



Climate change challenges the current conservation strategy for the giant panda



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ABSTRACT

The global total of protected areas to conserve biodiversity is increasing steadily, while numerous studies show that they are broadly effective. That said, how will current conservation strategies work, given the current and expected changes to the global climate? The giant panda is a conservation icon and exceptional efforts protect its remaining habitats. It provides a unique case study to address this question. There are many studies on the projected loss of habitats as climate warms, but few consider the geographical arrangement of future habitats, current protected area, and species' dispersal abilities. Most alarmingly, we expect much greater habitat fragmentation after climate change. Here, we combine long-term data on giant pandas with climate-change scenarios to predict future habitat loss and distribution in the Min Shan of Sichuan and Gansu, China. We employ metapopulation capacity as a mechanistic measure of a species' response to habitat fragmentation. The results show that climate changes will lead to 16.3 ± 1.4 (%) losses of giant panda habitats. Alarmingly, 11.4% of the remaining habitat fragments would be smaller than the extinction threshold area as the extent of fragmentation increases nearly four-fold. The projected fragmentation of giant panda habitats predicts 9% lower effectiveness inside the protected area network compared with that outside of reserves. A 35% reduction will occur in future effectiveness of reserve networks. The results challenge the long-term effectiveness of protected areas in protecting the species' persistence. They indicate a need for integrating both natural processes and dynamic threats over a simple reliance on individual static natural reserves.

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1. Introduction

The Earth's climate has already warmed rapidly over the past century. Climate change will rearrange the current global distribution of climatic conditions. Some climates will disappear entirely, and new climates will appear across wide regions (Loarie et al., 2009). Evidence from the paleoecological record of past climate change, together with recent observed range shift and modelled simulations of future range shifts, indicate that species are moving

their ranges. They will do so increasingly in the future. This geographic rearrangement of species will substantially alter present-day patterns of biodiversity (Bellard et al., 2012; Bennie et al., 2013; Early and Sax, 2011; Hole et al., 2009; Parmesan, 2006).

Protected areas are the cornerstones of biodiversity conservation (Joppa et al., 2008). Presently, there are more than 155,584 terrestrial protected areas worldwide, covering 18.4 million km² (12.5%) of the terrestrial realm (Watson et al., 2014). Such approaches typically protect the present-day snapshot of species distributions and assume that threats to species are static (Hannah et al., 2007; Hole et al., 2009; Pressey et al., 2007; Thomas et al., 2012).

Shifting geographic ranges are likely to have profound consequences for the effectiveness of the protected area networks as

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species shift their ranges outside a site's boundaries in response to their individual climatic tolerances (Hole et al., 2009). This will overestimate the effectiveness of protected areas in promoting the species' persistence, and underestimate species' susceptibility to anthropogenic drivers of global change. Combined these raise the spectre of even greater extinction rates than those presently (Pressey et al., 2007; Thomas et al., 2004).

It has not been clear how effective will be the present protected areas in promoting the species' persistence remain as the climate changes. Moreover, while many studies predict how habitats will shrink as the climate warms, few do so against the realities of where protected areas are, how habitats are fragmented, how these will change, and how species will disperse between them. These are among the most compelling challenges to conservation efforts in protecting the species' persistence.

To address these, we consider the case study of the giant panda (*Ailuropoda melanoleuca*) in the Min mountains of Sichuan, China (henceforth, simply the Min Shan). An extensive protected area network exists here. It provides a unique opportunity to ask: how the effectiveness of protected area networks will change in promoting the species' persistence as the climate warms? In particular, we show that understanding the existing and future distributions of habitat fragments provides essential insights.

2. Methods

2.1. Min Shan protected area networks for giant pandas

The giant panda is one of the world's most endangered and instantly recognized flagship species. It once lived throughout most of the lowland subtropical evergreen forests of eastern and

southern China, northern Vietnam, and northern Myanmar (Hu, 2001). Now, they remain in bamboo-forest habitats across six mountain ranges at the edge of the Tibetan Plateau in the western Chinese provinces of Gansu, Shaanxi, and Sichuan (Fig. 1) (Hu, 2001; Schaller, 1993). Climate change, habitat loss and fragmentation during the last two centuries have reduced their distribution and fragmented their populations (Hu, 2001; Li and Shen, 2012). Currently, the majority of wild populations survive in about 30 isolated populations. Thirteen of these have fewer than 10 individuals. Such isolated, small populations have a high risk of extinction. Some 10–20% of these populations have disappeared since the 1970s (Li and Shen, 2012).

Min Shan is a transitional zone between the Tibetan and the Sichuan plains in the upper Yangtze ecoregion of China. It covers an area of 34,623 km² (31°25'N–33°42'N, 102°45'E–105°38'E). We chose the Min Shan for three main reasons. First, these mountains support half of the giant pandas. Second, from 1951 to 2008, the temperature in the Min Shan increased by 0.16 °C per decade, for a total of 0.8 °C. The mean precipitation decreased by 34.6 mm per decade (Wang et al., 2010). Climatic variation and change along the altitudinal gradient from 496 m to 5588 m provide an excellent natural laboratory to investigate the role of potential impacts of climate change. Third, the Min Shan is a “flagship” protected area network. By 2009, 22 nature reserves had been established protecting 71% of the panda population and 57% of their habitats (Li and Shen, 2012). Giant pandas have received exceptional financial and technical support from the Chinese government and many international organizations such as the World Wildlife Fund. The performance of protected areas networks in the Min Shan stand for the success or failure of unprecedented conservation efforts made by the Chinese government and many international organizations.

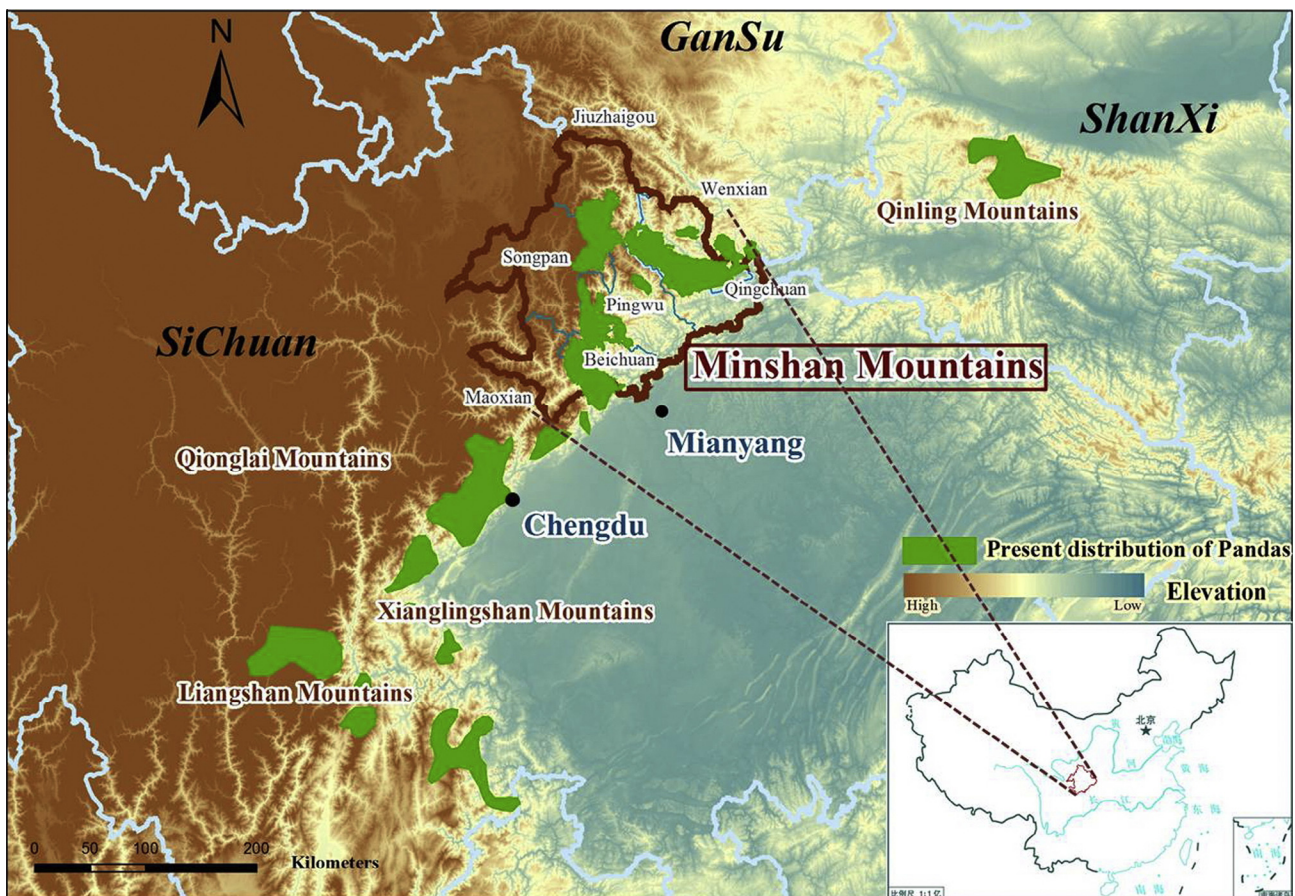


Fig. 1. Present distribution of giant pandas and the Min Shan in China.

2.2. Giant panda distribution data

We assembled the database on giant panda occurrence, representative of the distribution of each giant panda in the Min Shan, from the third (1999–2003) and second (1985–1988) national surveys, and from annual monitoring data. The third national survey involved all panda habitat, and used Global Positioning System, Remote Sensing and Geographic Information System to identify the panda's distribution. A stratified random sample of 2-km² grids across the Min Shan was laid out, and at least one continuous U-shape or Z-shape transect line of at least 0.75 km on each grid was designed (State Forestry Administration, 2006). The transect lines covered all the known and potential panda habitats. The second survey calculated the number of pandas based on a sample area, and then extrapolated the distribution from this figure. Since 1997, the monitoring surveys in Min Shan were conducted four times a year across more than 150 permanent transect lines (Gu et al., 2004).

We estimated panda numbers through a comprehensive analysis of the individuals seen in the wild, measurement of bamboo-bites in their droppings, home range, and interviews with local people (State Forestry Administration, 2006). The average bite-size of an individual panda did not vary by more than a few millimetres, and different individual pandas had different average bite sizes (Yin et al., 2005). Therefore, it was possible to collect and measure the average bite-size of bamboo pieces in faeces collected during the survey. Combining this information with average home range sizes for pandas, we can determine the minimum number of pandas in a given habitat block (State Forestry Administration, 2006).

2.3. Environmental variables

Feeding habitats, land cover, bamboo cover, topographical factors (such as elevation, slope and aspect), human activities (distance from residential areas and roads) and climate all affected the panda's presence (Liu et al., 1999; Loucks et al., 2003; Shen et al., 2008; Xu et al., 2006). Bamboo constituted 99% of its diet (Dierenfeld et al., 1995; Schaller, 1993; Zhu et al., 2011). Pandas must ingest large amounts (10–18 kg) of bamboo daily (Dierenfeld et al., 1995; Hu, 2001). Bamboos were dominant plants in the understory of the temperate montane broad-leaved forests, the temperate montane broad-leaved and conifer mixed forests, and the subalpine conifer forests to which pandas are now restricted (Li and Shen, 2012; Taylor et al., 2004). We derived the bamboo cover from the second (1985–1988) and third (1999–2003) national survey for giant pandas.

Forests provided shade for bamboo clones and dens for the panda (Li and Shen, 2012). Without forest shade, elevated evapotranspiration likely stresses bamboos (Taylor et al., 2004), with the bamboo culms becoming stunted and very dense. Pandas avoided such places when feeding (Schaller, 1993). Being so densely packed, bamboos precluded any canopy tree regeneration (Taylor et al., 2004). We obtained the land-cover data including the forest types from six Landsat Thematic Mapper images (2000–2001) from the Remote Sensing Satellite Ground Station, Chinese Academy of Sciences. We employed 1:50,000 topographic maps to georeference the images, and used an unsupervised classification. A 1:50,000 land-use map (1990s) was used to guide interpretation. In order to refine and correct the classification, we organized a workshop with local experts on land-cover, remote sensing and GIS. Ground-truthed surveys with 450 GPS points provided validation. We classified the forest types as coniferous forest, mixed coniferous and deciduous broad leaf forest, deciduous broad leaf forest, evergreen broad leaf forest, brush, grassland, and croplands. The accuracy of the land-cover classification was 84% (Shen et al., 2008).

Giant pandas showed strong preferences for relatively level terrain when feeding. Level ground makes it easier for them to sit while manipulating bamboo, and likely minimizes the energetic costs of moving on steep slopes (Hu, 2001; Schaller, 1993). We developed elevation, slope and aspect data that were representative of the topography from the digital elevation model (DEM) with a resolution of 30 m based on 1:50,000 topographic maps. We obtained the DEM data from the National Geomatics Center of China (NGCC).

Human activities had large impacts on the persistence of giant pandas. Distances from residential areas and roads measured the degree of human activities, and the impacts to giant pandas decreased with increasing distance (Liu et al., 1999; Shen et al., 2008; Xu et al., 2006). We obtained the residential areas and road distribution data from the Forestry Bureaus of Counties in the Min Shan. We compiled the climate, bamboo cover, land-cover, topographic and anthropogenic geographic information systems (GIS) layers, and resampled them to an oblique Mercator projection at 30 m resolution using ArcGIS, which ensuring that all layers were aligned at the same resolution.

We employed six climatic variables to model the potential distribution of giant pandas: total annual rainfall, mean annual temperature (MAT), mean maximum temperature, mean minimum temperature, mean relative humidity and minimum relative humidity. The China Meteorological Administration supplied the meteorological data from 1951 to 2008 for the 12 weather stations in the Min Shan. The modern nation-wide network of weather observation stations in mainland China was established in the 1950s, so the 12 selected stations all had data available since then. We generated the layers of climatic variables through thin-plate spline interpolation of monthly climate data from climate stations at 30 m × 30 m resolution. The quality of the data was controlled using the method described by Feng et al. (2004). Missing data were filled using linear regressions based on data from neighbour stations. The data time series had no missing data and the highest correlation with the former data during the same period (Dong et al., 2012).

2.4. Climate scenarios

We modelled the environmental suitability for giant pandas under climate change scenarios for the periods of 2011–2100 according to China's National Assessment Report on Climate Change (The Committee of China's National Assessment Report on Climate Change, 2011). The Committee of China's National Assessment Report on Climate Change made the climate assessment based on the BCC-CSM and FGOALS models, and concluded that the assessment results were robust with high reliability. We estimated the mean annual temperature increase as 1.2 °C from 2011 to 2040, 2.6 °C from 2041 to 2070, and 4.4 °C from 2070 to 2100 under scenario 1. The mean annual temperature increases for scenario 2 increase by 1.2 °C, 2.3 °C, and 3.3 °C respectively. We estimated that the total annual rainfall will increase by 1%, 6%, and 10% for these periods under scenario 1, and by 3%, 4%, and 7% under scenario 2. Scenario 1 depicted a more heterogeneous world with a continuously increasing population and an atmospheric CO₂ concentration of 0.72 mg g⁻¹ in 2080. Scenario 2 focused on sustainability involving slower growth of the human population and an atmospheric CO₂ concentration of 0.56 mg g⁻¹ in 2080 (The Committee of China's National Assessment Report on Climate Change, 2011).

2.5. Modelling

We modelled the environmental suitability of giant panda under climate change scenario 1 and 2 based on the maximum

entropy algorithm (MaxEnt) (Phillips et al., 2006). Based on environmental data and presence-only occurrence data, MaxEnt, the general-purpose machine-learning program, predicts environmental suitability for a particular species (Phillips et al., 2006). Through choice of feature classes and regularization of environmental parameters, MaxEnt captures and controls the complexity of the model, even though the input data are noisy, or the parameters are correlated (Luo et al., 2015; Phillips et al., 2006). Thus, when estimating species potential distributions, MaxEnt showed excellent performance. It outperforms many other algorithms, such as GLM, Bioclim, GARP, and Occupancy Model (Phillips and Dudik, 2008). These models are inefficient in dealing with data acquired from different sampling methods (Phillips et al., 2006).

We considered that MaxEnt is an effective means by which we could estimate the impacts of climate change on giant panda distribution patterns. We employed MaxEnt to estimate the probability that giant panda was present in a site, conditional on environmental variables based on the presence-background data (Hijmans and Graham, 2006; Phillips et al., 2006). We ran the models by randomly generating 70% of the giant panda occurrences as a training dataset and the remaining 30% reserved for testing the model results. We measured the model fit by the area under the curve (AUC) from the receiver operating characteristic curve (ROC). For a more robust estimate of the predictive performance, we ran ten cross-validation replicates and calculated the average AUC of the cross-validations. We examined the reliability of the independent dataset due to incorrect assigning of giant panda presence by the model training through the occurrence records.

We first input the training data and test data, the thirteen environmental variables layers (mean annual temperature (Tmean), mean maximum temperature (Tmax), mean minimum temperature (Tmin), annual precipitation (Ptotal), mean relative humidity (Mmean), minimum relative humidity (Mmin), elevation, slope, aspect, land-cover, bamboo cover, residential areas and roads distribution) into the model. Then, we ran the model by inputting the giant panda occurrence data and the environmental variables, with Jackknife testing. We used the logistic output of MaxEnt with suitability values ranging from 0 (unsuitable habitat) to 1 (suitable habitat). We chose the 10th percentile training presence as a suitability threshold, and we assumed that a grid cell was suitable if its suitability score was greater than the 10th percentile of training points. We adopted a jack-knife procedure to evaluate the relative importance of each predictor variable and the ability to predict correctly new ranges in the model. For the models, the ROC analyses revealed good performance by MaxEnt for both training AUC values (0.962 ± 0.0002) and test AUC values (0.940 ± 0.0013).

2.6. Giant panda's range responses to climate change

We quantified the potential range loss (currently suitable areas in terms of the number of 30 m grid cells projected to be lost), range gain (areas projected to become suitable), and range retained based on current potential ranges. We first extracted the altitude and latitude information of the centre position of each grid cell suitable for giant panda distributions through spatial analysis tools in ArcGIS. We then categorized and summed the total range area (number of grid cells) per altitudinal and latitudinal band. We qualified the shift of habitat using overlay, tabulate area and near tools in ArcGIS9.2.

2.7. Fragmentation and metapopulation capacity

We calculated the sizes of the habitat fragments in which pandas currently survive and in which they are likely be following climate change. We assessed the effectiveness of the protected areas by integrating the intersection of ecological process (dispersal) and

dynamic threats (climate change) in fragmented landscapes. We employed metapopulation capacity to quantify the landscape quality as a way of assessing the effectiveness of the protected area networks in supporting giant pandas (Hanski and Otso, 2000; Schnell et al., 2013). Metapopulation capacity measured the contribution of the spatial extent configuration of a landscape of habitat patches to the long-term persistence of a species living in those patches. Unlike statistics that simply described the distribution of fragments sizes, this metric incorporated information on a species' ability to disperse, the patch areas and their separation (Hanski and Otso, 2000).

Dispersal was the key process enhancing the long-term persistence of metapopulations in heterogeneous and dynamic landscapes (Hanski and Otso, 2000). We defined the inter-patch distances as the basis for the metapopulations colonization function in metapopulation models. To get metapopulation capacity for giant pandas in present and future habitats under climate scenarios 1 and 2, we first constructed the metapopulation functions, which required a survival function as a function of inter-patch distance. To get the metapopulation functions, we extracted the patch area and inter-patch distance functions of the landscapes into a matrix M with terms, and summarized them as a single value λm , the leading eigenvalue of the matrix m .

$$m = \begin{cases} f(D_{ij})A_jA_i^z & j \neq i \\ 0 & j = i_{ij} \end{cases}$$

where D_{ij} was the inter patch distance matrix. $f(D_{ij})$ was the function of the distance between patches i and j . A was the patch area matrix of the giant panda habitats. We chose $f(D_{ij}) = e^{-0.48D_{ij}}$ as the survival functions (Fig. 2) for giant pandas. The function was the exponential decay functions (Pan, 2002; Schnell et al., 2013; Van Houtan et al., 2007), which implied small survival at long distance movement for giant pandas in fragmented habitats.

So the survival matrix was the survival functions, that means the survival matrix = $f(D_{ij}) = e^{-0.48D_{ij}}$,

And $M = \text{survival matrix} * \text{transpose}[\{\text{patch areas}\}]$
 $\cdot \{\text{patch areas}^{0.5}\}$

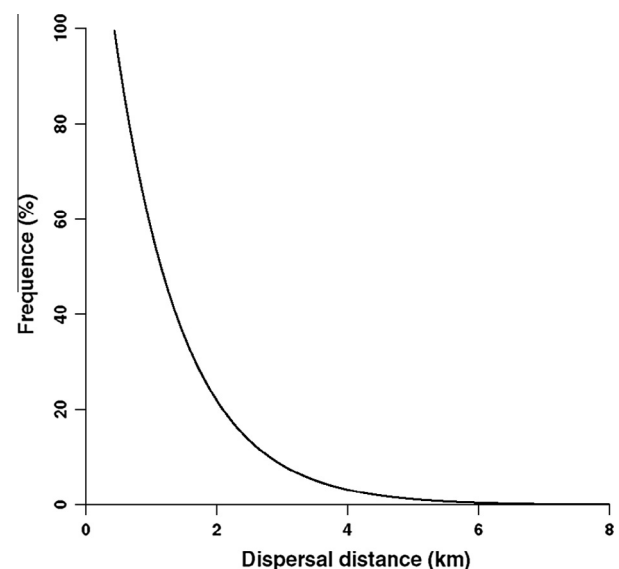


Fig. 2. Survival function for giant pandas. Metapopulation functions require a survival function that is a function of inter-patch distance. The percentage of the captured giant pandas (Y-axis) decreases with increasing distance from original capture (X-axis) (according to Pan, 2002). The survival function is an exponential decay function, $y = e^{-0.48x}$, ($r^2 = 0.979$), y = the percentage of the captured giant pandas, x = inter patch distance matrix.

Then we calculated the metapopulation capacity by the leading eigenvalue of M .

3. Results

We explored how the metapopulation capacity changed under climate change, and whether the protected area networks can increase the metapopulation capacity for supporting the giant pandas or not. We based the analysis on the nearly 30 years of field-work on life history, population dynamics, social behaviour, and habitat requirements for giant pandas in the Min Shan and other mountains (Hu, 2001; Li and Shen, 2012; Shen et al., 2008; State Forestry Administration, 2006).

3.1. Declines in habitat ranges

Giant pandas would experience both pole-ward and elevation shifts in their ranges. From 2011 to 2100, climate change would drive 67% of the panda range upward on average $358 (\pm 64)$ m or northward by $563 (\pm 131)$ m (Fig. 3) in the Min Shan. Overall, we predicted that pandas would experience larger range contractions than range expansions. The projections indicated that 16.3 ± 1.4 (%) loss of giant panda habitats would occur in the Min Shan (Fig. 3). We predicted that 85% loss of habitats would be at elevations lower than 3000 m, where the distributions of giant panda were centred in the Min Shan. Some, 17.5 ± 1.2 % of the losses would occur in the nature reserve network (Figs. 3 and 4). By comparison, only 5% of panda habitat would be added in the Min Shan (Fig. 4).

We identified seven potential panda habitats (PH 1–7) under climate change scenarios that should be protected in the future. The potential habitat area was 55–255 km², distributed from 1100 m to 3000 m in elevation. The forest coverage of the potential habitats was more than 30%, but the bamboo coverage was less than 20%, some less than 10% (PH 3, 4, 5) (Table 1).

3.2. Habitat fragmentation and extinction threshold

The projections showed that giant panda habitats would greatly fragment from 2011 to 2100 under climate change scenarios. The mean patch size (1568 ± 730 ha) of future (2011–2100) habitats was significantly smaller ($p < 0.05$) than that of the present

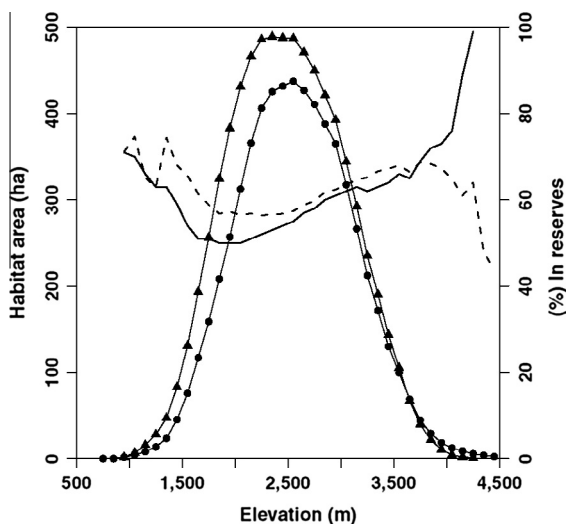


Fig. 3. The area of the present (solid line, triangles) and future habitat (2011–2100) (solid line circles), and the percentage of the areas in natural reserves (solid line) under climate change scenarios (dashed line) along different elevations in Min Shan.

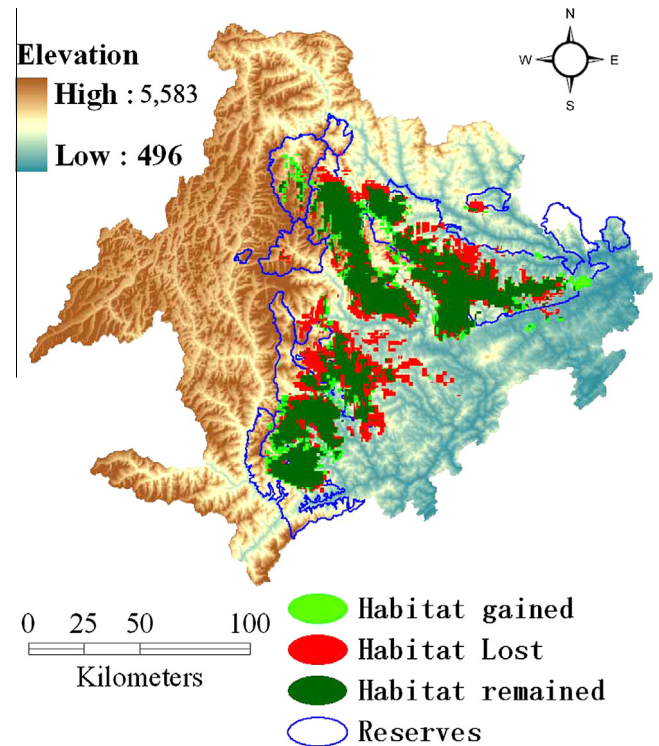


Fig. 4. Habitats lost and gained for giant pandas under climate change scenarios from 2011 to 2100 in Min Shan. Current habitat is the dark green areas plus the red ones and future (2011–2100) habitats are dark green plus light green. The metapopulation capacity decreases because while the panda loses some small (<400 ha) isolated patches (red), its potential gains (light green) include even smaller (<400 ha) and relatively isolated ones. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Proposed potential habitats (PH) for giant panda conservation outside nature reserves under climate change in the Min Shan.

PH	Area (km ²)	Elevation (m)	Slope (°)	Forest cover (%)	Bamboo area (%)
PH 1	70.1	2525 ± 569	36.8 ± 11	48	13.1
PH 2	130.3	3277 ± 496	35.6 ± 9	37	11.8
PH 3	55.1	1100 ± 192	30.1 ± 10	69	0.2
PH 4	102.9	1709 ± 293	33.0 ± 9	60	2.2
PH 5	33.3	1552 ± 232	32.9 ± 10	28	4.5
PH 6	66.8	2031 ± 304	29.0 ± 9	82	12.2
PH 7	254.5	2379 ± 578	35.0 ± 10	62	20.1

(3859 ± 1095 ha) (Fig. 5). Habitat loss and fragmentation would make it less likely to meet the threshold condition supporting viable populations in the Min Shan. Previous work shows that the extinction threshold area – the minimum area of habitat required for one giant panda to persist in a landscape – is 400 ha (Hu, 2001; Shen et al., 2008). At present, only 3% of the patches were smaller than this extinction threshold area. From 2011 to 2100, however, 11.4% of the patches would fragment into patches less than this size (Fig. 5). With climate change, the extent of fragmentation increased nearly fourfold.

3.3. Effectiveness of the protected area network

Climate changes would lead to habitat loss – especially the isolated patches of less than 400 ha – and increased fragmentation. Both reduce the giant panda's metapopulation capacity within

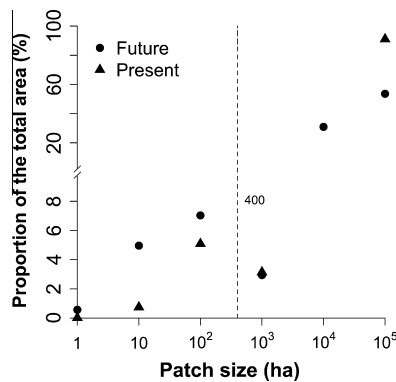


Fig. 5. The patch areas of different patch size for the present and future habitats (2011–2100) under climate change scenarios for giant pandas in Min Shan. Four hundred ha (400 ha) indicates the minimum area of habitat required for one giant panda to persist in a landscape.

the landscape of the Min Shan. We found that when integrating the dispersal processes of giant panda between fragmented patches into the climate change projections, the present metapopulation capacity of the landscape for giant pandas in protected area networks was 9% lower than that outside the protected area networks in Min Shan. Moreover, compared with present capacity, the 21st-century projections under scenarios indicated that the climate change would lead to 35 (± 2)% ($p < 0.001$) decline in the metapopulation capacity of protected areas networks during the next 90 years from 2011 to 2100. Furthermore, from 2011 to 2100, the metapopulation capacity in protected areas networks was 40 (± 14)% ($p < 0.01$) lower than that outside the networks of protected areas under climate change scenarios in Min Shan. Climate change would diminish the effectiveness of the protected area network in the 21st-century in the Min Shan.

4. Discussion

The giant panda enjoys a protected area network of 67 nature reserves. For nearly 15 years, China has implemented the Natural Forest Conservation Program (NFCP) and complemented it with the Grain-to-Green policy to protect all the remaining forests and to restore the degraded forests throughout the panda's range (Li and Shen, 2012). The forest area has expanded and non-forest area had decreased greatly across the giant panda's range (Liu, 2011). Yet, habitat loss and fragmentation continued to threaten its future (Hu, 2001; Li and Shen, 2012; Shen et al., 2008; Xu et al., 2006). Our results found that climate change would increase the giant panda habitat loss and fragmentation.

Our results show that climate change would drive 67% of the giant panda range to move upward or northward in the Min Shan, and 16% of their habitats would be lost in this century. In the Qin Ling, the climate change would reduce the extent of a suitable habitat for giant pandas by up to 62%, and the minimum elevation of panda habitat would rise by 500 m (Fan et al., 2014). Other recent studies of the entire giant panda distribution area showed that 53–71% of the current habitats would be lost under the climate scenarios. They predict that future suitable habitats would likely be located in high-elevation areas in the Min Shan and Liang Shan (Li et al., 2015), and the suitable habitat gradually moves north under projected global climate change (Jian et al., 2014).

Bamboo and giant pandas had developed co-evolutionary traits that ensured their survival (Liu and Viña, 2014). Bamboo species have unusual extended sexual reproduction intervals, limited seed dispersal ability and limited vegetative dispersal ability (Taylor

et al., 2004; Yang et al., 2015). Bamboo may not be able to keep pace with the giant panda in response to climate change at the same velocity as they move in higher elevations or latitudes (Liu and Viña, 2014; Tuanmu et al., 2013). Consequently, the climate change would alter the present feeding interaction between giant pandas and bamboos. The consequences of such disruption may cause decoupled trophic interaction and the co-evolutionary traits between giant panda and bamboo, which would alter the composition and structure of ecological food chain (Lavergne et al., 2010). Pandas are strict dietary specialists and do not consume alternative foods, bamboo has no substitute in the giant pandas diet (Hu, 2001; Li and Shen, 2012). So the spatial mismatch of trophic interaction between the giant pandas and bamboo in turn could ripple through the entire panda-bamboo food chain, and multiply the extinction risks of giant pandas (Lavergne et al., 2010; Zarnetske et al., 2012).

Our assessments of potential climate-change impacts on giant pandas were limited, at least partially, by the uncertainty associated with bamboo dispersal ability. However, our definition of giant panda habitat was based on not only the presence of bamboo species, but also many other factors, such as forest cover, human activities and pandas' climatic tolerance and dispersal ability. Giant pandas forage on different bamboo species in different seasons. A single bamboo species may not be able to support giant pandas year-round (Tuanmu et al., 2013).

We found that from 2011 to 2100 under climate change scenarios, the mean patch size of future (2011–2100) habitats in Min Shan would be significantly smaller than that of the present (Fig. 5). A recent study on the whole giant panda distribution area suggested that the mean patch size of habitats would decrease from the current 652 ha to 531 ha, and the most severe fragmentation would drive the mean patch size of the habitats decreased by 30% (Li et al., 2015). The decreased mean patch size (451 ha) of the habitat in the whole giant panda distribution area would not be smaller than the extinction threshold area 400 ha under future climate changes. In the Min Shan, we found that at present, only 3% of the patches were smaller than the extinction threshold area of 400 ha. From 2011 to 2100, however, 11.4% of the patches would fragment into patches less than the extinction threshold area (Fig. 5). Similar problems affect other species. For instance, for African great apes suitable environmental conditions across the continent-wide African have dramatically declined in recent years, and the loss was caused mainly by patch size reduction (Junker et al., 2012).

Networks of protected areas remain the most valuable resource for conserving the species' persistence (Gaston et al., 2006; Hole et al., 2009; Joppa et al., 2008; Watson et al., 2014). We integrated dispersal between fragmented patches as the ecological process and the dynamic threats from climate change in metapopulation capacity models, to simulate the range expansion and metapopulation capacity of the giant panda within a "flagship" protected area network. We found that the present metapopulation capacity of the landscape for giant pandas in protected area networks was 9% lower than that outside the protected area networks. Climate change would lead to 35% decline in the metapopulation capacity of protected areas networks. The metapopulation capacity in protected areas networks would be 40% lower than that outside the networks of protected areas in the Min Shan during the next 90 years from 2011 to 2100.

Nature reserves have protected 67% of the giant panda population and 54% of the giant panda habitats (State Forestry Administration, 2006), but only 55% of the core habitats (Shen et al., 2008). Most of the nature reserves were designated based on the giant panda population size and their current distribution pattern. Moreover, reserves have been established often on economically marginal land based on non-strategic and usually

politically expedient decisions (Cowling et al., 1999). In most case, dispersal process of the giant panda or the connectivity between the fragmented habitats was ignored (Li and Shen, 2012). Dispersal plays a crucial role in tracking favourable environmental conditions for giant pandas. Metapopulation persistence (Lavergne et al., 2010), enhances the long-term persistence in heterogeneous and dynamic landscapes at regional scales in the context of a changing environments (Van Houtan et al., 2007). So outwardly, it look like that most of the giant pandas have been protected by the reserves, but some of their habitats have been fragmented severely by road isolation, bamboo flowering, bamboo shoots cutting, grazing and mining et al. (State Forestry Administration, 2006).

Our empirical tests, based on long-term monitoring data of giant panda population, habitat and meteorological data, supported the hypothesis that ignoring the intersection of ecological process such as dispersal and dynamic threats overestimated the effectiveness of protected area for giant pandas, and climate warming would amplify this overestimation remarkably. Our results have parallels in other studies. Jaguar (*Panthera onca*) in the eastern coast of Nicaragua are declining in habitat use due to agricultural encroachment, and the lack of effective habitat protection within Wawashan Nature Reserve is especially alarming (Petracca et al., 2014). Creation of large reserves free of hunting is the preferable solutions to achieve viable wild populations of California condors. Although some acquisitions of foraging habitat have been made, these reserves are still much too limited to effectively counter the lead poisoning threat to condors (Meretsky et al., 2000). Climate change predictions suggest that protected area systems for whooping cranes are designed based on current stable climatic conditions. They should be re-evaluated in light of current knowledge and future expectations. This is particularly true in regards to whooping cranes whose increasing population is no longer limited to present day protected area boundaries, particularly during migrations (Chavez-Ramirez and Wehtje, 2012).

Our findings highlighted the risks of ignoring the intersection of ecological process and dynamic threats in response to climate change for giant pandas. Giant panda habitats are a mosaic of habitats. Designing landscape mosaics by moving conservation from a site-based activity to landscape activity would complement the existing reserve network (Shen et al., 2008). It is necessary to enlarge the current reserves as well as to generate new reserves. Particularly vital will be corridors in the north-western Min Shan. The corridors would facilitate giant panda migration and colonization among the different habitat blocks to allow a response to climate change. These new reserves could potentially serve as stepping-stones or corridors to facilitate giant panda migration to the emerging new habitats (Li et al., 2015). To ensure long-term survival, it is necessary to restore the diminishing habitats in the giant panda reserves by forestry planning and protecting or introducing bamboos in climatically suitable areas. One of the approaches is to reforest the habitats with early succession pioneer species to create a canopy cover. After the canopy closure has occurred, species unable to tolerate open planting but representing a range of life forms and successional stages can be planted in the forests (Li and Shen, 2012).

Most studies for calculating species extinction risk assume that endangered species would go extinct when they no longer have suitable habitat (Hole et al., 2009). Yet, species extinction is often driven by synergistic processes (Pressey et al., 2007). Giant panda habitat, plants (including trees and bamboos), local residents, and policies are an integrated system, all of which, in turn, are influenced by macroscale factors, including climate, natural disasters (e.g., earthquakes, landslides) (Liu and Viña, 2014). Choosing a landscape-based approach, including both natural processes and dynamic threats in response to climate change over a simple

reliance on individual static natural reserves, may have important implications not only for giant panda in the Min Shan, but also for giant panda conservation in other areas of China. It may serve as a future framework for more comprehensive identification of habitats worthy of conservation in response to climate change, and help develop efficient landscape scale protection for other endangered animals worldwide. At the same time, collaboration across disciplines, which will require new administrative structures, new political agreements, jointly implemented research agendas, technology transfer, and training, is needed to answer the complex issues surrounding giant panda and other endangered animals worldwide conservation responses to climate change adequately (Hannah, 2010).

5. Conclusion

Our results targeted how climate change would interact with habitat fragmentation to threaten giant pandas and diminish the effectiveness of current conservation actions. We found that climate change would cause the loss and fragmentation of giant panda habitat. If the minimum amount of habitats continues to decrease beyond the threshold, it would increase the extinction risks of giant pandas. The results challenge the long-term effectiveness of protected areas, and indicated the urgency for integrating both natural processes and dynamic threats over a simple reliance on individual static natural reserves.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2015.05.004>.

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