



The hidden risk of using umbrella species as conservation surrogates: A spatio-temporal approach

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ABSTRACT

The use of a charismatic umbrella species as surrogate for sympatric species is often advocated as an efficient approach. However, comprehensive evaluations from a spatio-temporal perspective are few, leaving the long-term effectiveness of such practices remain uncertain. We modeled the habitat change for giant panda and eight sympatric mammalian species using observations from extensive camera trap surveys and remotely-sensed environmental predictors during two time periods, early 2000s and early 2010s. We found that the degree and spatial pattern of the habitat suitability change varied among species. The overall habitat suitability improved between the early 2000s and early 2010s for seven target species including giant panda *Ailuropoda melanoleuca*, suggesting positive effects of several recent conservation projects in restoring natural landscapes for certain species groups. However, the current nature reserve system designed for giant pandas did not adequately cover critical landscapes for several species, including the two species who experienced net habitat loss, Endangered forest musk deer *Moschus berezovskii* and Vulnerable Asiatic black bear *Ursus thibetanus*. To conserve multiple species simultaneously in this region, we recommend establishing nature reserves for other threatened species who share dissimilar habitat needs with giant panda, and adding a widely distributed omnivores, Asiatic black bear, as a surrogate species in central and southwest China. These findings reveal the risk of using umbrella species as a conservation shortcut in protecting animal communities in China, and have substantial implications for other regions where the majority of the conservation funds are directed toward a single charismatic species.

1. Introduction

Managing natural resources to ensure the long-term persistence of fauna and flora species is a central theme in modern conservation sciences (Wiens and Hobbs, 2015). A commonly used strategy to guide conservation planning is the umbrella species approach, where one or few charismatic species, usually large-bodied animals at higher trophic level, are used as a surrogate for the conservation of entire biodiversity

pools (Caro, 2010). This umbrella species approach was originally based on the assumption that providing protection for a species with large area requirements (e.g. lion, tiger) will also shelter a suite of other species with smaller spatial needs (McNab, 1963). In a variant of this concept, the umbrella species criteria are broadened to consider other attributes besides home-range size, such as habitat connectivity or the distribution of critical resources (Breckheimer et al., 2014). However, under either formulation, the umbrella species approach is inevitably limited by

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differences in the ecological conditions required by the individual species, and the more extensive the suite of sympatric species, the more likely their needs will differ from those of the umbrella species (Wang et al., 2018). Seddon and Leech (2008) suggested seven criteria that conservation managers should apply when selecting umbrella species, including well-known biology, high probability of population persistence, and management needs that are beneficial to co-occurring species. The species selected as umbrella species are often the so-called 'flagship species', who can easily garner public attention and funding support, but do not necessarily represent the habitat needs of other focal species (Sattler et al., 2014). In regions where conservation policies are primarily developed for single surrogate species (e.g. common chimpanzee *Pan troglodytes*, Indus river dolphin *Platanista gangetica minor*, giant panda *Ailuropoda melanoleuca*), it is therefore crucial for decision maker to evaluate the effectiveness of such practices for a broad spectrum of species and to propose alternative management plans to fill in the conservation gaps.

Selecting appropriate study designs and analytical pathways for these types of assessments is challenging (Sattler et al., 2014; Seddon and Leech, 2008), and, furthermore, availability of species occurrence information for the sympatric species is often limited (Breckheimer et al., 2014). Often, the broad-scale habitat overlap between the umbrella and sympatric species is used to evaluate the utility of the umbrella species approach, but this approach ignores the fact that landscape change may impact some species more than others (Wang et al., 2018). For example, Hitt and Frissell (2004) argued that bull trout *Salvelinus conuentus* is not an appropriate umbrella species for the protection of cutthroat trout *Oncorhynchus clarkilewisi*. Even though at large scale the two species occupy the same region, at a fine-scale their habitat selection does not overlap. An additional concern is that most previous studies only focused on habitat status for a single, usually short, time period and failed to consider changes over time in species habitat and viability (Yang et al., 2017). Given the nature of landscape change (e.g. deforestation, nature reserve establishment, agricultural expansion), temporal shifts in suitable habitat will likely occur at different rates for different species (Renwick and Rocca, 2015). To address this challenge, it is essential that conservation policy, and specifically the effectiveness of the umbrella approach, be evaluated from a spatio-temporal perspective.

Conservation planning in central and southwest China is an ideal example of landscape management that could benefit from a multi-species focus. Native mammal species in this biodiversity hotspot (Myers et al., 2000) include Endangered (forest musk deer *Moschus berezovskii*), Vulnerable (giant panda *Ailuropoda melanoleuca*, Asiatic black bear *Ursus thibetanus*, takin *Budorcas taxicolor* and Chinese goral *Naemorhedus griseus*), Near Threatened (tufted deer *Elaphodus cephalophus* and Chinese serow *Capricornis milneedwardsii*) and Least Concern (Reeve's muntjac *Muntiacus reevesi* and wild boar *Sus scrofa*) (IUCN, 2016). The potential of the extinction of one of the most iconic species, the giant panda, prompted the creation of a network of 67 nature reserves, under the assumption that increased habitat for giant pandas would also provide shelter for other species (Li and Pimm, 2016; State Forestry Administration, 2006). For example, nine of the seventeen nature reserves were established or upgraded between 2003 and 2010 in Qinling Mountains (e.g. Niuweihe Nature Reserve in 2004, Huangbaiyuan Nature Reserve in 2006), and the systematic annual wildlife monitoring and patrolling activities started in 2004. In addition to the establishment of the nature reserve system, Payment for Ecosystem Services (PES) programs such as Grain-to-Green (GTG) and Natural Forest Conservation (NFC) instituted a range-wide logging ban that have improved the habitat conditions for giant pandas (Ouyang et al., 2016). Partly as a result of these conservation efforts, giant pandas were recently downlisted from Endangered to Vulnerable on the IUCN Redlist (Swaigood et al., 2018). However, in spite of these habitat improvements for giant pandas, several of the sympatric species (e.g. Asiatic black bear, Chinese serow, forest musk deer) appear to have recently

experienced drastic population declines (Table 1, IUCN, 2016). Thus, previous studies may have overestimated the poser of giant panda to serve as an umbrella species for these sympatric species (Li and Pimm, 2016; Xu et al., 2014). Additionally, not enough attention has been paid to the differences in the change of habitat over time for different species. Without an explicit assessment of how well the giant panda represents the conservation needs of the sympatric species, the umbrella species approach may not be effective for conserving sympatric mammals.

Here we present the first analysis of multi-species habitat trends and nature reserve effectiveness for this region. Since the systematic annual wildlife monitoring and monthly patrolling activities started since 2004, we chose two time periods, 2001–2003 and 2011–2013, to investigate species habitat change before and after the intensive conservation effort. We integrate remotely-sensed vegetation phenology information, land features, and anthropogenic indices with an extensive camera trapping dataset to evaluate the habitat dynamics for one umbrella species and eight sympatric species between the two time periods. Our objectives are to: (1) compare the habitat suitability of the nine mammal species between the two time periods; (2) evaluate the effectiveness of current giant panda nature reserves for the conservation of the sympatric species; and (3) investigate the associations between species habitat requirements and conservation or development activities. We propose alternative approaches to support the sustainability of sympatric mammal populations. The results of this study have substantial implications for the conservation of wildlife communities in China as well as other regions throughout the world where the majority of the conservation funds are directed toward a single charismatic species.

2. Material and methods

2.1. Study area

We conducted our field surveys in Qinling and Minshan Mountains in central and southwest China (Fig. 1). Forty two giant panda nature reserves are located across these mountain ranges, harboring more than 60% of the remaining giant panda population (Shaanxi Forestry Department, 2017; Sichuan Forestry Department, 2015). The natural landscapes have been significantly altered by agriculture, commercial logging, highway construction, and other human activities, and since the late 1990s have been under protection and restoration through the implementation of conservation programs such as GTG and NFC (Liu et al., 2016). We generated a 20 km buffer zone around our survey locations, and used the merged buffer zone as our study area. It covers an area of approximately 15,000 km², representing the best wildlife habitat in and around eight nature reserves.

Table 1
Species list and conservation statuses.

Order	Common name	Scientific name	IUCN status ^a	Population trend ^b
Carnivora	Giant panda	<i>Ailuropoda melanoleuca</i>	VU	Increasing
	Asiatic black bear	<i>Ursus thibetanus</i>	VU	Decreasing
Artiodactyla	Wild boar	<i>Sus scrofa</i>	LC	Unknown
	Tufted deer	<i>Elaphodus cephalophus</i>	NT	Decreasing
	Reeves' muntjac	<i>Muntiacus reevesi</i>	LC	Decreasing
	Forest musk deer	<i>Moschus berezovskii</i>	EN	Decreasing
	Takin	<i>Budorcas taxicolor</i>	VU	Decreasing
	Chinese serow	<i>Capricornis milneedwardsii</i>	NT	Decreasing
	Chinese goral	<i>Naemorhedus griseus</i>	NT	Decreasing

^a EN: endangered; VU: vulnerable; NT: near threatened; LC: least concern.

^b Population trend according to IUCN Red List.

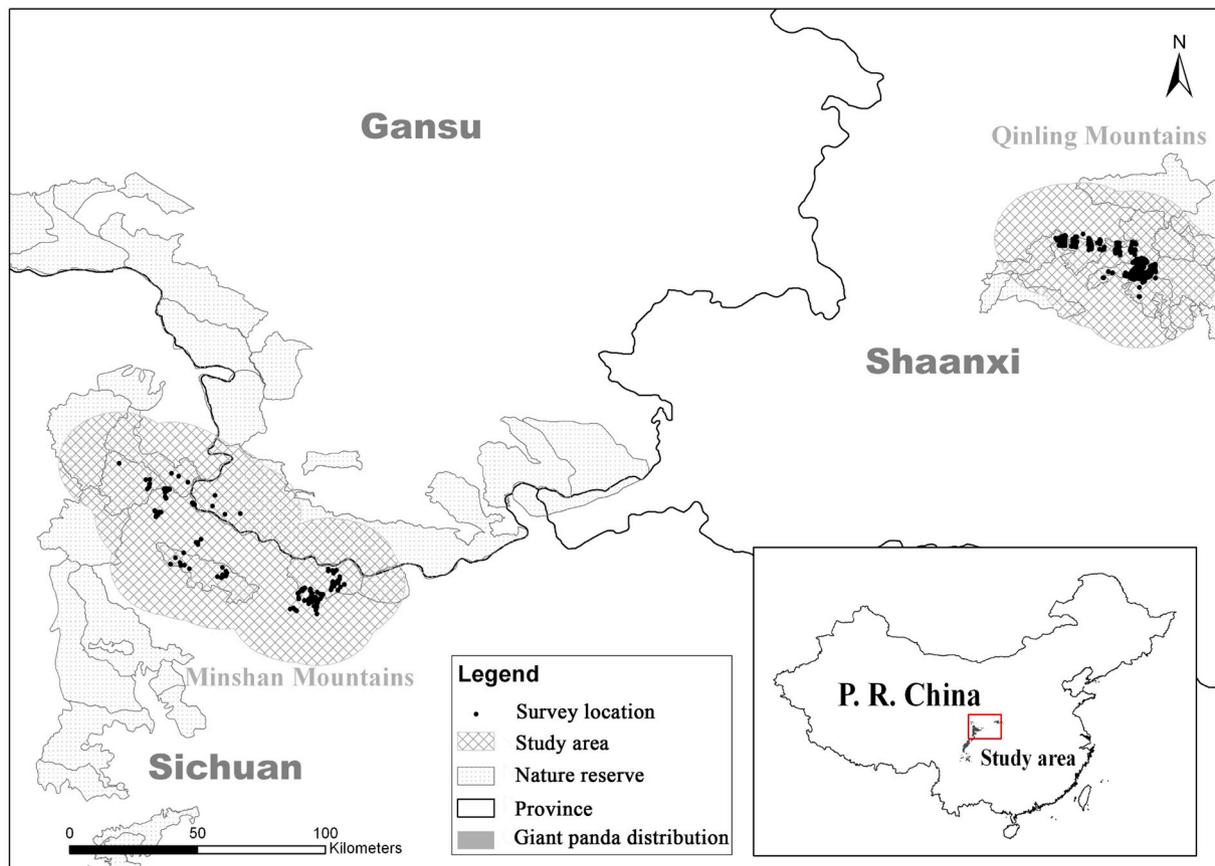


Fig. 1. Map of region and study design. 556 survey locations were investigated using camera-trapping during 2011–2013 in Qinling and Minshan mountain ranges. 304 locations were inside and 252 locations were outside nature reserves.

2.2. Data collection

2.2.1. Camera trap survey

Our camera trap surveys were conducted in and around eight nature reserves (Qinling Mountains: Changqing, Huangbaiyuan, Niuweihe and Pingheliang; Minshan Mountains: Wanglang, Tangjiahe, Xiaohegou and Laohegou) located in Sichuan and Shaanxi provinces (101.54° – 110.28° E, 26.22° – 35.49° N, Fig. 1) between March 2011 and March 2013. To ensure the sampling locations could cover different habitat types, we created 10 km^2 sampling arrays along the elevational gradient in and outside each nature reserve, and divided the arrays to 1 km^2 grid cells. We then conducted camera-trap surveys in randomly selected grid cells. Two simple rules were followed to avoid spatial autocorrelation: 1) no concurrent sample locations being placed within 500 m; and 2) no repeated survey in the same grid cell during any 3-month period. (Li et al., 2012; Wang et al., 2015). We conducted a camera trap survey at 556 locations along the elevation gradient, among which 304 locations were located inside nature reserves. Cameras (Reconyx™ PC800/900, Reconyx Company, USA or Huangwu™ Cam QL1, HW Company China) were mounted on trees at 40 cm height and operated 24 h per day. Scent lure (Carman's Magna-Glan Lure, Montgomery Fur Company, UT, USA) was used at 485 camera trap survey locations upon deployment to slow animal movement around the camera to ensure sufficient reaction time for the camera sensor (Mills et al., 2019). To ensure our field survey locations are able to cover different landscapes, at the end of each survey period (30–50 days, with a mean of 36 days) the cameras were moved to different grid cells. Three variables that could potentially affect the detection probability of camera traps (temperature, camera model and scent lure application) were recorded for each location.

2.2.2. Remotely sensed environmental predictors

We acquired the timeseries Moderate Resolution Imaging Spectroradiometer (MODIS) imagery (eight-day L3 Global 250 m product, MOD09Q1) between 2001 and 2003, and between 2011 and 2013. We then calculated the Wide Dynamic Range Vegetation Index (WDRVI, Gitelson, 2004) for each eight-day composite image (Yang et al., 2017). By enhancing the dynamic range while using the same bands as the widely used Normalized Difference Vegetation Index (NDVI), the WDRVI exhibits less saturation under conditions of high vegetation biomass and is therefore more suitable for detecting phenological change in areas with high vegetation biomass, such as bamboo forest in giant panda habitat (Tuanmu et al., 2010). We used TIMESAT 3.2 (Jönsson and Eklundh, 2007) to generate annual dynamic curves of the WDRVI, and obtained 11 phenology metrics based on the shape of the annual WDRVI dynamic curves (Fig. S1, see Tuanmu et al., 2010). Phenology indices include the length of growing season, the maximum and base value of annual WDRVI curves, the annual accumulative WDRVI layer and other seven other variables (Table 2). These phenological metrics can provide insight into the landscape characteristics that are important for our targeting species, including landscape change (e.g. deforestation, crop land abandonment, urbanization), vegetation seasonality, and the productivity of forest, shrub land and other vegetation types (Viña et al., 2010).

2.2.3. Land features and anthropogenic predictors

We reviewed previous studies, and identified land feature (e.g. elevation) and anthropogenic (e.g. road density) variables (Table 2) that have been suggested to associate with focal species' habitat suitability (Zhang et al., 2004; Lu et al., 2007; Guan et al., 2015; Wang et al., 2018). We used a 30-m resolution digital elevation model (Aster, 2009) to delineate the slope using ArcToolbox in ArcGIS 10.2 (ESRI, 2011). Geo-

Table 2
Variables for species habitat modelling and their multi-collinearity.

Name	Description	VIF
Phenological		
Base level	The base value of the annual dynamic curves of the Wide Dynamic Range Vegetation Index (WDRVI)	1068.73 (1.43) ^b
Maximum level ^a	The maximum value of the WDRVI	2327.42 (excluded)
Amplitude ^a	The difference between maximum and base level of WDRVI	1465.22 (excluded)
Date of the start of growing season	The number of days when growing season starts	98.71 (2.01)
Date of the middle of growing season ^b	The number of days of the middle of growing season	38.94 (excluded)
Date of the end of growing season ^b	The number of days when growing season ends	191.81 (excluded)
Length of growing season	The duration of growing season	91.43 (6.23)
Large integral ^a	The accumulative WDRVI of a year	111.08 (excluded)
Small integral	The base level WDRVI of a year	47.09 (6.89)
Increase rate	WDRVI growth rate	7.13 (3.81)
Decrease rate	WDRVI decrease rate	4.55 (2.24)
Land feature		
Elevation ^a	Numeric (m)	3.92 (excluded)
Slope ^a	Numeric (°)	146.69 (excluded)
Anthropogenic		
Human population	Numeric (/km ²)	1.21 (1.17)
Distance to residential area ^a	Numeric (km)	46.28 (excluded)
Road density	Numeric (km ²)	2.63 (1.54)
Detection		
Temperature	Categorical (<5 °C, 5–15 °C, >15 °C)	NA
Camera model	Categorical (Reconyx, Huangwu)	NA
Scent lure	Categorical (applied, not applied)	NA

^a Covariates that had a VIF >7 excluded for later analyses in giant panda modelling.

^b Values in brackets indicate the VIF value after excluding other correlated variables.

referenced data of human population and roads were obtained from State Forestry Administration (data available upon request).

2.2.4. Modelling habitat suitability for early 2010s

The detection history (detection/non-detection by camera traps) is assumed to represent species' habitat suitability of each species and was used for habitat modelling (MacKenzie et al., 2002). Prior to modelling species habitat suitability, we used a Variance Inflation Factor (VIF) method (García et al., 2015), and excluded any variable that had a VIF value greater than 7 from further analyses (Table 2) (Shiu, 2006). We constructed occupancy models to estimate species-environment relationship and map habitat suitability (MacKenzie, 2006). Occupancy models use information from repeated observations at each site to estimate detection and occupancy probabilities, adjusting for imperfect detectability in camera trap surveys (MacKenzie, 2006). We divided the camera-trap period at each survey location into five-day segments to generate an observation history (Wang et al., 2018). For each segment, a species was labeled "detected" if any detection was made during the five-day segment and "not-detected" otherwise.

To calculate the detection probability of each species, we included all environmental predictors for each model, and added all possible combinations of the three detection variables. We then selected the detection variable(s) in models that had the lowest AIC values in subsequent steps (see full model details in Wang et al., 2018). To estimate the species-environment relationship and predict species' occurrence probability, all possible combinations of the environmental predictors were then combined with the selected detection variables and ranked the

models according to their AIC value (Erb et al., 2012). We selecting all top models with a delta AIC values <3 to best model (lowest AIC) (Richards et al., 2011), and used a weighted model-averaging approach to create a final occupancy model (Posada and Buckley, 2004). This process was completed for each species, and the final model was used to generate species-specific probability maps for early 2010s (Richards et al., 2011).

All occupancy modelling was conducted using the "unmarked" package in R (Fiske and Chandler, 2011). We used a 10-fold method to randomly select 90% of camera trap locations (n = 500) for model training, and used the remaining locations (n = 56) for model validation. We constructed Receiver Operating Characteristic curves for each species and calculated the Area Under the Curve (AUC) to evaluate the models' predictive accuracy (Allouche et al., 2006).

2.2.5. Investigating habitat change between the early 2000s and early 2010s

We assumed that the species' habitat preference remained consistent during 2001–2013, and extrapolated the species-environment association from occupancy models created with the 2011–2013 camera trap data and remotely sensed environmental predictors to the 2001–2003 remotely-sensed environmental predictors to simulate habitat suitability for the early 2000s period. To evaluate the discriminative ability of our habitat suitability models, we obtained distribution information of giant panda and takin from the Shaanxi and Sichuan Forestry Department, and used a 10-fold cross validation method and calculated the AUC value (LeDell et al., 2015). The forestry departments recorded giant panda and takin signs along 736 transects (approximately 3140 km total length) in 2010 and 665 transects (approximately 2440 km total length) in 2000 that covered all our study areas in Qinling and Minshan Mountains. Giant pandas and takins were labeled "present" if any signs (e.g. fecal and foraging site) were recorded. We used a 10-fold cross validation method. Although this evaluation dataset potentially has imperfect detection, and does not include all species tested in this study, it offers the best available information for model validation of some species.

To quantify the change in habitat quality for each species, we first calculated the difference in the Habitat Suitability Index (HSI) for every pixel across the study area between the two periods (Yen et al., 2012). We used a Ward's hierarchical clustering analysis to classify each species Δ HSI, and established a dendrogram using Ward's hierarchical clustering of a Gower dissimilarity matrix (Bohlenbaugh et al., 2011; Murtagh and Legendre, 2014). Pairwise dissimilarities between species Δ HSI in each grid cells were measured using Gower distance, and species with similar Δ HSI patterns were categorized into same cluster (Gower and Warrens, 2014).

To evaluate whether the giant panda nature reserve system adequately covered the conservation needs for giant panda and sympatric species, we used the maximum value of the standard deviation of species HSI variation among different model runs as the threshold, and categorized species habitat change into "improved" (Δ HSI >0.2), "stable" ($-0.2 > \Delta$ HSI >0.2), and "decreased" (Δ HSI < -0.2). We then compared species habitat change in and outside nature reserves.

3. Results

Giant panda was detected at 103 among 556 camera trap locations, other large and medium sized mammal species include one large-bodied omnivore (Asiatic black bear, 49 locations), three large-bodied herbivores (takin, 173 locations; Chinese serow, 54 locations; and wild boar, 127 locations), and four medium-sized herbivores (tufted deer, 88 locations; Chinese goral, 125 locations; Reeve's muntjac, 72 locations; and forest musk deer, 48 locations).

Six phenological variables and two anthropogenic variables were included in habitat models after the multi-collinearity test (Table 2). Model construction for each species identified a unique set of important

environmental variables (Table 3). Human population had negative or no association with habitat suitability for all species except Chinese serow. Habitat suitability was higher in areas with higher base value of the annual WDRVI for forest musk deer, giant panda, Reeve's muntjac and tufted deer, while the habitat suitability of Asiatic black bear, Chinese goral, Chinese serow, takin and wild boar had negative association with the base value of the annual WDRVI. Giant panda and takin habitat suitability had significant negative association with annual WDRVI curve decrease rate. The habitat suitability for Chinese serow, forest musk deer, Reeve's muntjac and wild boar was high at locations where the increase rate of annual WDRVI curve was high. Takin, tufted deer and Asiatic black bear habitat had negative association with road density. Model validation results show that the early 2010s habitat suitability maps for all species (Table S1), and the early 2000s maps for giant panda (AUC 0.825 ± 0.028) and takin (AUC 0.808 ± 0.031), exhibited high accuracies.

The degree and spatial pattern of the HSI change varied among species (Fig. 2). Comparing the spatial HSI change patterns among species using hierarchical clustering analysis, takin, Chinese goral, wild boar, and tufted deer had a similar spatial pattern to the change experienced by giant panda (Fig. 3). Forest musk deer, Asiatic black bear, Chinese serow and Reeve's muntjac consisted another cluster. For areas that had positive HSI change for forest musk deer, Asiatic black bear, Chinese serow and Reeve's muntjac, there was less overlap with areas with positive HSI change for giant panda, and vice versa (Fig. 2).

The net habitat improvements (percentage of grid cells that had HSI change >0.2 minus percentage of grid cells that had HSI change <-0.2) is highest for Chinese goral (30%), followed by takin (27%), wild boar (27%), giant panda (14%) and Reeve's muntjac (13%) (Fig. 4). Among all species, forest musk deer (3%) and Asiatic black bear (8%) were the only species that experienced net habitat loss. Forest musk deer had the least habitat improved grid cell percentage (6%), and Asiatic black bear had highest habitat decreased grid cell percentage (18%). All other species had an amount of habitat increase higher than 15%, and net habitat improvements higher than 7% (Fig. 4).

Comparing the habitat change pattern at locations inside or outside nature reserves, all species but forest musk deer, Asiatic black bear and tufted deer had higher net habitat improvements inside (mean: 26%) than outside (mean: 18%) nature reserves. Forest musk deer had 3% net habitat loss outside nature reserves, and 7% net habitat loss inside nature reserves. Asiatic black bear had 8% net habitat loss at locations far from nature reserves, and 23% net habitat loss inside nature reserves.

4. Discussion and conclusions

In assessing the effectiveness of using giant panda as an umbrella species to protect sympatric mammals, we found that Vulnerable Asiatic black bear and Endangered forest musk deer had minimum or none net habitat improvements even under intensive conservation effort, and the current giant panda nature reserve system do not cover areas where these two species had habitat improvements. In addition, we found that the where forest musk deer, Asiatic black bear, Chinese serow and Reeve's muntjac had positive habitat changes had less overlap with areas with positive HSI change for giant panda, and vice versa. Our results differed from previous studies (Li and Pimm, 2016; Xu et al., 2014), which either compared giant panda habitat within the known geographic range of other species (Li and Pimm, 2016), or the ratio of overlap between giant panda reserves and other species' potential habitat (Xu et al., 2014). We found two major limitations in previous approaches: 1) simply overlapped giant panda and other species habitat maps, but ignored the different habitat preference and ignored the potentially different habitat trends; and 2) used a forest layer to represent species vegetation needs, but ignored the fact that different species have different preference to specific vegetation characteristics (e.g. length of growing season, understory bamboo, and etc.). As a result of the above limitations, previous studies were relatively general and

Table 3

Top models for predicting the occupancy probability of focal species.

Rank	Model ^a	K	LL	AIC	delta AIC ^b
Asiatic black bear					
1	Inc, Pop, Roa, Sos	21	-209.36	462.46	0.00
2	Bas, Len, Roa, Sma, Sos	23	-208.10	464.27	1.81
3	Pop, Roa, Sos	19	-212.46	464.34	1.88
4	Bas, Roa, Sma	19	-212.77	464.95	2.49
5	Bas, Dec, Roa, Sma	21	-211.05	465.43	2.97
Chinese goral					
1	Bas, Dec, Len, Sma	21	-632.07	1307.88	0.00
2	Bas, Dec, Len, Pop, Sma	23	-630.11	1308.30	0.42
3	Bas, Dec, Len, Pop, Roa, Sma	25	-628.07	1308.59	0.71
4	Bas, Dec, Len, Roa, Sma	23	-630.57	1309.22	1.34
5	Bas, Dec, Len, Sma, Sos	23	-631.40	1310.88	3.00
Chinese serow					
1	Bas, Dec, Len, Roa, Sma	22	-250.42	546.75	0.00
2	Bas, Roa	16	-257.00	547.02	0.27
3	Bas, Roa, Sma	18	-255.27	547.82	1.07
4	Roa	14	-259.64	548.05	1.31
5	Bas, Pop, Roa	18	-255.50	548.28	1.53
6	Dec, Inc., Pop, Roa, Sma, Sos	24	-249.11	548.48	1.74
7	Bas, Dec, Inc., Len, Roa	22	-251.37	548.65	1.90
8	Len, Roa, Sma	18	-255.71	548.69	1.94
9	Roa, Sma	16	-257.89	548.78	2.03
10	Pop, Roa	16	-258.07	549.14	2.40
11	Bas, Dec, Len, Roa, Sos	22	-251.67	549.24	2.49
12	Bas, Inc., Len, Roa	20	-253.85	549.26	2.52
13	Bas, Pop, Roa, Sos	20	-253.90	549.38	2.63
14	Dec, Roa	16	-258.21	549.44	2.69
15	Len, Roa	16	-258.31	549.63	2.89
16	Bas, Pop, Roa, Sma	20	-254.08	549.73	2.99
Forest musk deer					
1	Dec, Inc., Len, Pop, Roa, Sos	25	-88.96	230.37	0.00
2	Bas, Dec, Inc., Len, Pop, Roa, Sos	27	-86.75	230.37	0.00
3	Bas, Dec, Inc., Len, Pop, Sos	25	-89.53	231.52	1.15
4	Bas, Dec, Inc., Len, Roa, Sos	25	-89.72	231.91	1.54
5	Dec, Len, Pop, Sma	21	-95.28	233.29	2.92
Giant panda					
1	Bas, Dec, Pop, Roa	21	-425.74	895.21	0.00
2	Bas, Dec, Roa	19	-429.22	897.86	2.65
3	Bas, Dec, Inc., Pop, Roa	23	-425.42	898.91	2.87
4	Bas, Dec, 7%, Pop, Roa, Sos	23	-425.60	899.27	2.96
Reeve's muntjac					
1	Bas, Dec, Inc., Roa, Sos	22	-277.71	601.33	0.00
2	Bas, Dec, Roa, Sma, Sos	22	-278.42	602.74	1.41
3	Bas, Dec, Roa, Sos	20	-281.14	603.86	2.53
4	Bas, Dec, Inc., Len, Roa, Sos	24	-276.80	603.87	2.54
5	Bas, Dec, Inc., Roa, Sma, Sos	24	-276.81	603.88	2.55
6	Inc, Pop, Roa, Sos	20	-281.32	604.22	2.89
Tufted deer					
1	Bas, Dec, Inc., Pop, Roa, Sos	25	-499.02	1050.51	0.00
2	Bas, Dec, Inc., Roa	21	-503.65	1051.03	0.53
3	Bas, Dec, Inc., Roa, Sos	23	-501.62	1051.32	0.82
4	Bas, Dec, Inc., Pop, Roa	23	-501.63	1051.34	0.83
5	Bas, Dec, Inc., Len, Pop, Roa, Sos	27	-497.27	1051.42	0.91
6	Bas, Dec, Inc., Pop, Roa, Sma, Sos	27	-497.88	1052.62	2.12
7	Bas, Dec, Inc., Len, Roa, Sos	25	-500.41	1053.28	2.77
8	Bas, Dec, Inc., Roa, Sma	23	-502.61	1053.29	2.79
9	Bas, Inc., Pop, Roa, Sma, Sos	25	-500.46	1053.39	2.88
Takin					
1	Bas, Dec, Inc., Pop, Roa, Sos	25	-1056.58	2165.61	0.00
2	Bas, Dec, Inc., Pop, Roa, Sma, Sos	27	-1055.04	2166.96	1.35
3	Bas, Dec, Inc., Len, Pop, Roa, Sos	27	-1055.12	2167.12	1.51
4	Bas, Dec, Inc., Roa, Sma, Sos	25	-1057.71	2167.87	2.26
5	Bas, Inc., Len, Pop, Roa, Sos	25	-1058.02	2168.49	2.88
Wild boar					

(continued on next page)

Table 3 (continued)

Rank	Model ^a	K	LL	AIC	delta AIC ^b
1	Bas, Dec, Pop, Sma, Sos	22	-683.21	1412.33	0.00
2	Bas, Dec, Pop, Roa, Sma, Sos	24	-681.37	1413.00	0.67
3	Dec, Pop, Sma, Sos	20	-686.41	1414.40	2.07
4	Bas, Dec, Len, Pop, Sma, Sos	24	-682.40	1415.07	2.74
5	Bas, Dec, Len, Pop, Roa, Sma, Sos	26	-680.33	1415.32	2.99
6	Dec, Pop, Roa, Sma, Sos	22	-684.72	1415.34	3.02

^a Bas: The base value of the annual dynamic curves of the Wide Dynamic Range Vegetation Index (WDRVI); Dec: WDRVI decrease rate; Inc.: WDRVI growth rate; Len: duration of growing season; Pop: human population; Roa: road density; Sma: The base level WDRVI of a year; Sos: The number of days when growing season starts.

^b For brevity, top models presented up to delta AIC = 3.

ambiguous about conservation gap in using giant panda as a surrogate species to conserve other species. Here we demonstrate a spatio-temporal approach, and our result is fundamentally different with previous ones (Fig. 2). We believe that our findings provide an important empirical base for using phenological metrics over time to fit species distribution models, and is applicable to other regions where the majority of the conservation funds are directed toward a single charismatic species (Mikoláš et al., 2017).

We found that the net habitat loss inside nature reserves is 200% higher for Asiatic black bear and 80% higher for forest musk deer than outside nature reserve, while all other species had higher net habitat increase in than outside nature reserves (Fig. 4). We found that these two

species had positive associations with high base level and increase rate of annual WDRVI curve. Since currently nature reserve system for giant panda was primarily located at higher elevation with aged mixed forest, we speculate that the low-land deciduous forest and shrubland outside reserves could better meet the habitat need for species such as Asiatic black bear and forest musk deer. Our results were consistent with previous studies that focused on single-species conservation planning (Liu et al., 2011; Yao et al., 2015). According to a regional-scale study on the conflict between Asiatic black bears and humans, there was no significant effect of the proximity of giant panda nature reserves on bear occurrence in any region of Sichuan Province (Liu et al., 2011). However, although the vegetation may be better outside nature reserves, species are facing much serious threats including poaching, livestock grazing, tourism and construction (Wang et al., 2015; Li et al., 2017; Zhang et al., 2017). For example, Yao et al. (2015) used distance sampling and strip-transect methods to survey forest musk deer population in southern China, and reported low population density, which was a result of illegal poaching outside nature reserves. To summarize, we suggest a better designed reserve network to promote the long-term persistence of multiple species simultaneously.

An interesting result in nature reserves was that giant panda had relatively high percentage of habitat with positive HSI change (21%) and lowest percentage of habitat with negative HSI change among all species tested (1%). Such result was contradicted to the general perception that habitat recovery for giant pandas is slow. As a habitat specialist, giant panda is believed to have much stricter environmental requirements than many sympatric species (e.g. the need for bamboo, less steep slope, and stronger avoidance to anthropogenic interference, see Zhang et al., 2011; Hull et al., 2014; Pan et al., 2014). When

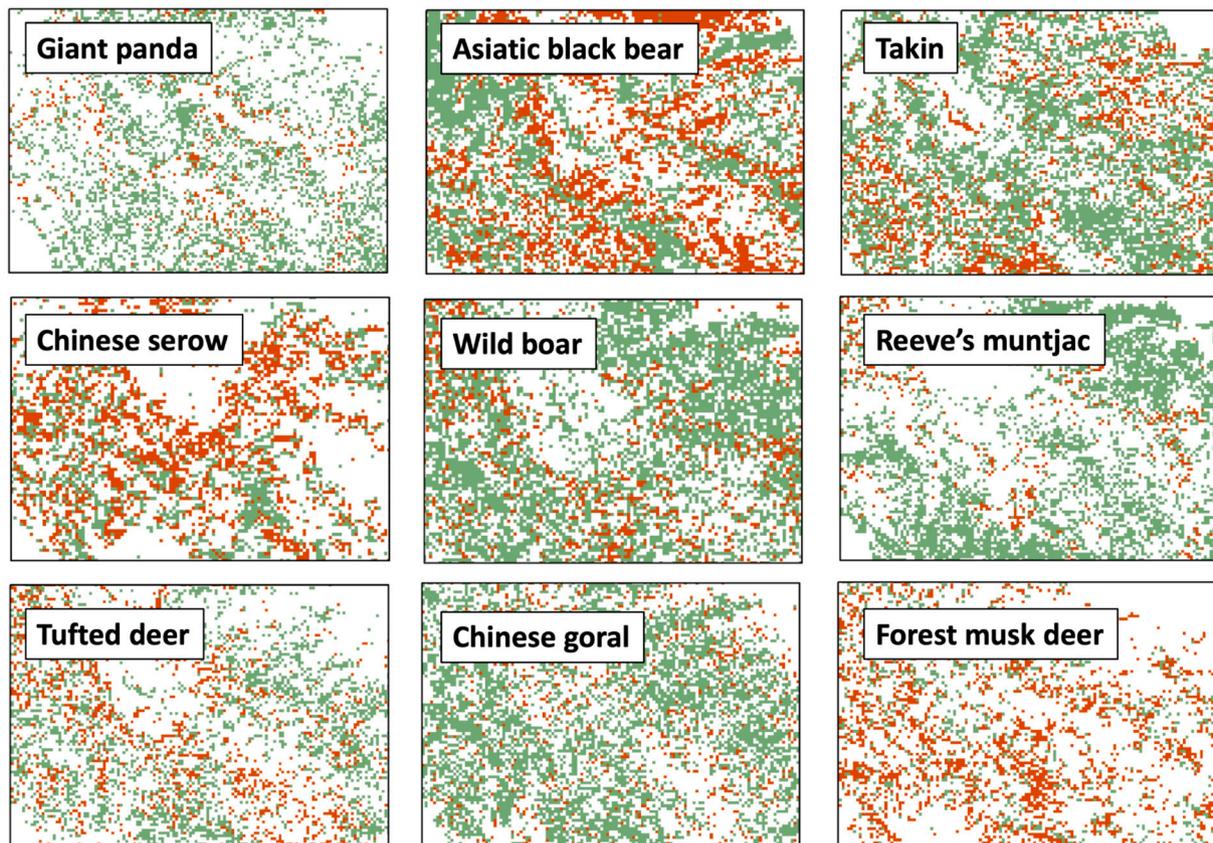


Fig. 2. The habitat suitability change of different. Red color indicates habitat suitability decrease (habitat suitability decrease >0.2), and green color indicates habitat suitability improvements (habitat suitability increase >0.2). Using southern Minshan as example, the degree and deviation of habitat change vary among species. For forest musk deer, Asiatic black bear, Chinese serow, and Reeve's muntjac, areas that had positive habitat suitability change did not overlap with those areas where habitat suitability improved for giant panda, and vice versa. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

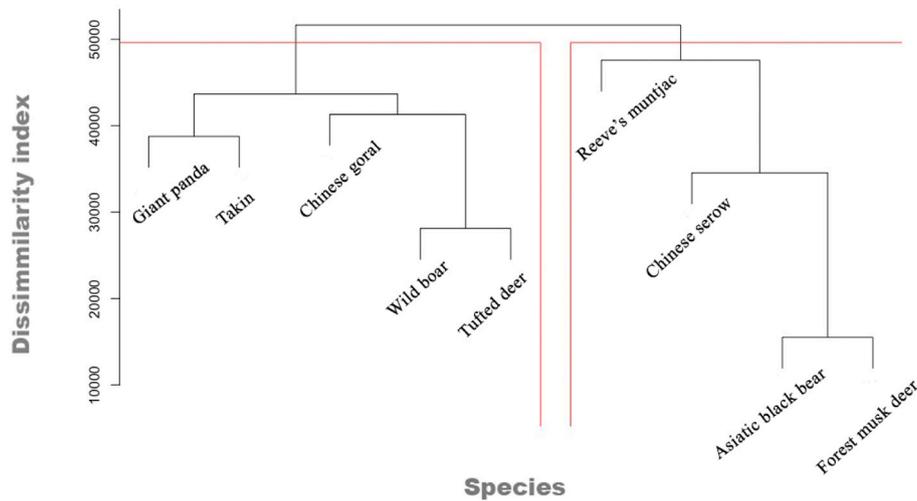


Fig. 3. The similarity of species' habitat change patterns between early 2000s and 2010s. Four species (Asiatic black bear, forest musk deer, Chinese serow, and Reeve's muntjac) formed a cluster, indicating these species had different habitat change patterns compared with the giant panda and other sympatric species.

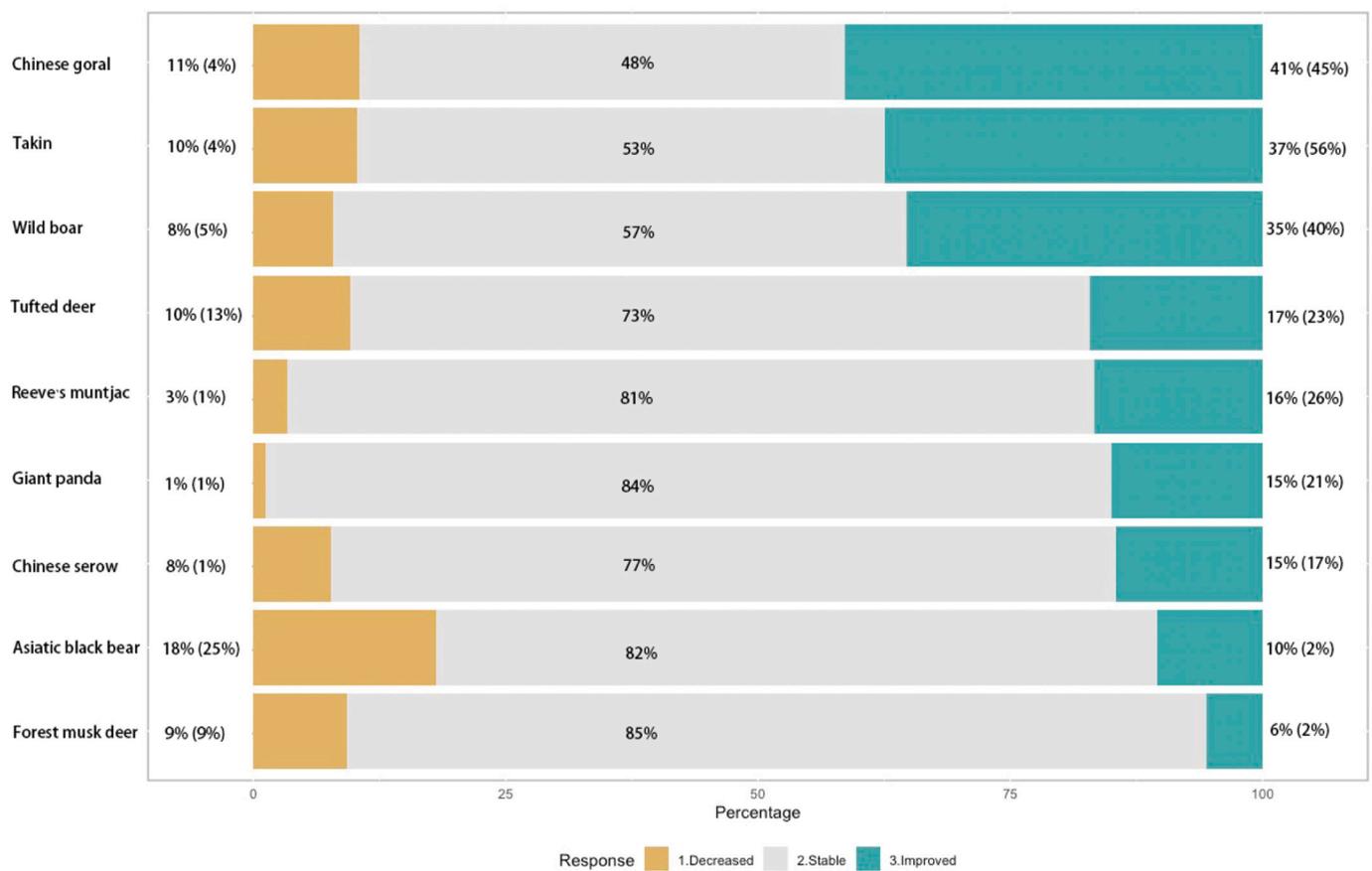


Fig. 4. Overall habitat suitability change and changes inside nature reserves (in brackets). Across the entire study area, Chinese goral and takin exhibited the most habitat improvements (percentage of habitat had suitability change >0.2). Forest musk deer had the least habitat decrease (percentage of habitat had suitability change < -0.2). Forest musk deer and Asiatic black bear had net habitat loss (percentage of grid cells had habitat improved minus decreased) of 8% and 3%, while other species' net habitat improvements were higher than 7%. In comparing the habitat changes in and outside nature reserves, all species but Asiatic black bear, forest musk deer, and tufted deer had higher net habitat improvements (percentage of grid cells had positive habitat suitability change minus negative) inside nature reserves than outside. Asiatic black bear had 23% net habitat loss in nature reserves, and forest musk deer had 7% net habitat loss in nature reserves.

conservation efforts such as GTG and NFC programs and nature reserve establishment have successfully led to giant pandas being downlisted from Endangered to Vulnerable on the IUCN Redlist, there was a common believe among reserve managers that similar or more significant

population recovery would be happening to sympatric habitat generalist such as Asiatic black bears. However, similar habitat recovery may only happen to species whose habitat preference is similar to giant pandas, for example, takin and wild boar. In a study that analyzed the giant

panda movement behavior, Wan et al. (2005) reported a steady takin population growth in a giant panda nature reserve in northern Sichuan Province. During a most recent provincial giant panda census, wild boar were found to be overpopulated near giant panda nature reserves (Xiaofeng Zhang, personal communicate). For the animals whose habitat is not highly associated with conifer or mixed forest with bamboo understory, their population recovery could therefore be much slower than anticipated (Wang et al., 2018).

Given the fact that the proposed Giant Panda National Park will soon be officially established (Xu et al., 2017), it is crucial that park managers incorporate multi-species habitat restoration plans into the development and management of this new park system. A practice promoted by other researchers for ecosystems outside China has been to select additional umbrella species to maximize biodiversity conservation (Caro, 2010; Sattler et al., 2014). Ideally, umbrella species should be species that are habitat generalists with large home ranges, whose presence is easy to sample, and that are only moderately sensitive to human interference (Seddon and Leech, 2008). We recommend using widely distributed omnivores, such as the Asiatic black bear, as an additional surrogate species in central and southwest China because it meets most of the above criteria (IUCN, 2016), and is in urgent need for more strict poaching control in areas outside of current nature reserves (Liu et al., 2011; Malcolm et al., 2014).

CRedit authorship contribution statement

Fang Wang: Conceptualization, Methodology, Formal analysis, Writing - Original Draft, Writing - Review & Editing

Julie Winkler: Methodology, Validation, Writing - Review & Editing

Andrés Viña: Methodology, Writing - Review & Editing

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Sheng Li: Investigation

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Zhiqiang Zhao: Conceptualization, Methodology

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Ying Tang: Writing - Review & Editing

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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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.2020.108913>.

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