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Forest-cover change rather than climate change determined giant panda's population persistence

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ABSTRACT

Climate and land-use change are two primary drivers of global biodiversity loss, which increase the risks of extinction for giant panda, an umbrella and one of the most heavily invested species in conservation. Understanding how giant panda responds to these environmental changes thus is critical for developing long-term effective conservation strategies. However, until now most studies focused on only the effects of either climate change or land-use change on giant panda. So, if the potential combined effects of these processes are greater than either of them, the current conservation recommendations would be inappropriate or misleading. Here, based on two national survey data on giant panda occurrences across nearly thirty years, we quantified the variation of giant panda's population persistence as a function of land-use (measured as forest-cover) change, climate (measured as annual mean temperature (MAT), annual mean summer temperature (MAST) and annual mean precipitation (MAP)) change, and the synergistic effect of land-use and climate change. We found forest-cover change explained 38.1% of giant panda's persistence variation, while climate change explained 20.1% of the variation, and the synergistic effect of land-use and climate change explained only 1.5% of the variation. We confirmed that forest-cover change surpassed climate change or the synergistic effect between them as the greatest force driving giant panda's population persistence. Our findings highlighted the urgent need for a more comprehensive understanding of the relative effects of climate change by integrating climate change and land-use change rather than just focusing on climate change in tackling global biodiversity loss.

1. Introduction

Stepping up action to safeguard biodiversity is an essential part of the achievement for the Sustainable Development Goals (Secretariat of the Convention on Biological Diversity, 2020). Climate and land-use change are the main drivers of biodiversity loss (Sala et al., 2000). From 1500 to 2005, habitat conversion and degradation had led to a decline in global biodiversity, with an average reduction of 13.6% in local richness and 10.7% in total abundance (Newbold et al., 2015). More recently, climate change has been recognized as the major driver of contemporary biodiversity loss (Northrup et al., 2019; Yalcin and Leroux, 2018). Evidence suggested that 20–30% of global plant and animal species faced a serious risk of extinction due to climate warming (Parry et al., 2007), and the continued warming will drive 16% of species to extinct by approximately 2100 (Urban, 2015). Growing evidence suggested that climate change will negatively interact with habitat loss and habitat fragmentation and synergistically contribute to the degradation of biological diversity (Brook et al., 2008).

As both the flagship and umbrella species, giant pandas (*Ailuropoda melanoleuca*) are facing great threats and challenges from habitat fragmentation and climate change (Li and Pimm, 2016; Swaisgood et al., 2017). Giant panda's habitats have become severely contracted and fragmented, and the habitat fragmentation creates small populations with increased spatial isolation, which increases giant panda's risks of extinction (Zhu et al., 2010). On the other hand, giant panda's habitat was becoming warming, and the warming had induced potential heat

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stress expand by 38–218% from 1960s to 2000s within the densely populated giant panda habitat (Zang et al., 2017), which is expected to amplify the effect of giant panda's habitat fragmentation (Zang et al., 2020).Yet most studies focused on the effects of climate change on giant panda (Fan et al., 2014; Shen et al., 2015; Tuanmu et al., 2012) or the effects of habitat loss and fragmentation on giant panda (Xu et al., 2017; Zhu et al., 2010) in isolation (Wang et al., 2018; Zhang et al., 2018). If the potential combined effects of these processes are greater than one of them, then the current conservation recommendations for giant pandas would be inappropriate or even misleading (Chazal and Rounsevell, 2009; Mantyka-pringle et al., 2012).

It is becoming increasingly clear that a single stressor perspective is inadequate when species are threatened by multiple, co-occurring stressors (Darling et al., 2010). Habitat loss and climate change are being the key threatening processes driving giant panda's population persistence (Swaisgood et al., 2017). Yet, until now, it is difficult to determine which stressor is the more important driver for long-term giant panda's population trends, and little is known about their synergistic effects on giant panda's populations due to the complexity underlying both processes (Zhang et al., 2018). If the combined effects of habitat loss and climate change are greater than the effects of each threat individually, or the effects of habitat loss outweighs the climate change, or vice versa, in determining giant panda's population trends, current conservation management strategies may be inefficient and even misleading.

Therefore, it is urgent to identify whether the interacting effects between climate change and habitat loss exist and, if so, to quantify the magnitude of climate change, habitat loss and their combined impact on giant panda's population. Here, we quantified the relative effects of climate change, habitat loss and their interaction in determining giant panda's population by integrating thirty-year time-series of giant panda's occurrences with land-use and climate change data. We used the generalized additive model (GAM) to quantify the variation in giant panda's local colonization and local extinction in each grid as a function of land-use change (forest-cover), climate change (annual mean summer temperature (MAST), annual mean temperature (MAT) and annual mean precipitation (MAP)), and the synergistic effect of land-use change and climate change. Understanding the effects of climate and land-use change on giant panda's population will inform us what actions we should take in the coming decades, which has critical implications for our ability to support and incorporate climate change adaptation measures into giant panda and other species' policy development and management response.

2. Materials and methods

2.1. Study area

We chose the Min Shan as the study area. Min Shan is a transitional zone between the Qinghai-Tibetan and the Sichuan plains. The total area spans approximately 9713 km^2 (31°25′N–33°42′N, 102°45′E–105°38′E). The protected area network composed of 27 nature reserves had been established for giant panda covering 42.8% of the giant panda's population and 26% of their habitat (Shen et al., 2015).

2.2. Giant panda occurrence data

We obtained giant panda occurrence data in the Min Shan from the second (1985–1988) and fourth (2011–2014) national survey on giant panda. The second national survey used lateral density estimation of biological populations to identify giant panda's occurrence. The fourth national survey identified giant panda's occurrence based on global positioning system, remote sensing, and geographic information system (National Forestry and Grassland Administration, 2021).

We estimated the change of giant panda occurrence by comparing the giant panda occurrence in each grid during the two national survey periods (1985–1988 and 2011–2014). We defined the spatial resolution of grids as 2000 × 2000 m, the minimum habitat area of giant panda (Shen et al., 2008; Shen et al., 2015; Zang et al., 2017). We assumed that the occurrence of giant pandas in a grid was present at the grid during the second or fourth survey period. Conversely, the lack of occurrence in a grid represented absence of giant pandas in the grid. We summarized the occurrence differences of giant pandas in each grid during the two national survey periods. We made four scenarios: 1) a “persistence” scenario if giant panda was present in a grid in the second national survey period (1985–1988) and giant panda remained present in the grid in the fourth national survey period (2011–2014) (i.e. this grid was always occupied); 2) a “loss” scenario when giant panda was absent in the grid in the fourth national survey period (2011–2014) (i.e. this grid was initially occupied but later unoccupied so it was presumed that giant panda in this grid was locally extinct); 3) an “absence” scenario if giant panda was absent in a grid in the second national survey period (1985–1988), and remained absent in the grid in the fourth national survey period (2011–2014) (i.e. this grid was always unoccupied); 4) a “gain” scenario when giant panda was present in the grid in the fourth national survey period (2011–2014) but that the grid was initially unoccupied in the second national survey period (1985–1988). We referred to the “gain” and “loss” of giant panda as the local colonization and local extinction, respectively (Fig. 1).

We generated giant panda's local colonization probability or extinction probability based on generalized additive model (GAM). The colonization probability was the colonized probability of the empty grid by giant pandas, and the extinction probability was the unoccupied probability of the occupied grid due to giant panda's absence. In the local colonization model, we chose the gained grids to analyze giant panda's colonization pattern across the second and fourth survey periods. In the local extinction model, we chose the lost grids to explore giant panda's extinction pattern across the second and fourth survey periods.

Additionally, we developed giant panda density distribution maps by performing a point density analysis, based on giant panda occurrence data from the second (1985–1988) and fourth (2011–2014) national survey through the spatial analyst tools in ArcGIS 10.2. We calculated giant panda's population persistence variation based on the density variation of each grid between the second (1985–1988) and fourth (2011–2014) national survey periods through the spatial analyst tools in ArcGIS 10.2.

2.3. Forest-cover change data

We obtained land-use data across Min Shan in 1980 and 2010 from the Resource and Environment Data Cloud Platform (Data Cente for Resources and Environmental Sciences, n.d.). The land-use data was interpreted from cloud-free Landsat MSS/TM images and classified into 6 primary categories and 25 subcategories with the spatial resolution of 30 × 30 m (Liu, 1996; Liu et al., 2005; Xu et al., 2014). The forests were classified into 4 subcategories with the accuracy greater than 90%, including the forest land with canopy coverage >30%, sparse woods with canopy coverage between 10% and 30%, shrub with canopy coverage >40% and height <2 m, and woodlands such as slash land and nurseries. We extracted the forest land with canopy coverage >30% in 1980 and 2010, respectively, and generated the forest land raster layers for giant panda's second and fourth national survey period.

We calculated the forest-cover of each grid with 2000 × 2000 m spatial resolution according to [((numbers of forest land cell with 30 m × 30 m resolution in the grid with 2000 × 2000 m resolution) × (30 m × 30 m)) / (2000 m × 2000 m)] * 100% during the second (1985–1988) and the fourth national survey (2011–2014) by using the “spatial join” analysis in ArcGIS 10.2. Then we estimated the change of forest-cover of each grid with 2000 × 2000 m spatial resolution as the difference of the forest-cover between the two national survey periods.

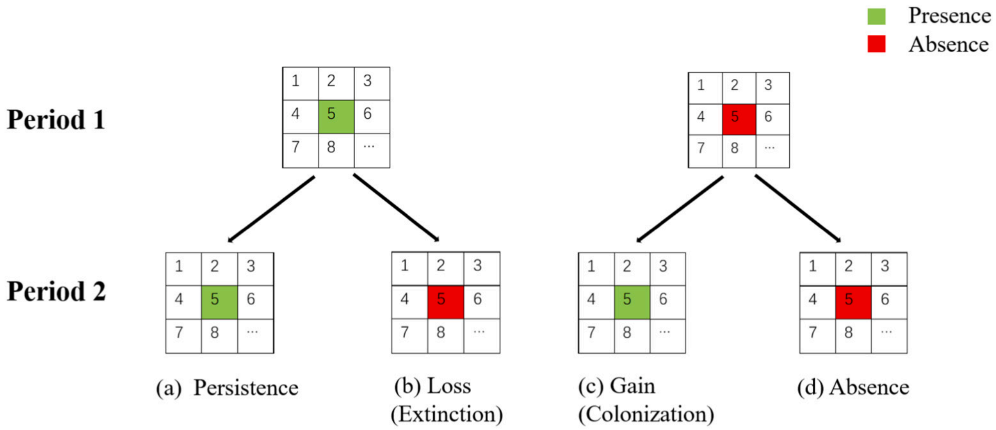

Fig. 1. The colonization and extinction of Giant Panda on the habitat patch. Four scenarios were set: (a) "persistence scenario", if the giant panda was present in a grid in the second national survey period (period1, 1985–1988) and the fourth national survey period (period2, 2011–2014) (this grid was always occupied); (b) "loss scenario", giant panda was present in a grid in the second national survey period but absent in this grid in the fourth national survey period (this grid was initially occupied and finally unoccupied, the giant panda in this grid was extinct). Conversely, (c) "gain" scenario, the giant panda was absent in a grid in the second national survey period but present in this grid in the fourth national survey period (this grid was initially unoccupied and finally occupied, the giant panda in this grid was colonized); (d) "absence" scenario, giant panda was absent in a grid in the second national survey period, and the giant panda remained absent in this grid in the fourth national survey period (this grid was always unoccupied). We referred to the "gain" (grid was initially unoccupied [0] and finally occupied [1]) (c) and "loss" (this grid was initially occupied [1] and finally unoccupied [0]) (b) of the giant panda as the local colonization(c) and local extinction (b), respectively.

2.4. Climate change data

We obtained the raster data of annual mean temperature (MAT) and annual mean precipitation (MAP) with a spatial resolution of 500 × 500 m across China during 1960–2015 from China Meteorological Station (Data Cente for Resources and Environmental Sciences, n.d.). The MAT and MAP were generated by spatially interpolating the daily recorded temperature or rainfall from more than 2000 meteorological sites across China. We extracted and calculated the average values of the MAT and MAP in each grid in Min Shan during 1965–1985 as the MAT and MAP for giant panda's second national survey period, and the average values of the MAT and MAP in each grid in Min Shan during 1991–2010 as the MAT and MAP for giant panda's fourth national survey period.

We obtained climate data of the annual mean summer temperature (June through August) (MAST) during 1960–2010 throughout the giant panda distribution area from China Meteorological Administration (2017). Temperatures, including daily maximum, minimum, and mean surface air temperature, were recorded daily at 02:00, 08:00, 14:00, 20:00. Daily maximum was the record at 14:00, daily minimum was the record at 02:00, and daily mean surface air temperature was the mean of these records. Less than 1% of the temperatures were missing. We used a simple linear interpolation algorithm to fill the data gaps spanning up to seven consecutive days. We used stepwise regressions to fill the data gaps based on the data with no missing data during the closet 5 years from stations. The data spanned more than seven consecutive days. We also examined the homogeneity of the daily maximum, minimum, and mean surface air temperature series for each station by the short-cut Bartlett test. Finally, we removed data from the nonhomogeneous stations to generate a final temperature dataset of daily maximum, minimum, and mean surface air temperature. We interpolated the temperatures of meteorological stations by performing a raster surface analysis in ArcGIS 10.2. We interpolated the temperatures by the linear lapse rate adjustment method, and we eliminated the interpolation errors of temperature resulted from elevation effects. After spatial interpolation of temperatures, we extracted and obtained over 18,628 maps of Min Shan for daily maximum, minimum, and mean surface air temperature, respectively (Zang et al., 2017).

Finally, we estimated the difference of MAST, MAT and MAP of each grid between 1965–1985 and 1991–2010 as the changes of the MAST, MAT and MAP between the two national survey periods. All climate change variables (MAST, MAT and MAP) of each grid were standardized to have a mean of 0 and a standard deviation of 1.

2.5. Statistical analyses

We tested the effects of forest-cover change, climate change, and the synergistic effect of forest-cover change and climate change on the local colonization and extinction of giant panda. We used GAM to explore the variation of giant panda persistence in each grid as the function of forest-cover change, climate change (MAST, MAT, MAP) and the synergistic effect of forest-cover change and climate change.

Since the local colonization or local extinction was subject to binomial distribution, we fitted a logistic GAM against forest-cover, climate and the synergistic effect of forest-cover and climate with the formula

$$log\left(\frac{Y_{it}}{1-Y_{it}}\right) = a_t + b_tF_{it} + c_tT_{it} + d_tF_{it} : T_{it} + s(Lon_i, Lat_i) + \varepsilon_{it}$$

where Y_{it} was the local colonization probability or local extinction probability of giant panda in the ith grid (For the local colonization, 0 denoted the absence of giant panda in the grid, i.e., extinction; 1 denoted the presence of giant panda in the grid, i.e., survival; conversely, for the local extinction, 1 denoted the absence of giant panda in the grid, i.e., extinction; 0 denoted the presence of giant panda in the grid, i.e., survival.) at time t (1985–1988 and 2011–2014); F_{it} was the forest-cover variable; T_{it} was the climate variable (MAST, MAT and MAP); $F_{it} : T_{it}$ was the interaction between the forest-cover and climate; $s(Lon_i, Lat_i)$ was a 2D smoothing function (with k value, dimension of the basis = 4) for modeling the spatial autocorrelation effects, and ε_{it} was uncorrelated random errors of zero mean and finite variance; a, b, c and d were constants (a was the intercept; b, c and d represented associations of forest-cover, climate, and the synergistic effect of forest-cover and climate with the local extinction or local colonization of giant panda). The forest-cover and climate variables were the average values of the standardized forest-cover and standardized MAST, MAT and MAP of last 20 years during the periods of 1985–1988 and 2011–2014.

We ran the logistic GAM to calculate the probability of giant panda's local colonization or extinction. Then, we explored the variation of giant panda's local colonization, local extinction and persistence in each grid as the function of forest-cover change, climate change, and the synergistic effect of forest-cover change and climate change (R package: mgcv). The forest-cover and climate change were calculated as the difference between the forest-cover, MAST, MAT and MAP in 1985–1988 with the forest-cover and MAST, MAT and MAP in 2011–2014. We used the variance analysis to assess the importance of forest-cover change, climate change, and the synergistic effect of forest-cover change and climate change. We performed the model diagnostics to test the basis dimensions of the smoothing terms and the residuals of GAM (R function: gam.check()) (Fig. A1).

3. Results

3.1. Giant panda's local colonization

Both forest-cover change and the synergistic effect of forest-cover change and MAP change significantly affected giant panda's local colonization probability, while the MAST change, MAT change, MAP change and the synergistic effect of forest-cover change and MAST change or MAT change were not significant ($p > 0.05$) (Table 1). The increase of forest-cover accelerated giant panda's colonization, and giant panda's local colonization probability increased by 50% when the extent to which forest-cover increased by 65% (Fig. 2a). Meanwhile, the synergistic effect of forest-cover and MAP change promoted giant panda's local colonization. Giant panda's local colonization probability increased by 50% when the extent to which the synergistic effect of forest-cover and MAP change increased by 80% (Fig. A2b). Forest-cover change exceeded climate change (MAST, MAT, MAP) or the synergistic effect of forest-cover change and climate change (MAST, MAT, MAP) as the greatest global force driving giant panda's colonization (coefficient = 0.01249) (Table 1).

3.2. Giant panda's local extinction

Forest-cover loss and the MAP change significantly affected giant panda's local extinction probability, while the effects of MAST change, MAT change and the synergistic effect of forest-cover and MAST change, MAT change or MAP change were not significant ($p > 0.05$) (Table 1). The loss of forest accelerated giant panda's extinction, but with the slowdown of the extent of forest-cover loss, giant panda's local extinction probability decreased (Fig. 2a). Giant panda's local extinction probability decreased by 50% when the extent to which forest-cover loss reduced 35% (Fig. 2a). The increase of MAP accelerated giant panda's extinction, and giant panda's local extinction probability increased by 50% when the extent to which MAP increased by 33% (Fig. 2b). Forest-cover change surpassed climate change (MAST, MAT, MAP) or the synergistic effect of forest-cover and climate change (MAST, MAT, MAP) as the greatest global driving force for giant panda's extinction (coefficient = −0.18050) (Table 1).

Table 1

Associations of forest-cover change (FC), annual mean summer temperature change (MAST), annual mean temperature change (MAT), annual mean precipitation change (MAP) and their interaction with the local colonization probability, the local extinction probability, and the persistence variation of the giant panda[a].

Factor		Colonization	Extinction	Persistence variation
Forest-cover change	FC	1.249e-02[***]	−1.805e-01[***]	3.285e-01[*]
Climate change	MAST	−2.748e-03	3.701e-02	−1.161e-01[***]
	MAT	−2.072e-03	1.299e-02	−2.932e-03.
	MAP	−9.992e-03.	1.829e-03[***]	−1.774e-04[***]
Interaction between forest-cover change and climate change	FC: MAST	9.714e-03	−3.253e-02	−6.266e-02[***]
	FC: MAT	4.662e-03.	1.117e-03	5.816e-04
	FC: MAP	1.246e-02[*]	1.128e-09	4.118e-05

[a] The analysis was conducted using generalized additive model (GAM) for 3 responses: the local colonization probability, the local extinction probability and the persistence variation of giant pandas in the Min Shan. Boldfaced values indicate statistically significant regression coefficients. ** $p < 0.01$.

[*] $p < 0.05$.

[***] $p < 0.001$.

3.3. Giant panda's population persistence

Forest-cover change, MAST change, MAP change and the synergistic effect of forest-cover and MAST change all significantly affected giant panda's persistence (Table 1). The GAM explained 59.7% of giant panda's persistence variation (Fig. 4a), in which forest-cover change, climate change (MAST, MAT, MAP) and the synergistic effect of climate change and forest-cover change explained 38.1% ($R^2 = 0.381$), 20.1% ($R^2 = 0.201$) and 1.5% ($R^2 = 0.015$) of the variation, respectively (Fig. 4b). The increase of forest-cover significantly promoted giant panda's population persistence ($p < 0.05$), and with the extent to which forest-cover increased by 50%, giant panda's population density increased by 50% (Fig. 3a). The climate change had a significantly negative association with giant panda persistence variation ($p < 0.001$), and with the extent to which MAST increased by 33%, or MAP increased by 38%, giant panda's population density decreased by 50% (Fig. 3b, c). Meanwhile, the synergistic effect of MAST and forest-cover change had a significantly negative association with giant panda persistence variation ($p < 0.001$). Giant panda's density decreased by 50% when the extent to which the synergistic effect of MAST change and forest-cover change increased by 51% (Fig. A2a). Forest-cover change overtook climate change (MAT, MAST, MAP) or the synergistic effect of forest-cover change and climate change (MAT, MAST, MAP) as the greatest force driving giant panda's persistence (coefficient = 0.32850) (Table 1).

4. Discussion

Climate change and land-use change have been the two greatest threats to the loss of global biodiversity (Sala et al., 2000). Understanding how species respond to the changes is critical for developing effective conservation strategies (Tingley et al., 2013). Our study confirmed that it was the forest-cover change rather than climate change or the synergistic effect of climate change and forest-cover change that determined giant panda's population persistence. Our study further highlighted the irreplaceability of forest-cover for giant panda's population persistence.

The sixth assessment report of the Intergovernmental Panel on Climate Change demonstrated the Earth's global surface temperature has increased by around 1.1 °C compared with the average in 1850–1900, and projected the increase of 2.1–3.5 °C by the end of the 21st century (Masson-Delmotte et al., 2021). Climate change had caused 20–30% of global plant and animal species face serious risk of extinction (Parry et al., 2007). And the continued warming would drive 16% global species to extinct around 2100 (Urban, 2015). In the past 50 years, China's land surface temperature had risen by 1.40 °C, almost twice the global average temperature (0.72 °C) (Ren et al., 2017). The climate change had advanced the phenological time of wild plants and animals (Ge et al., 2015), undermined biodiversity conservation and the effectiveness of the established protected area network, and thus increased species loss risks (Xu et al., 2009; Zomer et al., 2015). Giant panda's habitat was significantly warming, and the warming intensified giant panda's habitats loss and fragmentation (Shen et al., 2015; Zang et al., 2017), thus compromised giant panda's population persistence (Zang et al., 2020).

However, most of the studies about the impacts of climate change on giant panda's population persistence focused only on climate change, and overshadowed the relative effects of climate change by combining the effects of climate change with the effects of land-use change, which had been proved the primary driver of contemporary biodiversity loss (Newbold et al., 2015). Our study found that climate change had explained 20.1% of the giant panda's population persistence variation ($R^2 = 0.201$) when integrating the effects of climate change with the effects of land-use change. This proved that the effect of climate change on giant panda's population persistence was not as strong as the previous

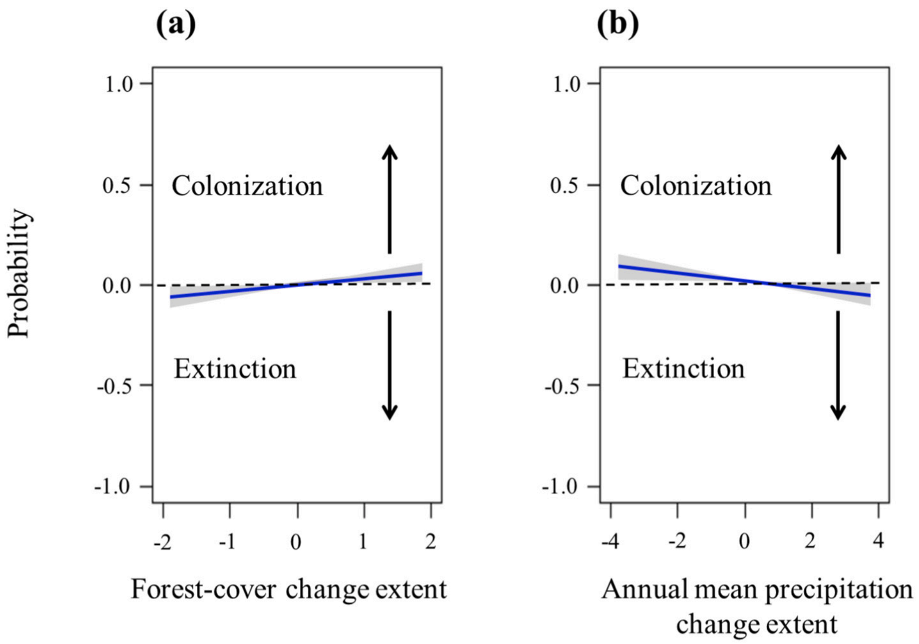

Fig. 2. The quantified effect of forest-cover change and climate change on giant panda local colonization probability (value represented as greater than zero) and the extinction probability (value represented as less than zero) using generalized additive model (GAM). (a) The relationship of the local colonization probability and local extinction probability of giant panda with the forest-cover change. The X-axis denotes standardized forest-cover change extent, and the Y-axis denotes the local colonization (value represented as greater than zero) or local extinction probability (value represented as less than zero) (shading, 95% CI). (b) The relationship of the local colonization probability and local extinction probability of giant panda with the climate change. The X-axis denotes standardized annual mean precipitation change extent, and the Y-axis denotes the local colonization (value represented as greater than zero) or local extinction probability (value represented as less than zero) (shading, 95% CI).

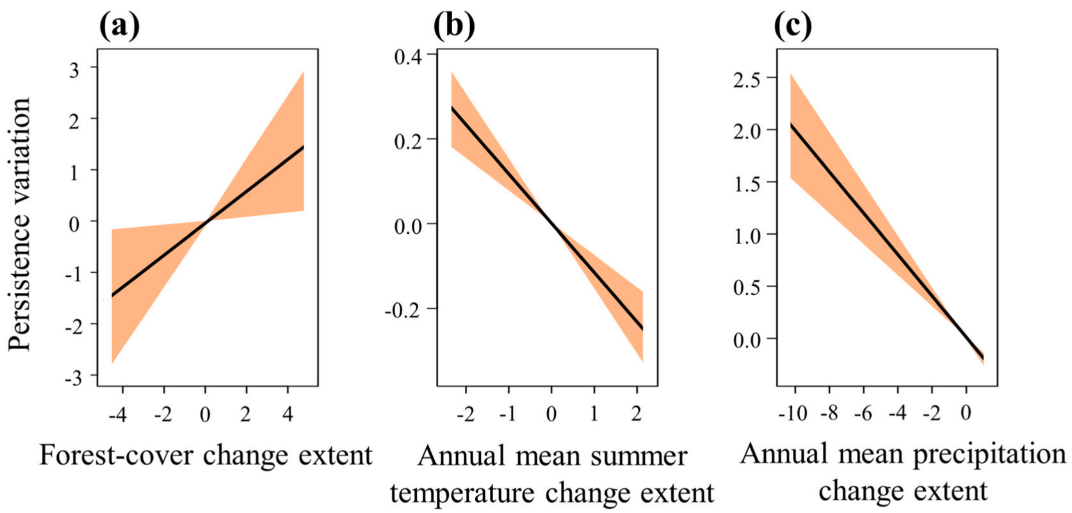

Fig. 3. The quantified effect of forest-cover change and climate change on giant panda's persistence variation using generalized additive model (GAM). (a) The relationship of the giant panda's persistence variation with the forest-cover change. The X-axis denotes standardized forest-cover change extent, and the Y-axis denotes the extent of density increase (value represented as greater than zero) and the extent of density decrease (value represented as less than zero) (shading, 95% CI). (b) The relationship of the giant panda's persistence variation with the temperature change. The X-axis denotes standardized annual mean summer temperature change extent, and the Y-axis denotes the extent of density increase (value represented as greater than zero) and the extent of density decrease (value represented as less than zero) (shading, 95% CI). (c) The relationship of the giant panda persistence variation with the precipitation change. The X-axis denotes standardized annual mean precipitation change extent, and the Y-axis denotes the extent of density increase (value represented as greater than zero) and the extent of density decrease (value represented as less than zero) (shading, 95% CI).

studies (Fan et al., 2014; Tuanmu et al., 2012; Zang et al., 2020), most of which ignored the relative contribution of climate change or land-use change. In contrast, forest-cover change explained 38.1% of variation in giant panda's population persistence ($R^2 = 0.381$). Crucially, we found that the synergistic effect of climate change and forest-cover change only explained 1.5% of variation in giant panda's population persistence ($R^2 = 0.015$), although lots of studies had indicated the strongly synergistic effects of habitat loss and climate change across a wide range of species and landscapes (Northrup et al., 2019).

Actually, the truth was that it was the forest-cover that sheltered giant panda from climate change. Forests constituted the crucial components of giant panda's habitats by mitigating climate change through physical, chemical, and biological processes (Bonan, 2008; Tuanmu et al., 2012). Old growth forest was just as good an indicator that giant pandas live in the area as the presence of bamboo (Liu et al., 2001; Zhang et al., 2011). Younger forest also provided suitable shelter for giant pandas, and their maturation drove giant pandas to expand geographical ranges (Wei et al., 2020). Importantly, forest loss and fragmentation induced the giant panda's loss of genetic diversity, thus threatening giant panda viability heavily (Liu et al., 2001; Loucks et al., 2003; Xu et al., 2006; Yang et al., 2015).

In particular, forest-cover was indispensable for the survival of giant panda's staple food bamboo (Li and Shen, 2012). Giant panda was extreme dietary specialists for bamboo, and giant panda and bamboo

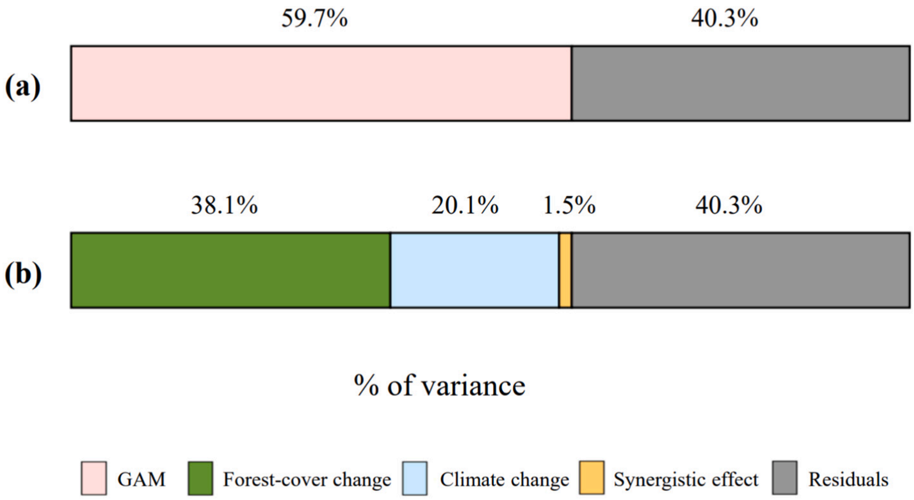

Fig. 4. The summary of the variance model on the persistence variation of giant pandas in the Min Shan. (a) The total variance on the persistence variation of giant pandas explained by the generalized additive model (GAM). (b) The effect of forest-cover change, climate change, and the synergistic effect of climate change and forest-cover change on the persistence variation of giant pandas examined by GAM in the Min Shan.

species had developed co-evolutionary trails that ensured their survival (Li and Shen, 2012; Liu and Viña, 2014). Bamboo was a particularly conspicuous feature in the understory of the forests of the panda geographic range (Schaller et al., 1989). Forest canopy composition and density influenced the patterns of understory bamboo distribution, dominance and abundance (Taylor et al., 2004). Changes in bamboo's abundance and spatial distribution could cause food shortage for panda (Liu and Viña, 2014). Interactions between tree species life history, canopy type, and bamboo life-cycles created heterogeneous conditions that influenced tree and bamboo regeneration, and contributed to the coexistence of the integrated system consisting of tree species, bamboo and giant panda (Li and Shen, 2012; Taylor et al., 2004; Tuanmu et al., 2012).

Deforestation and forest degradation threatened the survival of giant panda's staple food bamboo, and the ongoing climate change intensified the threat to bamboo's growth and regeneration (Tuanmu et al., 2012). Many bamboo species were vulnerable to climate change because their unusual extended sexual reproduction intervals, along with limited seed dispersal ability, which rendered them less capable of adjusting their distributions to the rapidly changing climate (Tuanmu et al., 2012). In addition, understory staple food bamboo limited vegetative dispersal ability, which left them less capable of quickly expanding their range (Zang et al., 2020). So, if there was no forest covering giant panda's habitats, or only degraded or fragmented forest covered the patches, giant panda would be exposed to ambient warming or drought environment. When ambient temperature increased beyond giant panda's suitable thermal range, giant panda would suffer from prolonged exposure to heat or drought stress, thus facing the increased risk of extinction (Zang et al., 2020). Multi-taxon reviews had suggested that 20–30% of global plant and animal species could be at an increased risk of extinction due to climate warming (Parry et al., 2007), and continued warming would drive 16% species to extinction by 2100 (Urban, 2015).

To our delight was that Chinese government had started early to restore giant panda habitat by initiating a series of conservation programs. By the end of 2015, National Conservation Project for the Giant Panda and its habitat had created 67 “panda reserves”, protecting and restoring 1.4 million acres of panda habitat, covering 58% of giant panda's range (National Forestry and Grassland Administration, 2021). Since 1998, China began implementing the Natural Forest Conservation Program (NFCP). This initiative banned logging in natural forests, strengthened protection of existing forests, and implemented afforestation throughout much of China, including most of the panda's range (Swaisgood et al., 2017). The NFCP was complemented by the Grain-to-Green policy, which aimed to restore hillside agricultural lands into forest or grasslands (Zhang et al., 2011). As a result, the amount of available habitat for panda had been provided with strict protection to all the remaining forests throughout the panda's range (Loucks et al., 2001). Now, China has launched an ambitious program to establish a national park system that integrates current protected areas to resolve the problem of habitat fragmentation (Li et al., 2020).

Our study had provided one of the few empirical tests of the relative and combined effect of global change drivers on giant panda's population persistence. However, 40.3% of the variation in giant panda's population persistence had not been explained by forest-cover change, climate change and the synergy between them. The unexplained residual variation in our models suggested that other human disturbance drivers may play some role in the local colonization and extinction of the giant panda. Although, the established nature reserves were effective on protecting giant panda and their habitats, human disturbance such as livestock, roads, farming, and other disturbance activities, coupled with the ongoing habitat fragmentation were still threatening giant panda's population persistence (Wei et al., 2018; Xu et al., 2017).

Our analysis had provided an empirical evidence that only focusing on the underlying effect of climate change rather than the comprehensive effects of land-use and climate change would overestimate the absolute fatal effects of climate change on giant panda's population persistence, which could lead to inappropriate conservation recommendations (Guo et al., 2018; Sirami et al., 2016; Wang et al., 2018). However, we still couldn't be too optimistic and ignored the critical role of climate change played in the giant panda's protection, especially in facing the continued forest fragmentation. After all, the climate in giant panda's distribution area was indeed warming, moreover the warming was driving giant panda to leave suitable habitats (Wei et al., 2018; Zang et al., 2017). Our findings highlighted the urgent need for an understanding of the comprehensive effects of climate change and land-use change rather than just focusing on climate or isolating land-use change and climate change in tackling the global biodiversity loss.

CRediT authorship contribution statement

On behalf of my co-authors and myself, I hereby certify that this paper reflects our original work rather than copying, plagiarism and fraud. To the best of my knowledge and belief, neither the entire manuscript nor any part of its content has been published or has been accepted elsewhere. It is not being submitted to any other journal. We have participated sufficiently in the work to take public responsibility for the appropriateness of the method, the collection, analysis and interpretation of the data. All of the authors agree to the submission of this revised manuscript.

Declaration of competing interest

We declare that no conflict of interest exits in this manuscript.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2021.109436.

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