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Spatial models of giant pandas under current and future conditions reveal extinction risks

Lingqiao Kong[1], Weihua Xu[1], Yi Xiao[1], Stuart L. Pimm[2], Hao Shi[1] and Zhiyun Ouyang[1,3] ✉

In addition to habitat loss and fragmentation, demographic processes—the vagaries of births, deaths and sex ratio fluctuations—pose substantial threats to wild giant panda populations. Additionally, climate change and plans for the Giant Panda National Park may influence (in opposing directions) the extinction risk for wild giant pandas. The Fourth National Giant Panda Census showed pandas living in 33 isolated populations. An estimated 259 animals live in 25 of these groups, ~14% of the total population. We used individual-based models to simulate time series of these small populations for 100 years. We analysed the spatial pattern of their risk of extinction under current conditions and multiple climate change models. Furthermore, we consider the impact of the proposed Giant Panda National Park. Results showed that 15 populations face a risk >90%, and for 3 other populations the risk is >50%. Of the 15 most at-risk populations, national parks can protect only 3. Under the Representative Concentration Pathway 8.5 climate change scenario, the 33 populations will probably further divide into 56 populations. Some 41 of them will face a risk >50% and 35 face a risk >90%. Although national parks will probably connect some fragmented habitats, 26 populations will be outside national park planning. Our study gives practical advice for conservation policies and management and has implications for the conservation of other species in the world that live in isolated, fragmented habitats.

The giant panda (*Ailuropoda melanoleuca*) is the flagship species of global biodiversity conservation. According to the Fourth National Giant Panda Census, panda habitat has increased in recent decades. The International Union for Conservation of Nature (IUCN) changed the giant panda's status from endangered to vulnerable. A concern, however, is that it is in 33 isolated populations (Fig. 1; released by State Forestry Administration at http://www.forestry.gov.cn/main/4462/20150303/743596.html)[1]. Its habitat is becoming more fragmented[2,3] as a result of both natural and human factors. The natural factors include fragmented forest and bamboo and large rivers and tall mountains. The infrastructure and human activities include transportation networks, cropland, residential plots and tourism facilities and activity[3]. Climate change will exacerbate these problems[4], as will large-scale bamboo die-off after synchronous flowering[5]. Simply, habitat fragmentation and population isolation are substantial threats to its long-term survival[3,6]. Climate change may further degrade the spatial distribution of panda habitat, increasing habitat fragmentation in some areas. To restore and connect fragmented habitats, China is planning the Giant Panda National Park. In the context of ecological protection and climate change, the future survival risk of small populations living in fragmented habitats is of concern.

Here, we use individual-based models to assess the risk of extinction of the giant panda populations across the panda's entire range. Climate change and the protection afforded by the Giant Panda National Park are also considerations. Our goal is to understand the significance of these risks and provide advice for future conservation actions.

All populations experience two kinds of factors that cause them to vary over time: demographic accidents and environmental fluctuations[7]. The former are the unavoidable consequences of births, deaths and sex ratio fluctuations. Even an otherwise healthy population will produce varying numbers of young each year, there may not be equal numbers of males and females and, by chance alone, there will be more deaths in some years than others. While these vagaries may even out in a large population, they pose a substantial risk to a small one. A population of two males and two females has a one in eight chance of producing either all males or all females in the next generation, for example. The genetic consequences of inbreeding add yet further risks to small populations, motivating genetic rescue of populations by translocating individuals, as done for the Florida panther[8]. Finally, external environmental factors such as weather and the changing abundances of resources and predators can pose substantial risks, even for large populations.

In sum, small populations in fragmented and isolated habitat patches face a high risk of local extinction[3,9]—even in protected areas. With the increasing habitat fragmentation of wildlife globally[10], the increased risk of extinction of small panda populations is similar to risks many other species face worldwide[11,12].

Many studies have assessed panda habitat[3,13–15], the impact of climate change and human activities on panda habitat[16–19], design of the nature reserves and corridors[20–22] and panda conservation policies[23,24]. Population viability analysis[25,26], was undertaken using off-the-shelf products such as Vortex[27–32], Leslie matrix models[33–35] or a DNA-based model[36] for a specific mountain area or a nature reserve. They have not been applied range-wide. Our choice of individual-based models stems from the necessity of keeping track of individuals, their age and sex for populations as small as the ones we consider. Such factors play an increasingly important role in determining a population's fate as its size declines. Climate change studies predict that giant panda habitats will become more fragmented. We further simulate the extinction risks under scenarios of future climate change. Finally, we assess the impact of the Giant Panda National Park.

[1]State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing, China. [2]Nicholas School of the Environment, Duke University, Durham, NC, USA. [3]College of Resources and Environment, University of Chinese Academy of Sciences, Beijing, China. ✉e-mail: zyouyang@rcees.ac.cn

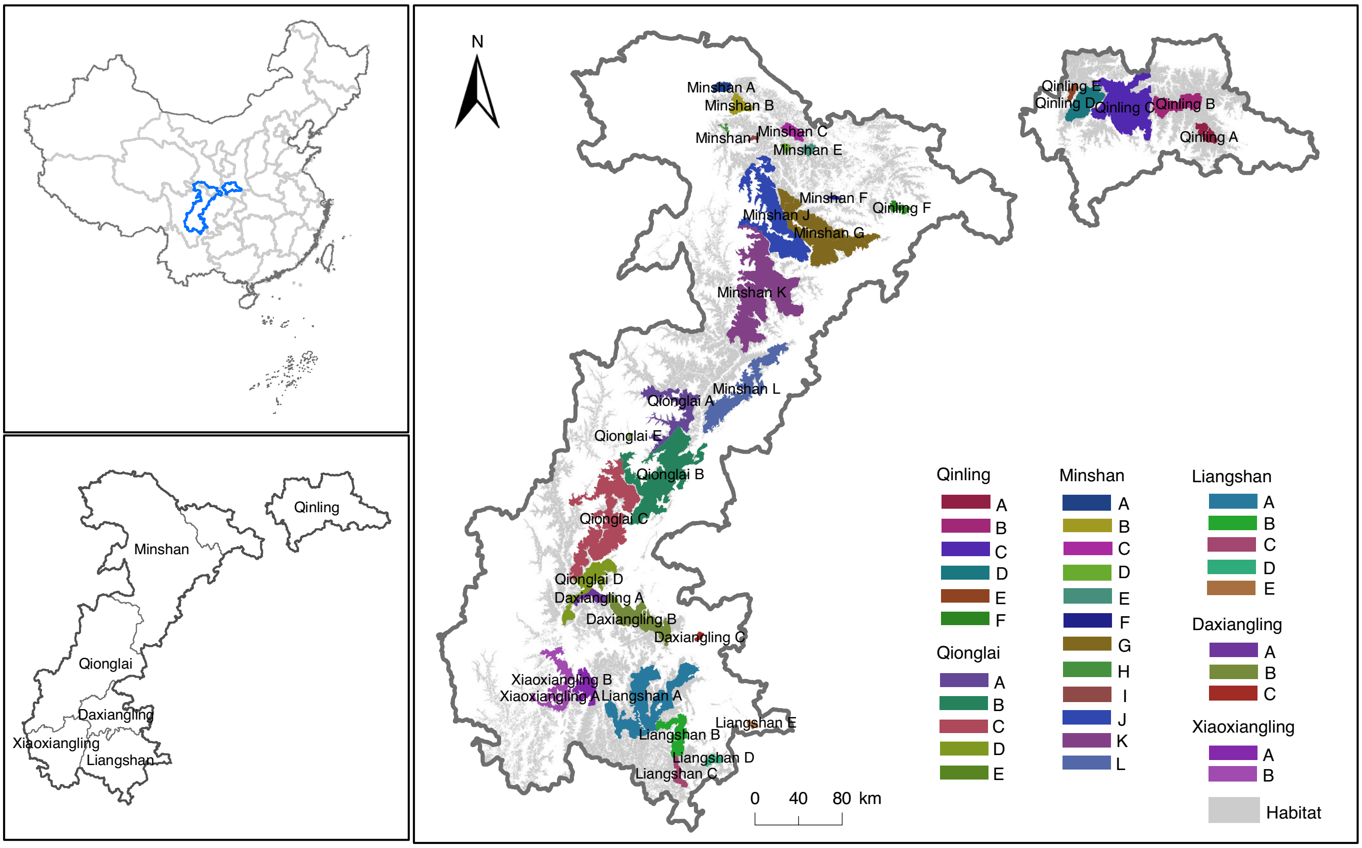

Fig. 1 | The 33 isolated populations of giant pandas. Map of wild giant panda populations showing six populations in Qinling (A–F), twelve in Minshan (A–L), five in Qionglai (A–E), three in Daxiangling (A–C), two in Xiaoxiangling (A and B) and five in Liangshan (Liangshan A–E).

Results

Population trends assuming total connectivity. Our models assume no external environmental factors—such as poaching, logging, livestock grazing, bamboo flowering, natural disasters and other human activities. Under such assumptions, our models predict that the general population of the wild giant panda should increase slowly eventually (Extended Data Fig. 1). This optimal scenario assumes that pandas can move readily between all populations within six mountain ranges. It is against this that we can contrast the fate of small populations when demographic effects increase local extinction risk.

By chance, animals may be mostly young ones or old ones or something in between in isolated populations. The transient dynamics depend on the initial conditions of age structure. We simulated different age structures, with juvenile age, adult age and old age predominating. (Supplementary Table 5 shows the specific compositions of different age structures.) We used the stable age structure simulated by our model's multiple operations, as described in the Methods. When old animals predominate, one can expect a rapid decline in numbers before the eventual, slow recovery.

Extinction risks under current conditions. Figure 2 shows the relationships of the fractions of simulations going extinct within 100 yr with the simulations for various panda population sizes under a stable age structure. Henceforth, we call this 'extinction risk' for simplicity. As expected, the extinction was high for small populations and decreased with increasing initial population size.

There are 25 populations with fewer than 35 individuals each on the Fourth Census; they total 259 individuals. Figure 2 shows that they face a risk of extinction of at least 15% in the next 100 yr. There are 15 populations and three others with extinction probabilities greater than 90 and 50%, respectively.

Next, we consider how different assumptions may alter these results.

First, we simulated the extinction risks under various age structures (Fig. 3). As expected from the results shown in Fig. 3, populations in which most individuals are old have a very high risk of extinction. All 25 populations have >90% probability of extinction in 100 yr. For the other three scenarios, the effect of the initial age structure was less dramatic.

Second, we changed the survival and reproduction rate parameters by ±10% for each age to see the uncertainty of the extinction rates. Variation in these parameters does not substantially alter our conclusions. Populations with <35 individuals have at least a 10% risk of extinction for almost all combinations of parameters. The exceptions are for simulations with high fecundity. Many combinations of parameters have substantially higher risks of extinction than shown in Fig. 3. New-born panda cubs are very weak and easily fall prey to natural predators. Their survival rate is sensitive. A small drop in the survival rate of cubs can lead to a notable increase in extinction risks. Age structure is particularly sensitive: when biased to old individuals, which may be the case for long-isolated populations, they have low population growth and the risks of extinction can be high even for populations with up to 60 individuals. We present the complete results in Extended Data Figs. 2, 3 and 4 and Supplementary Tables 1 and 2.

The spatial distribution of the populations at greatest risk causes alarm (Fig. 4). These populations are mostly peripheral to the main panda populations. They include 59 pandas in the northern Minshan and 32 pandas in the southern Liangshan, populations at the two ends of the species' distribution. Their chance of rescue by immigrants from larger populations is much less than if they were close to, and surrounded by, other populations.

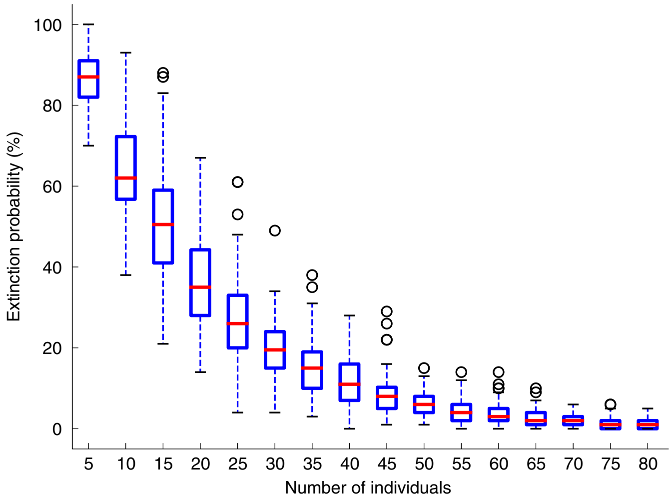

Fig. 2 | Relationship between population size and the fraction of simulations going extinct. In the boxplots, the horizontal line shows the median value of the fraction of simulations going extinct. The whiskers show the 25 and 75% quartile values.

Impact of climate change and the Giant Panda National Park. Climate change exacerbates these problems. We used the Coupled Model Intercomparison Project Phase 5 (CMIP5) model and the new emission scenario (Representative Concentration Pathways, RCPs) of the IPCC Fifth assessment report (AR5) to estimate future climate changes impacts on the spatial pattern of wild giant panda habitat. RCPs includes four scenarios: RCP 2.6, RCP 4.5, RCP 6.0 and RCP 8.5. Each scenario provides an emission path affected by socioeconomic conditions and climate. Under the four scenarios, the average global temperature increases respectively by 1.0, 1.4, 1.3 and 2.0 °C from 2046 to 2065 and increases by 1.0, 1.8, 2.2 and 3.7 °C from 2081 to 2100. We used the long-term simulated temperature and rainfall data of four scenarios to analyse the change of the giant panda population extinction risk. These data are then input to the giant panda habitat simulation to analyse whether the giant panda habitat may risk further fragmentation under future climate change.

For some populations, habitat fragmentation increases under climate change. Under the climate change scenarios of RCP 2.6, RCP 4.5 and RCP 8.5, the number of isolated populations will probably increase to 40, 39 and 56 in the year 2100, respectively. When considering the national park protection, the numbers could decrease to 23, 23 and 32, respectively. The park will probably connect the large area of habitat of the large populations and the surrounding populations in the south Minshan and Qionglai Mountains. In addition, the small populations in the Qinling, south Qionglai, Daxiangling and Xiaoxiangling Mountains will also benefit from the connection. Extinction risks of the populations within the national park will drop substantially. However, the populations in Liangshan and northern Minshan are outside the national park. What is more, under the climate change scenario of RCP 8.5, the number of populations with extinction possibilities greater than 90, 50 and 15% will increase to 35, 41 and 48, respectively. That is, they have more than doubled. In that case, although the national park can protect most large populations, there will still be 29, 26 and 20 populations with an extinction possibility greater than 15, 50 and 90%, respectively. Figure 5 shows the branch diagrams of populations and extinction possibilities in different scenarios. Extended Data Fig. 5 shows the detailed list of simulated future extinction possibilities of each wild giant panda populations under different scenarios.

The situation in Liangshan Mountain will be the worst, whether in the RCP 8.5 scenario or the national park scenario (Fig. 4). The current five populations will become 13 isolated populations. The large populations of this set will divide into eight small populations. In that case, 11 small populations will face extinction probabilities >50% and seven populations will face extinction probabilities >90% (Fig. 5).

The situation in Xiaoxiangling Mountain is also serious. Under the RCP 8.5 scenario, the current two small populations will further divide into five populations, four of which face extinction possibilities >90% (Fig. 4). When considering the national park, there will still be two small, isolated populations facing extinction possibilities >90% (Fig. 5).

For the Qionglai Mountain, the easternmost and the southernmost populations (Qionglai B and Qionglai D) will be most affected. Under RCP 2.6 and RCP 4.5 scenarios, there will be two small populations separated from Qionglai B, with extinction risks >75%. It is worse in the RCP 8.5 scenario, as three small populations will face extinction because of the complete habitat loss. The Qionglai D population will divide into five small populations, four of which will face an extinction risk >90% (Fig. 4). Most populations can connect within the national park to form a large population but two isolated pandas out of the national park will still struggle to survive (Fig. 5).

The current three small populations in Daxiangling Mountain will further divide into six populations, five of which face extinction possibilities >95% under the RCP 8.5 scenario (Figs. 4 and 5). One small population will be outside the national park.

For the Minshan and Qinling Mountains, the southernmost population (Minshan L) will probably divide into two populations unless there is the national park's protection. The Qinling F will probably divide into two populations and face higher risk in the RCP 8.5 scenario (Fig. 5). However, the national park will not mitigate the extinction risk of small populations in the northern Minshan mountains (Fig. 4). Although Qinling A and Qinling F are already inside the national park, roads or large rivers separate them from other populations and they are hard to connect.

Discussion

Currently, panda habitat covers less area and is more fragmented than it was 30 yr ago. Its small, isolated populations are facing a high risk of regional extinction[3]. The Giant Panda National Park should increase the connectivity of panda habitat. In contrast, climate change will aggravate habitat loss in local areas, posing a threat to small, local populations. A quantitative analysis of extinction risk across the giant panda geographic range considering both the protection and climate change was necessary. This study revealed the extinction risk of each isolated population and the spatial pattern of extinction risk under current condition, the future climate change scenarios and the benefits of a national park to connect populations. We pay particular attention to small populations whose extinction risk was very high.

Our study showed that 25 populations face some degree of extinction risk at present and 15 populations with fewer than five individuals face near-immediate extinction. The survey results of the Third National Giant Panda Census[37] and the Fourth National Giant Panda Census confirmed these concerns. Pandas in four isolated populations decreased; each had no more than 17 wild pandas. One isolated population with three pandas decreased to only one. Three isolated populations disappeared; each had no more than two pandas.

Our results echo previous studies, such as Zhu et al.[36,38] but they are optimistic. They do not include the additional risks of inbreeding, which can doom small populations or external factors that cause even large populations to fluctuate. In short, they suggest the best-case scenarios. Actual populations will have higher risks. Inbreeding, bamboo flowering, food capacity and other natural

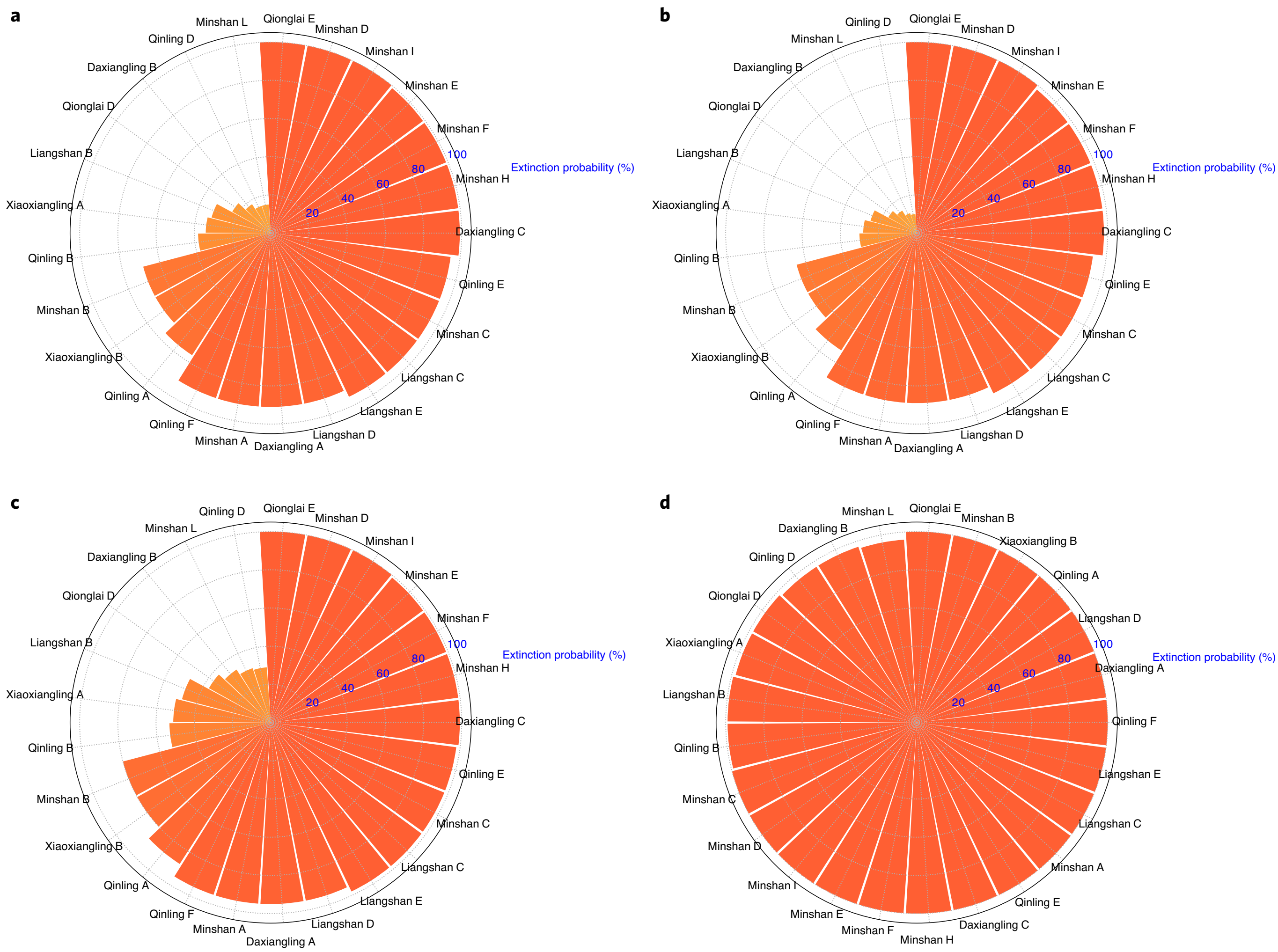

Fig. 3 | Radar charts of fraction of simulations of giant panda populations going extinct in 100 yr. a–d, Fractions of simulations of giant panda populations going extinct under various conditions: the initial state of stable age structure (**a**); the initial state of youth majority age structure (**b**); the initial state of adult majority age structure (**c**); and the initial state of old majority age structure (**d**).

disasters (such as earthquakes) will increase the extinction risks of the small, isolated populations. It is essential to study the influences of these disturbances on extinction risks for isolated populations in the future. Since the population information is limited, we simulated the extinction risk without considering the population parameter differences in the different six mountains. Further efforts should study the local differences in the extinction risk.

Improvement of habitat connectivity for wild panda populations can reduce the extinction risk of small populations. Pandas find it very difficult to walk long distances. This limitation makes them lose the directions to return to the nest domain. They have difficulties in communicating far away, even in the same habitat patch[39]. In addition, it is not easy to connect the habitats separated by mountains >4,000 m and by major rivers such as the Minjiang, Daduhe and Jialingjiang. In this study, the habitat in the Northern Minshan Mountains will probably increase under climate change. This increase is consistent with the conclusion of previous studies[17,40]. That said, the northern Minshan small populations will not easily connect to the large southern population because of roads, rivers or long distances. For southern populations such as Liangshan, Xiaoxiangling, Daxiangling and southern Qionglai mountains, climate change threatens their habitat, so there is an urgent need for habitat connectivity.

It is more feasible within the Giant Panda National Park to fill the habitat gaps caused by degraded vegetation, cropland or roads by corridors. This national park will be the most strictly protected unit in the Nature Reserve System in China. The varied causes of population isolation determine the different habitat connection strategies that managers should fully consider in national park planning. For the populations separated by forest degradation and cropland, the fragmented habitats should be connected by reforestation and bamboo recovery, and the forest protection by sufficient eco-compensation payments[41]. If roads separate the habitats, road tunnels could reconnect them[3]. In the area where tourism facilities and activities separate the panda population, improving facility location and management on the basis of panda behaviours could be a method to connect the habitats. For instance, there might be no access to the panda habitat, limits to the number of tourists and careful management for tourism to avoid disturbing the pandas. Although the Giant Panda National Park could protect most large populations, small populations would be hard to connect inside because of roads or natural barriers. These include Qinling A and Qinling F, which need conservation investments. A way to supplement the wild population of Qinling A would be by reintroduction. The population trend of Qinling F and its habitat needs to be monitored. It could be relocated to a nearby large population if the

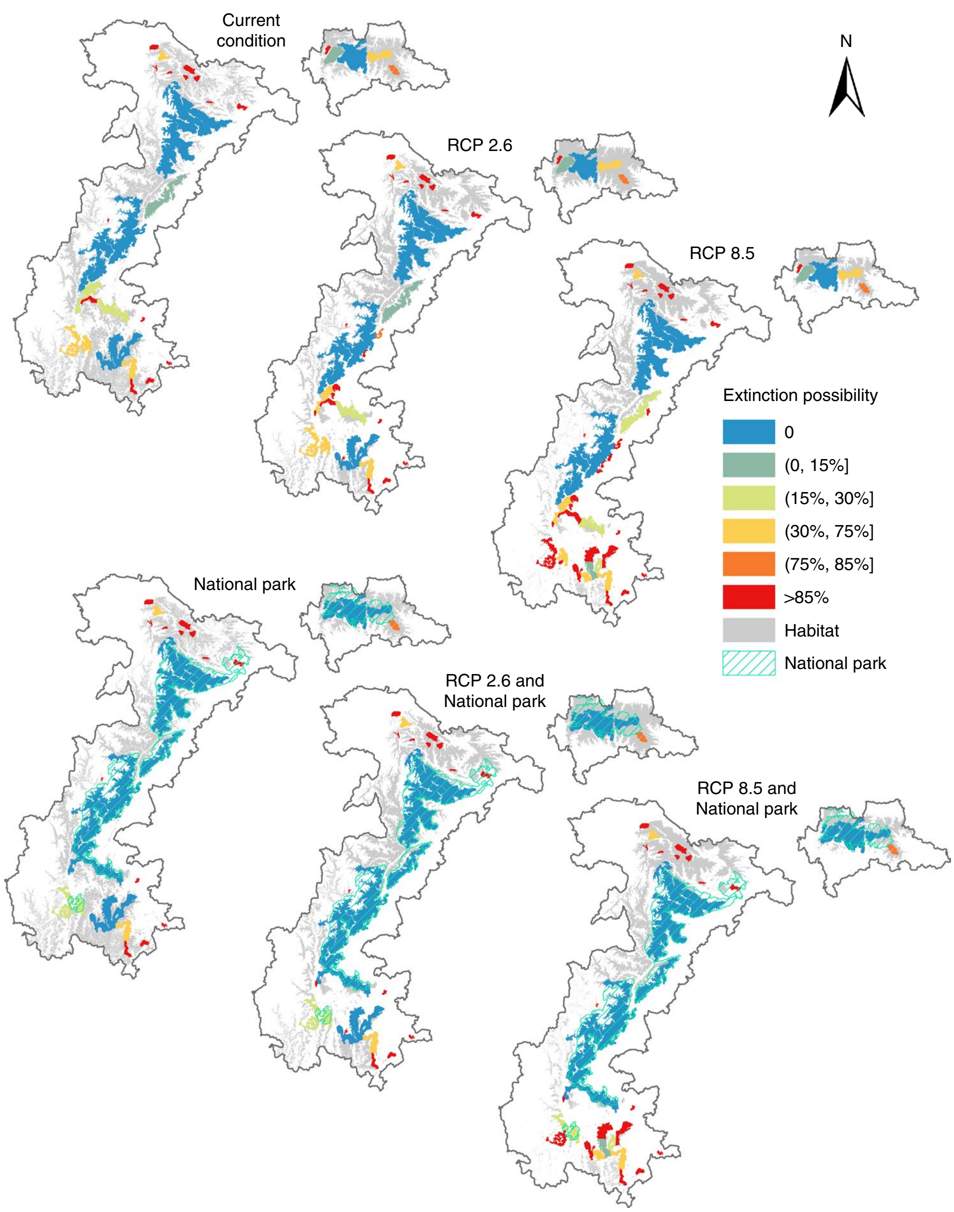

Fig. 4 | The spatial pattern of extinction risks under different scenarios of climate change and Giant Panda National Park. Maps showing the spatial patterns of extinction possibilities under six scenarios (current conditions, RCP 2.6 and RCP 8.5 scenarios, and their corresponding national park scenarios).

habitat cannot be improved. Although the Xiaoxiangling populations are in the national park, habitat fragmentation is serious and the population extinction risk is high. It is necessary to strengthen habitat restoration and national park management. In addition, a lot of small populations are outside the national park's protection. These include those in the Liangshan, western Xiaoxiangling and northern Minshan Mountains. Here, the habitat will probably suffer severe loss and become extremely fragmented due to climate change. Therefore, these populations need to be connected. The Giant Panda National Park's scope should further expand to include the habitat range of these populations in the long term.

At present, measures should also be taken in these areas to restore fragmented habitats and build corridors for giant panda populations. To be specific, for the small populations in Northern Minshan, the Minshan A and Minshan B populations could be connected. Other small populations could be concentrated towards Minshan C. For Minshan L, whose habitat is highly fragmented, it will be necessary to strengthen habitat restoration to increase carrying capacity and build corridors to connect with the large populations. For Qionglai E, Daxiangling C and Liangshan E, the national survey showed that each population had fewer than three individuals. Their habitat is difficult to connect with the neighbour habitats. We recommended to recheck the population survey and consider relocating the populations. For the Liangshan populations, we recommend that Liangshan B and Liangshan A be connected as a large population and other small populations could be connected to it.

According to a primary estimation based on the comparison of panda population size and its occupied area of habitat[3,23], considering the panda's home range[39] and the impact of bamboo distribution on carrying capacity[42], 27 of 33 panda populations—about 54% of the total population—have some degrees of inbreeding. It could be possible to introduce pandas from the nearby large populations to increase population genetic diversity—as done for the Florida panther[8]. Such introductions might be particularly effective for the

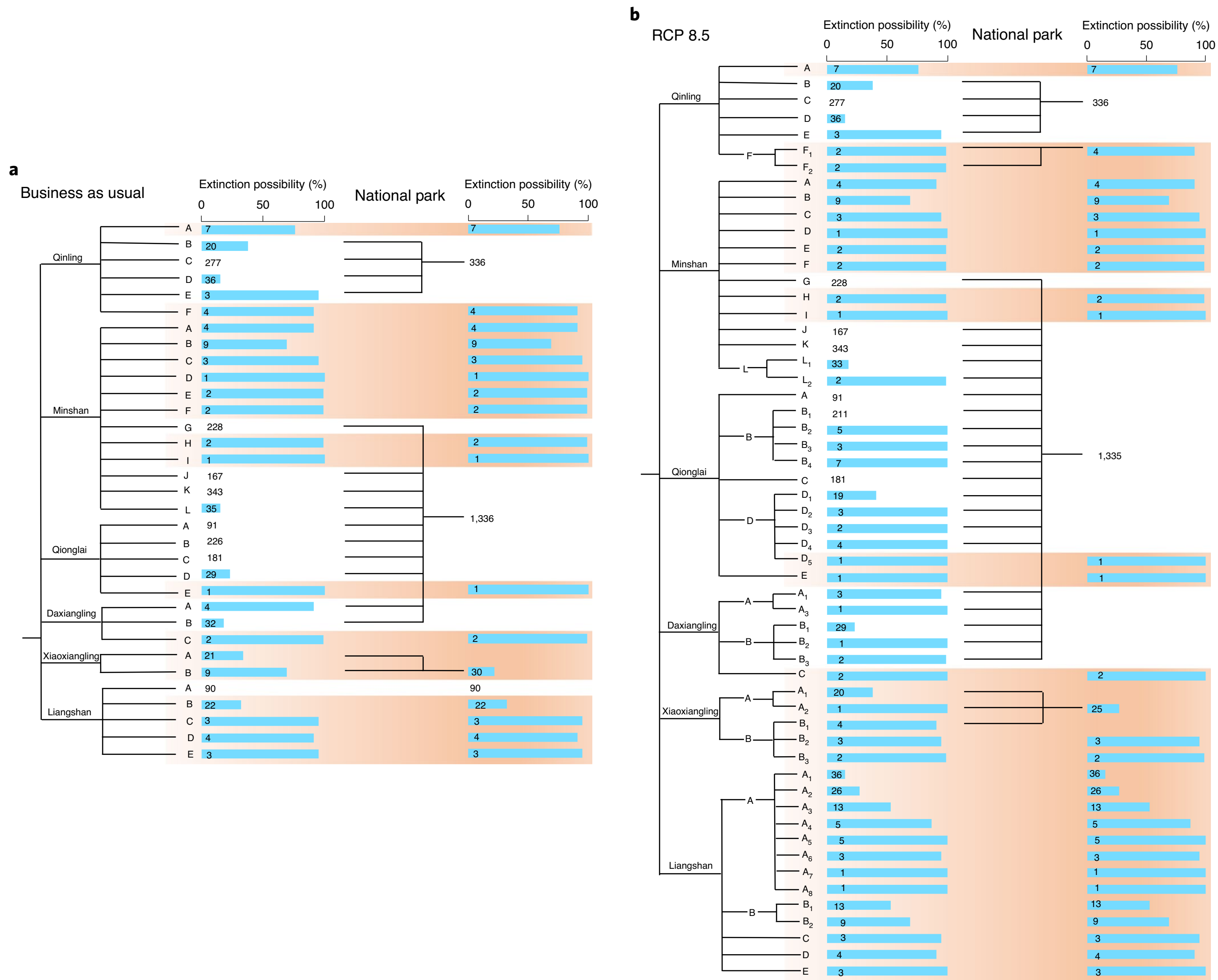

Fig. 5 | Branch diagrams of populations and their extinction possibilities under current conditions and RCP 8.5 scenario, and the corresponding national park scenarios. a,b, Branch diagrams of populations and extinction rates under current conditions and the national park scenario (**a**) and under RCP 8.5 and its corresponding national park scenario (**b**). The blue histograms show the extinction possibilities corresponding to the small populations. The number on the histogram is the number of individuals in the population. The populations within the orange area will be still at risk of extinction when considering the national park.

small populations with abundant habitats, such as the small populations in Northern Minshan and Liangshan. Studies of the impact of climate change on panda habitat indicated the northward shifts of suitable habitat[17,40]. This shift would also support the supplement of the small population in the northern Minshan Mountains. In addition, previous studies showed gene flow could be encouraged between isolated populations either through the natural corridors or genetic restoration[6]. Additionally, managers could reintroduce giant panda[43]. There are >600 captive giant pandas in the giant panda breeding centres in China. This number should increase by >30 per year, providing the possibility for reintroducing giant pandas to the wild. We recommend formulating technical guidelines for reintroduction and a sensible science-based plan by in-depth research, and also launching the reintroduction of giant pandas to supplement the giant pandas in small populations to reduce their risk of extinction.

With the increasing habitat fragmentation of wildlife globally, the high risks of small populations of giant pandas present a common situation that many other species face worldwide.

Methods

Simulation of the population trend and risk of extinction. We used an individual-based model[44–47] to simulate the population dynamics. Such models considered individuals as discrete and autonomous entities. First, we input the parameters (reproductive rate, death rate and sex ratio for each age category and birth intervals). The model then calculated whether each agent's life-history events, such as reproduction, birth or death, might occur at each step, doing so in a stochastic manner based on the individual's sex and age.

Following the procedure flow (Extended Data Fig. 6), the model repeats the following procedure each year for each individual until the population is extinct, recording its sex and age. We considered the population extinct if all the individuals were of the same sex or all the males and females were older than the maximum breeding age. For each simulation, we calculated the extinction probability in 500 simulations for 100 yr. For each population, we simulated the extinction probability 100 times and took the average. Then, we mapped the populations' extinction risk.

To determine the initial numbers of different ages for the simulation, we first ran the procedure for 500 yr to obtain the stable age structure. We used this as the input to our procedure. The Fourth National Giant Panda Census does not include the number of baby pandas in the population data, so we first simulate it according to the age structure. A literature review provided the other starting values for the model, including reproduction and death rates, birth intervals and sex structure. Supplementary Tables 3 and 4 summarize them, following the studies by Wei et al.[48] and Hou[49]. The model does not consider factors such as poaching or disease that may alter age or sex structures. They arise purely from life-history events of all individual pandas across the entire span of simulation runs.

Simulation of climate change scenarios. The climate projection data were from the China Meteorological Administration (bcc-csm1-1 CMIP5 r1i1p1), with a spatial resolution of 2.8125°×2.7893° and a daily temporal resolution. These data were aggregated into a monthly time-step and downscaled into a $1\times1\,km^2$ resolution using the delta method and the WorldClim 2.0 Product (June 2016, http://worldclim.org) as reference.

We used a MaxEnt model to simulate the spatial patterns of giant panda habitat in 2015 and 2100. The input variables included altitude, slope, vegetation type, annual average temperature, maximum yearly temperature, minimum yearly temperature and annual rainfall. Under the four climate change scenarios, the area under curve values reached 0.8595. According to the simulated spatial patterns of separated pieces of habitat, we generated the corresponding spatial patterns of separated populations. Then, we simulated the future extinction risks of the isolated populations under different climate change scenarios using the individual-based model described above.

Simulation of national park scenarios. The Giant Panda National Park plans to restore giant panda habitat and construct corridors to increase panda habitat connectivity to alleviate fragmentation. We assumed that fragmented habitats could be connected and population exchange could be realized within the National Park unless roads, residential plots or natural barriers separated those isolated populations. By overlapping the spatial boundary of the planned national park with the habitat and the populations, we generated the spatial pattern of isolated populations under the national park's protection. The National Park Administration provided the Giant Panda National Park data (released at http://www.forestry.gov.cn/html/main/main_4461/20191017111923948546698/file/20191017112033510119113.pdf). We then simulated the future extinction risk of the separated populations by the individual-based model mentioned above to indicate the Giant Panda National Park's protective effects.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability
Data that support the findings of this study are available in the main text or the Supplementary Information.

Code availability
The main text describes the procedure flow of the individual-based algorithm. Code for running the model is available at https://github.com/konglingqiao/eco.

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References

1. Tang, X. et al. Scheme design and main result analysis of the fourth national survey on giant pandas. *For. Resour. Manag.* **1**, 11–16 (2015).
2. Swaisgood, R. R., Wang, D. & Wei, F. Panda downlisted but not out of the woods. *Conserv. Lett.* **11**, 1 (2018).
3. Xu, W. et al. Reassessing the conservation status of the giant panda using remote sensing. *Nat. Ecol. Evol.* **1**, 1635–1638 (2017).
4. Shen, G. et al. Climate change challenges the current conservation strategy for the giant panda. *Biol. Conserv.* **190**, 43–50 (2015).
5. Tian, Z. et al. The next widespread bamboo flowering poses a massive risk to the giant panda. *Biol. Conserv.* **234**, 180–187 (2019).
6. Lu, Z. et al. Patterns of genetic diversity in remaining giant panda populations. *Conserv. Biol.* **15**, 1596–1607 (2001).
7. Pimm, S. L. *The Balance of Nature* (Univ. Chicago Press, 1991).
8. Pimm, S. L., Dollar, L. & Bass, O. L. Jr The genetic rescue of the Florida panther. *Anim. Conserv.* **9**, 115–122 (2006).
9. Qing, J. et al. The minimum area requirements (MAR) for giant panda: an empirical study. *Sci. Rep.* **6**, 37715 (2016).
10. Haddad, N. M. et al. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* **1**, e1500052 (2015).
11. Fahrig, L. Relative effects of habitat loss and fragmentation on population extinction. *J. Wildl. Manag.* **61**, 603–610 (1997).
12. Simberloff, D. Habitat fragmentation and population extinction of birds. *IBIS* **137**, S105–S111 (1995).
13. Viña, A. et al. Range-wide analysis of wildlife habitat: implications for conservation. *Biol. Conserv.* **143**, 1960–1969 (2010).
14. Wang, T., Ye, X., Skidmore, A. K. & Toxopeus, A. G. Characterising the spatial distribution of giant pandas (*Ailuropoda melanoleuca*) in fragmented forest landscapes. *J. Biogeogr.* **37**, 865–878 (2010).
15. Xu, W. et al. Conservation of giant panda habitat in South Minshan, China, after the May 2008 earthquake. *Front. Ecol. Environ.* **7**, 353–358 (2009).
16. Gong, M., Guan, T., Hou, M., Liu, G. & Zhou, T. Hopes and challenges for giant panda conservation under climate change in the Qinling Mountains of China. *Ecol. Evol.* **7**, 596–605 (2017).
17. Songer, M., Delion, M., Biggs, A. & Huang, Q. Modeling impacts of climate change on giant panda habitat. *Int. J. Ecol.* **2012**, 108752 (2012).
18. Tuanmu, M. N. et al. Climate-change impacts on understorey bamboo species and giant pandas in China's Qinling Mountains. *Nat. Clim. Change* **3**, 249–253 (2013).
19. He, K. et al. Effects of roads on giant panda distribution: a mountain range scale evaluation. *Sci. Rep.* **9**, 1110 (2019).
20. Li, H. et al. Application of least-cost path model to identify a giant panda dispersal corridor network after the Wenchuan earthquake—case study of Wolong Nature Reserve in China. *Ecol. Model.* **221**, 944–952 (2010).
21. Qi, D. et al. Quantifying landscape linkages among giant panda subpopulations in regional scale conservation. *Integr. Zool.* **7**, 165–174 (2012).
22. Shen, G. et al. Proposed conservation landscape for giant pandas in the Minshan Mountains, China. *Conserv. Biol.* **22**, 1144–1153 (2008).
23. Kong, L. et al. Habitat conservation redlines for the giant pandas in China. *Biol. Conserv.* **210**, 83–88 (2017).
24. Zhang, J. et al. Natural recovery and restoration in giant panda habitat after the Wenchuan earthquake. *Ecol. Manag.* **319**, 1–9 (2014).
25. Boyce, M. S. Population viability analysis. *Annu. Rev. Ecol. Syst.* **23**, 481–497 (1992).
26. Possingham, H. in *Conservation of Australia's Forest Fauna* (ed. Lunney, D.) Ch. 3, 35–40 (Royal Zoological Society of New South Wales, 1991).
27. Lacy, R. C. VORTEX: a computer simulation model for population viability analysis. *Wildl. Res.* **20**, 45–65 (1993).
28. Wei, F., Fgeng, Z. & Hu, J. Population viability analysis computer model of giant panda population in Wuyipeng, Wolong Natural Reserve, China. *Int. Conf. Bear. Res. Manag.* **9**, 19–23 (1997).
29. Guo, J., Chen, Y. & Hu, J. Population viability analysis of giant pandas in the Yele Nature Reserve. *J. Nat. Conserv.* **10**, 35–40 (2002).
30. Jiang, H. & Hu, J. Population viability analysis for the Giant Panda in Baoxing County, Sichuan. *Sichuan J. Zool.* **29**, 161–165 (2010).
31. Li, X., Li, D., Yong, Y. & Zhang, J. A preliminary analysis on population viability analysis for Giant Panda in Foping. *Acta Zool. Sin.* **43**, 285–293 (1997).
32. Yang, Z., Hu, J. & Liu, N. The influence of dispersal on the metapopulation viability of Giant Panda (*Aliuropoda melanoleuca*) in the Minshan Mountains. *Acta Zool. Acad. Sci. Hung.* **53**, 169–184 (2007).
33. Leslie, P. H. On the use of matrices in certain population mathematics. *Biometrika* **33**, 183–212 (1945).
34. Carter, J., Ackleh, A. S., Leonard, B. P. & Wang, H. Giant panda (*Ailuropoda melanoleuca*) population dynamics and bamboo (subfamily Bambusoideae) life history: a structured population approach to examining carrying capacity when the prey are semelparous. *Ecol. Model.* **123**, 207–223 (1999).
35. Xia, W. & Hu, J. On the trend of population dynamics in giant panda based on age structure. *Acta Theriologica Sin.* **9**, 87–93 (1989).
36. Zhu, L. et al. Conservation implications of drastic reductions in the smallest and most isolated populations of giant pandas. *Conserv. Biol.* **24**, 1299–1306 (2010).
37. State Forestry Administration P. R. C. *Report of the Third National Giant Panda Census* (Science Publishing House, 2006).
38. Zhu, L., Hu, Y., Zhang, Z. & Wei, F. Effect of China's rapid development on its iconic giant panda. *Chin. Sci. Bull.* **58**, 2134–2139 (2013).
39. Hu, J. *Research on the Giant Panda* (Shanghai Science and Technology Education Press, 2001).
40. Li, R. et al. Climate change threatens giant panda protection in the 21st century. *Biol. Conserv.* **182**, 93–101 (2015).
41. Yang, B. et al. China's collective forest tenure reform and the future of the giant panda. *Conserv. Lett.* **8**, 251–261 (2015).
42. Linderman, M. et al. The effects of understory bamboo on broad-scale estimates of giant panda habitat. *Biol. Conserv.* **121**, 383–390 (2005).
43. Yang, Z. et al. Reintroduction of the giant panda into the wild: a good start suggests a bright future. *Biol. Conserv.* **217**, 181–186 (2018).
44. Kaiser, H. The dynamics of populations as result of the properties of individual animals. *Fortschr. D. Zool.* **25**, 109–136 (1979).
45. Huston, M., DeAngelis, D. & Post, W. New computer models unify ecological theory. *BioScience* **38**, 682–691 (1988).
46. DeAngelis, D. L. *Individual-Based Models and Approaches In Ecology: Populations, Communities and Ecosystems* (CRC Press, 2017)
47. Uchmański, J. & Grimm, V. Individual-based modelling in ecology: what makes the difference? *Trends Ecol. Evol.* **11**, 437–441 (1996).

48. Wei, F. et al. A study on the life table of wild giant pandas. *Acta Theriologica Sin.* **9**, 81–86 (1989).
49. Hou, W. Revision of the giant panda life table and related data indicators. *Zool. Res.* **21**, 361–366 (2000).

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Author contributions

L.K., Z.O., W.X. and S.L.P. designed the research. L.K., W.X., Y.X. and H.S. performed the research. L.K., W.X., Y.X. and H.S. analysed the data. L.K., Z.O., S.L.P., W.X. and Y.X. wrote the paper.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to Z.O.

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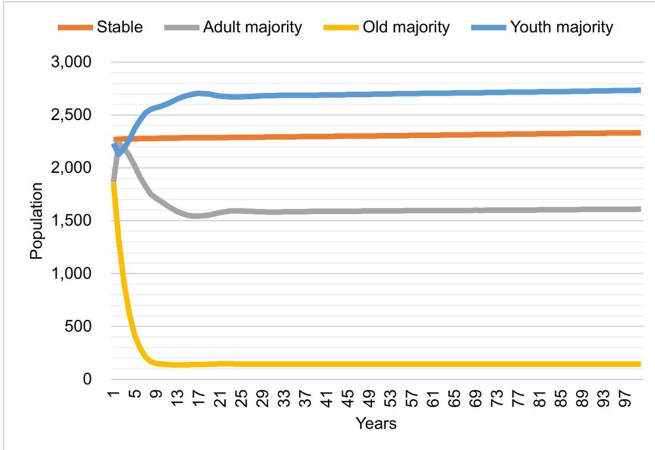
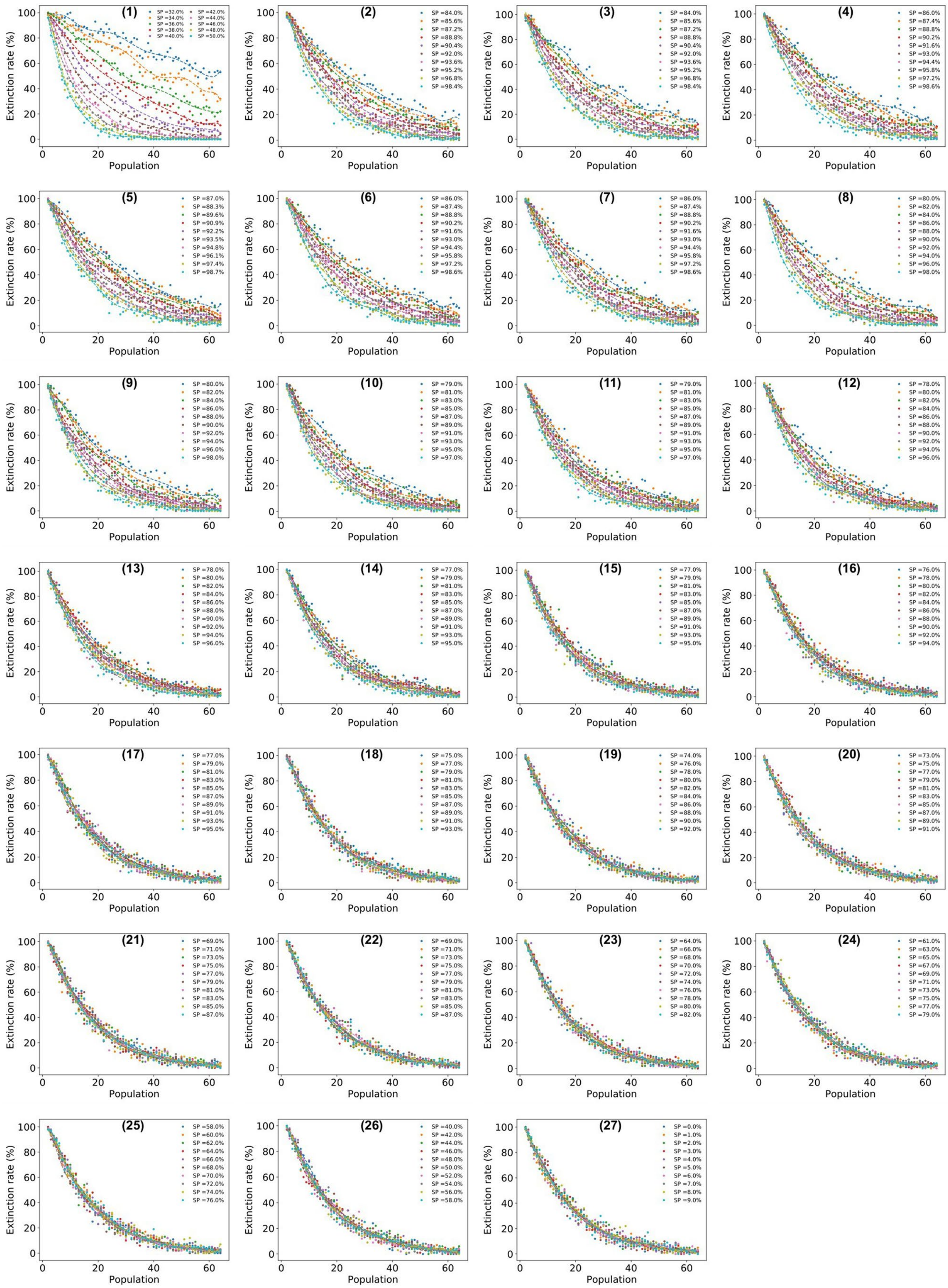
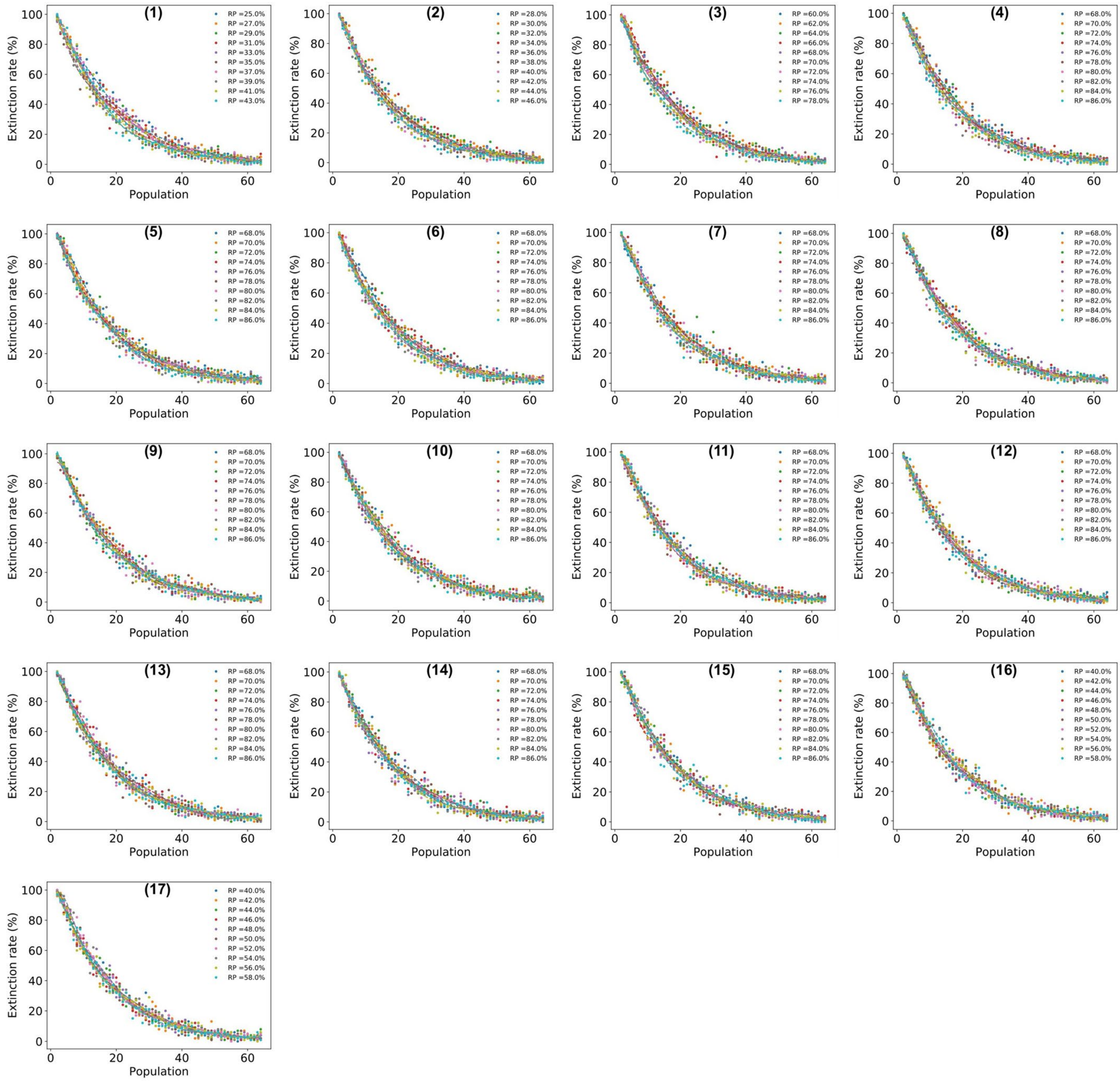


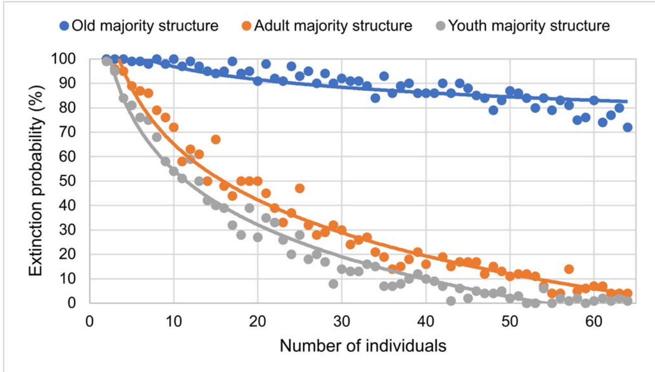
Extended Data Fig. 1 | Population dynamics of giant panda under optimal conditions. Different initial age structures (youth majority structure, adult majority structure, old majority structure and the stable age structure) are used to simulate population trends for 100 years. There is a dramatic decline for the old majority structure. Regardless of the initial age structure, the population will grow slowly and steadily when the age structure becomes stable in the long run.



Extended Data Fig. 2 | Uncertainty in Survival Probabilities (SP). (1): Uncertainty in the SP of the individuals under one year old. (2)-(27): Uncertainty in the SP of the individuals aged 1 to 26.



Extended Data Fig. 3 | Uncertainty analysis of Reproductive Probabilities (RP). (1)-(17): Uncertainty in the RP of the individuals aged 5 to 21.

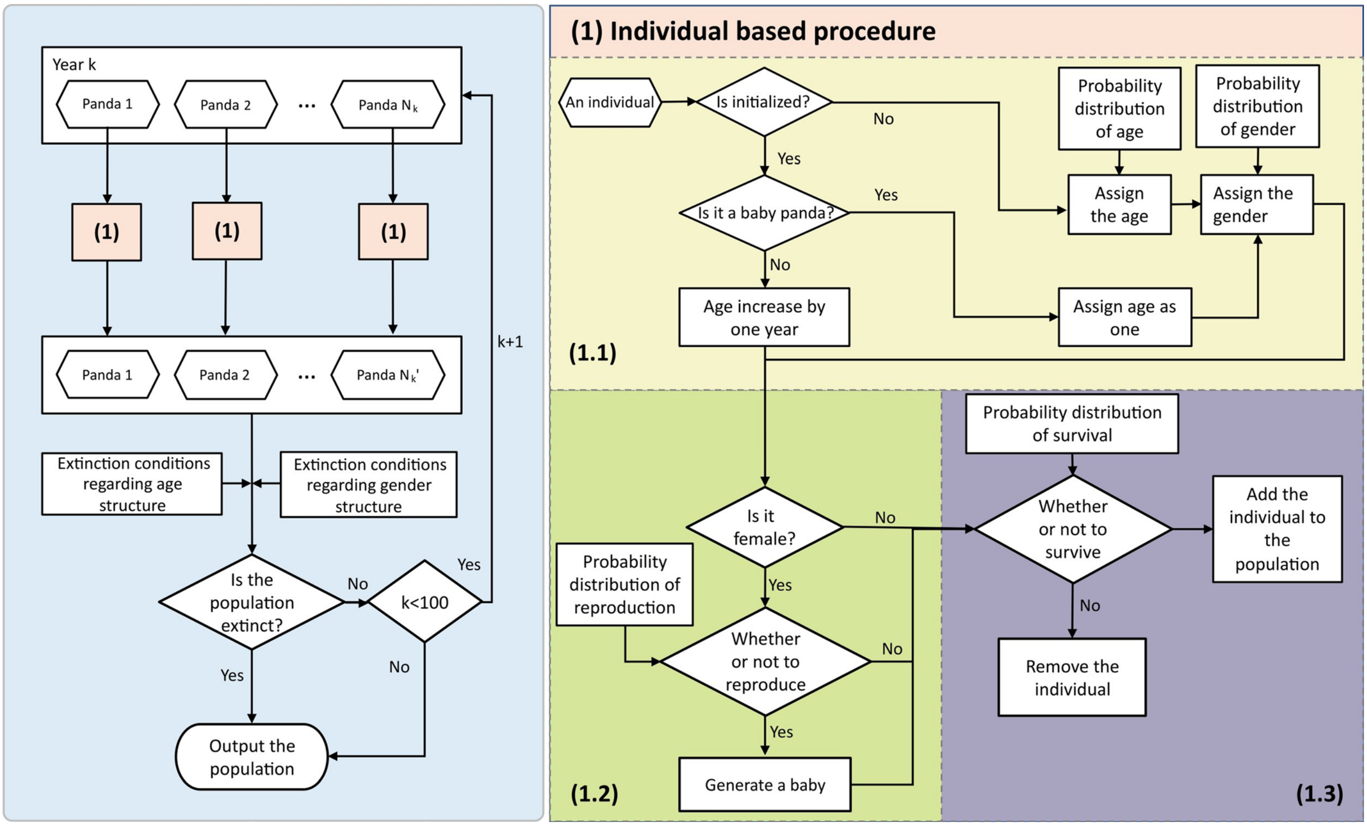


Extended Data Fig. 4 | Uncertainty Analysis of initial age structure. Extinction probabilities of populations with different numbers of individuals under different initial age structures.

Mountain	Panda population	Number of individuals	S1	S2	S3	S4	S5	S6	S7	S8
Qinling	A	7	76	76	76	76	76	76	76	76
	B	20	38	38	38	38	0	0	0	0
	C	277	0	0	0	0				
	D	36	15	15	15	15				
	E	3	95	95	95	95				
	F	2	91	91	91	99	91	91	91	91
		2				99				
Minshan	A	4	91	91	91	91	91	91	91	91
	B	9	69	69	69	69	69	69	69	69
	C	3	95	95	95	95	95	95	95	95
	D	1	100	100	100	100	100	100	100	100
	E	2	99	99	99	99	99	99	99	99
	F	2	99	99	99	99	99	99	99	99
	G	228	0	0	0	0	0	0	0	0
	H	2	99	99	99	99	99	99	99	99
	I	1	100	100	100	100	100	100	100	100
	J	167	0	0	0	0	0	0	0	0
	K	343	0	0	0	0				
	L	33	15	15	18	18				
		2			99	99				
Qionglai	A	91	0	0	0	0	0	0	0	0
	B	211	0	0	0	0				
		5				100				
		3		95	95	100				
		7		76	76	100				
	C	181	0	0	0	0				
	D	19	23	41	27	41				
		3		95		100				
		2		99		100				
		4		91	91	100				
		1		100	100	100		100	100	100
	E	1	100	100	100	100	100	100	100	100
Daxiangling	A	3	91	91	91	95	0	0	0	0
		1				100				
	B	29	18	18	18	23				
		1				100				
		2				99				
	C	2	99	100	100	100	99	100	100	100
Xiaoxiangling	A	20	34	34	34	38	22	22	22	27
		1				100				
	B	4	69	69	69	91				
		3				95				95
		2				99				99
Liangshan	A	36	0	0	0	15	0	0	0	15
		26				27				27
		13				53				53
		5				87				87
		5				100				100
		3				95				95
		1				100				100
		1		100	100	100		100	100	100
	B	13	32	32	32	53	32	32	32	53
		9				69				69
	C	3	95	95	95	95	95	95	95	95
	D	4	91	91	91	91	91	91	91	91
	E	3	95	100	100	100	95	100	100	100
Number of isolated populations			33	40	39	56	21	23	23	32
Number of populations with extinction possibilities greater than 15%			25	32	31	48	17	19	19	29
Number of populations with extinction possibilities greater than 50%			18	25	24	41	15	17	17	26
Number of populations with extinction possibilities greater than 90%			15	21	20	35	13	15	15	20

Extended Data Fig. 5 | See next page for caption.

Extended Data Fig. 5 | Extinction possibility (%) of each population. Cells filled with colour show the extinction possibilities under different scenarios. S1: Business as usual; S2: RCP2.6; S3: RCP4.5; S4: RCP 8.5; S5: Giant Panda National Park; S6~S8: (RCP2.6, RCP4.5, RCP 8.5) & Giant Panda National Park. The darker the red, the higher the extinction possibility, and the darker the blue, the lower the extinction possibility. The second column corresponds to the current giant panda populations in Fig. 1 in the main text.



Extended Data Fig. 6 | Procedure flow of extinction risk simulation of giant panda populations. (1.1) Individual assignment; (1.2) Reproduction simulation; (1.3) Judgement of survival.

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Corresponding author(s): Zhiyun Ouyang

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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	R (v.3.6.1)
Data analysis	We used the following software in this study: ArcMap (v.10.6), MaxEnt (v.3.4.1), python (v.3.7), matplotlib(v.3.2.2), and we also used custom algorithm of an Individual-based model which is described in the main text.

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All studies must disclose on these points even when the disclosure is negative.

Study description	We used an individual-based model to simulate the population dynamics, considering individuals as discrete and autonomous entities. The input parameters include age structure, reproductive rate, death rate and sex ratio for each age category and birth intervals. Our model calculated whether or not life-history events of each agent may occur at each step in a stochastic manner based on the individual's sex and age. It repeated the procedure each year for each individual until the population is extinct. For each simulation, we calculated the extinction probability in 500 simulations for 100 years. For each population, we simulated the extinction probability 100 times and took the average. The MaxEnt model was used to simulate the giant panda habitat and the input variables included altitude, slope, vegetation type, annual average temperature, annual maximum temperature, annual minimum temperature and annual rainfall.
Research sample	We studied all the 33 wild giant panda populations across the panda's entire range, and the population data was from the National Giant Panda Census.
Sampling strategy	We aimed at studying the extinction risk of all the 33 populations of wild giant panda within its entire range.
Data collection	Population data was from the National Giant Panda Census carried out by National Forestry and Grassland Administration. L.K, Y.X and H.S collected the altitude, slope, vegetation type data, and the future meteorological data. The altitude, slope, vegetation type data was from scientific database of the Chinese Academy of Sciences (http://www.csdb.cn/). Details of how future meteorological data was generated can be found in the main text.
Timing and spatial scale	Data collection was done between 2014-2016 and analysis was performed during 2017-2020. The spatial scope of the data is the entire range of wild giant pandas.
Data exclusions	No data were excluded.
Reproducibility	All data underlying our analyses are provided in the main text or the supplementary materials to facilitate future analyses.
Randomization	All the individual assignment, judgments of reproduction and survival were performed randomly according to the probability distributions of age, reproduction, and survival.
Blinding	Not directly relevant to the population dynamics simulation or habitat assessment

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study	
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☒	☐	Eukaryotic cell lines
☒	☐	Palaeontology and archaeology
☒	☐	Animals and other organisms
☒	☐	Human research participants
☒	☐	Clinical data
☒	☐	Dual use research of concern

Methods

n/a	Involved in the study	
☒	☐	ChIP-seq
☒	☐	Flow cytometry
☒	☐	MRI-based neuroimaging