supplementary Information for detailed methods and associated references.

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Author contributions

M-N.T., A.V., J.A.W and J.L. conceived the ideas and designed the analyses; M-N.T., A.V., Y.L., W.X. and Z.O. collected the data; M-N.T. built the models and performed the data analyses; all authors wrote the paper.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to J.L.

Competing financial interests

The authors declare no competing financial interests.