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Range-wide analysis of wildlife habitat: Implications for conservation

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ABSTRACT

The range-wide habitat status of many endangered species is unclear. We evaluated the status and spatial distribution of the habitat of the endangered giant panda (*Ailuropoda melanoleuca*) across its entire geographic range (i.e., six mountain regions located in Sichuan, Shaanxi and Gansu provinces, China) by integrating field and remotely sensed data to develop a habitat distribution model. Results suggest that current suitable habitat corresponds to ca. 1/4 of the habitat baseline (i.e., maximum amount of habitat possible). The highest proportion of suitable habitat relative to the baseline is in the Qinling mountain region. Overall, around 40% of the suitable habitat is inside nature reserves, but the proportion of habitat inside them varied among different mountain regions, ranging from ca. 17% (Lesser Xiangling) to ca. 66% (Qinling). The habitat model also predicted the occurrence of potentially suitable habitat outside the currently accepted geographic range of the species, which should be further evaluated as potential panda reintroduction sites. Our approach is valuable for assessing the conservation status of the entire habitat of the species, for identifying areas with significant ecological roles (e.g., corridors), for identifying areas suitable for panda reintroductions, and for establishing specific conservation strategies in different parts of the giant panda geographic range. It might also prove useful for range-wide habitat analyses of many other endangered species around the world.

1. Introduction

As many species are now facing unprecedented reductions in habitat availability due mainly to human actions, range-wide habitat analyses are becoming a necessity, particularly for endangered species and across political boundaries (Sanderson et al., 2002; Thorbjarnarson et al., 2006). Such analyses allow the identification of areas that require different conservation actions (e.g., establishment of new nature reserves, corridors and species reintroduction sites). However, for many threatened and endangered species the information regarding specific habitat characteristics and distribution across their entire geographic ranges is often inadequate (Odom et al., 2001). This is the case of the endangered giant panda (*Ailuropoda melanoleuca*), which is considered a global icon of biodiversity conservation (Liu et al., 2001; Loucks et al., 2001; Mackinnon and De Wulf, 1994).

Giant pandas once ranged throughout most of China, northern Vietnam, and northern Myanmar (Pan et al., 2001), but fewer than 1600 individuals in the wild are estimated to survive within six mountain regions (Qinling, Minshan, Qionglai, Greater Xiangling, Lesser Xiangling and Liangshan) in three provinces (Gansu, Shaanxi and Sichuan) of China (Hu and Wei, 2004; Mackinnon and De Wulf, 1994; Reid and Gong, 1999; State Forestry Administration, 2006) (Fig. 1). The drastic reduction in the geographic distribution of the species is mainly attributed to human activities [e.g., agricultural expansion, logging, infrastructure development, and residential development (Liu et al., 2003a)]. This has prompted the Chinese government and international non-governmental organizations to invest in the establishment of 63 giant panda nature reserves (protected areas specifically designed to conserve the species). As panda populations inside many of these nature reserves tend to be isolated (Viña et al., 2007; Xu et al., 2006), it is necessary to establish conservation blocks that integrate several nature reserves and enhance the habitat connectivity among them. However, giant panda habitat analyses have been performed mainly inside nature reserves (Linderman et al., 2005; Liu et al., 1999, 2001, 2005; Viña et al., 2007, 2008) or within single mountain regions (Feng et al., 2009; Loucks et al., 2003; Shen et al., 2008; Xu et al., 2006) and often using different criteria for characterizing the habitat of the species. Therefore, an analysis of the habitat status and distribution across the entire geographic range of the species is warranted.

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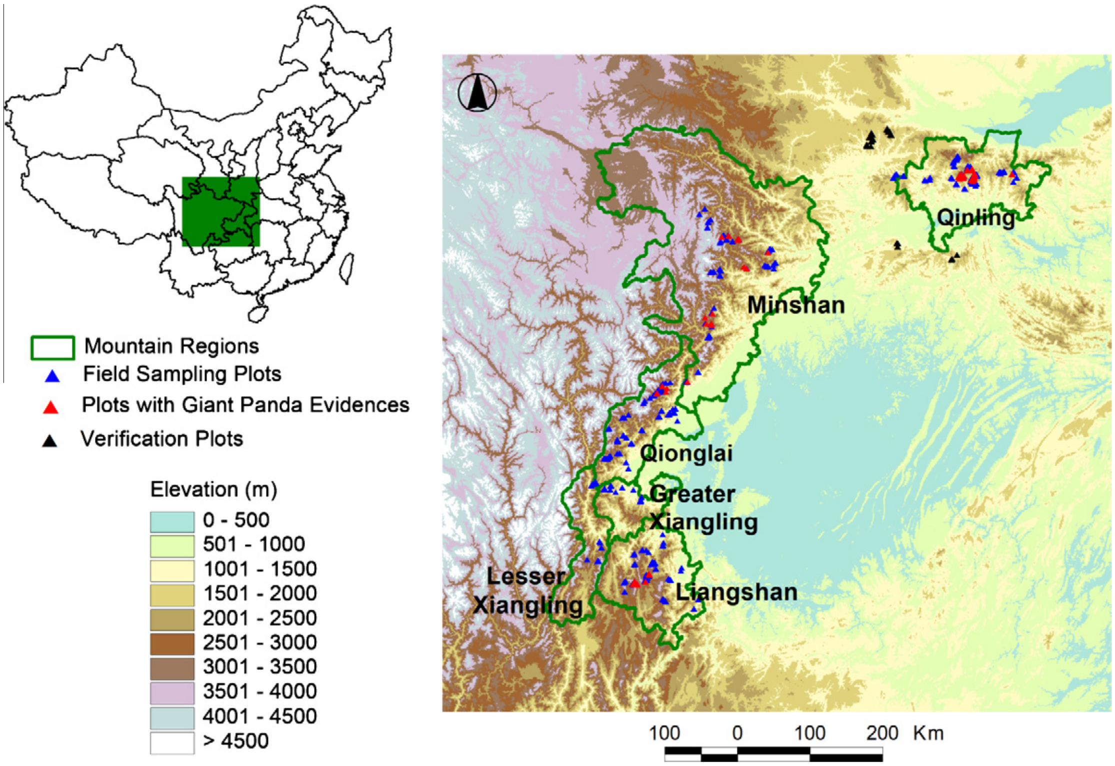

Fig. 1. Topographic map showing the location of the mountain regions currently inhabited by giant pandas (Hu and Wei, 2004; Mackinnon and De Wulf, 1994; Reid and Gong, 1999; State Forestry Administration, 2006). Also shown are locations of the 540 field sampling plots established for this study with 84 of them exhibiting evidences of the occurrence of giant pandas (i.e., tracks, feces, dens, sleeping sites), together with 34 plots established outside the mountain regions for model verification.

In this study we quantified the habitat of the giant panda across its entire geographic range. Our specific objectives were to establish the areal extent of the habitat, assess the degree of habitat connectivity, evaluate the amount of habitat inside 63 giant panda reserves, and identify potential sites for locating new nature reserves, corridors and reintroduction sites.

2. Methods

2.1. Study area

The study area (ca. 125,170 km^2) was defined by the six mountain regions currently inhabited by giant pandas (Fig. 1). These mountain regions are characterized by high mountains and deep valleys, with elevations between ca. 70 and 6250 m. Together with this strong elevational gradient there is high variation in climate and soils that leads to diverse flora and fauna. One of the world's top 25 Biodiversity Hotspots is included in the region, the Southwest China hotspot (Mittermeier et al., 2004; Myers et al., 2000). Natural vegetation is dominated by evergreen and deciduous broadleaf forests at lower elevations and subalpine coniferous forests at higher elevations. The dense understory of these forests is dominated by ca. 60 bamboo species, with approximately 35 of them being the preferred food of giant pandas (Hu and Wei, 2004; Li, 1997).

2.2. Habitat distribution model

2.2.1. Modeling approach

Models that predict the spatial distribution of the habitat of target species have generated great interest in recent years, as they help not only in the prediction of the locations of suitable habitat, but also aid in understanding niche requirements (Guisan and Thuiller, 2005). These models relate observations of the occurrence of the target species with environmental variables in order to establish the suitability of an area to meet the biological requirements of the target species. Many such models require information on the areas that exhibit both confirmed presences and absences of the target species. While the presence of the target species can be determined through direct observation or through the use of surrogates (e.g., fecal droppings), information on confirmed absences is more difficult to obtain. This is particularly true for vagile species with small population sizes, such as the giant panda, because the absence of individuals in a particular place does not necessarily mean that it is unsuitable habitat. Therefore, models specially designed for presence-only data have been developed in recent years (Hirzel et al., 2002; Phillips et al., 2006; Stockwell and Peters, 1999).

Several studies that compared the performance of different presence-only models have found that MaxENT, a general purpose machine-learning method for making predictions from incomplete information, constitutes one of the most accurate algorithms, particularly when using a small number of occurrence locations (Elith et al., 2006; Hernandez et al., 2006; Pearson et al., 2007; Phillips et al., 2006). Therefore, we used MaxENT as the modeling framework for mapping the spatial distribution of giant panda habitat. MaxENT estimates the probability of an area to be suitable habitat for the target species, by finding a probability distribution of maximum entropy (i.e., maximum uniformity) such that the expected value of each environmental variable matches its empirical average, defined by known occurrence locations. The algorithm runs a user-defined number of iterations or until a convergence limit is reached. The final output is a continuous habitat suitability index (HSI), ranging from 0 (unsuitable) to 1 (perfectly suitable).

2.2.2. Giant panda occurrence

The giant pandas are difficult to observe in the wild due mainly to their small population size in a large geographic area. Therefore, we used surrogates (i.e., tracks, fecal droppings, dens, sleeping sites) to determine their occurrence. Among these, fecal droppings were the most abundant and constituted a straightforward indicator of the occurrence of the species because they are deposited frequently (an average of four droppings/hour) and remain visible for several months (Schaller et al., 1985). We searched for these surrogates in 540 sampling plots (ca. 314 m^2 each) distributed throughout the study area (Fig. 1). To avoid areas where giant pandas are known to be absent, we concentrated our field sampling efforts in the geographic areas of each of the six mountain regions where surrogates of the species have been sighted in the past. Sampling plots were then distributed randomly within each of these geographic areas. The selection of geographic areas to randomly distribute our sampling plots was done with the aid of local guides. The center of each sampling plot was geo-referenced using a real-time differentially corrected global positioning system (GPS) receiver. Each of these plots was visited one time in either September–November of 2004, or in May–July of 2005, 2006 and 2007. Among the 540 plots surveyed, 84 exhibited evidences of the occurrence of giant pandas.

Although no giant panda sightings have been reported outside the six mountain regions comprising the study area in recent decades, 34 additional field plots were distributed outside them in order to verify if some of these areas constitute potential suitable habitat. The locations of these verification plots (Fig. 1) were established based on the results of the habitat model developed in the study (see below).

2.2.3. Environmental variables

The phenological characteristics of forest canopies together with the asynchronous phenologies of forests with and without understory bamboo have been used for identifying and mapping the areas that constitute giant panda habitat within a single nature reserve (Viña et al., 2008). Vegetation phenology has also been associated with the elevational migration of giant pandas (Beck et al., 2008). Therefore, we used vegetation phenology, as measured by a time series of images acquired by the Moderate Resolution Imaging Spectroradiometer (MODIS) satellite sensor system, as an environmental variable for modeling giant panda habitat. MODIS time series data were selected not only for their high temporal resolution (i.e., daily acquisition), but also because they cover vast areas, thus are suitable for analyzing the habitat status and distribution across the entire geographic range of the species. We used a time series of 8-day composite surface reflectance data acquired between January, 2004 and December, 2007 (a total of 184 images, 46 for each year) by the MODIS sensor system on board the National Aeronautics and Space Administration (NASA) Terra satellite (product MOD09Q1 – Collection 5). This geometrically corrected image dataset has surface reflectance values, corrected for the effects of atmospheric gases, aerosols and thin cirrus clouds (Vermote et al., 1997), collected in two spectral bands ($b1$: 620–670 nm; $b2$: 841–876 nm) with a pixel resolution of ca. 250 m × 250 m. A time series of the Wide Dynamic Range Vegetation Index (WDRVI) was calculated from these data using the formula:

$$\mathrm{WDRVI} = \frac{\alpha \cdot \rho_{b2} - \rho_{b1}}{\alpha \cdot \rho_{b2} + \rho_{b1}} \tag{1}$$

where ρ_{b1} and ρ_{b2} are surface reflectance values in bands 1 and 2, respectively, and α is a coefficient that down-weights the contribution of the near-infrared band ($b2$), making it comparable to that of the red band ($b1$) (Gitelson, 2004). We selected an $\alpha = 0.25$ as the optimum for the MODIS time series dataset used in the study (Henebry et al., 2004). The WDRVI constitutes a non-linear transformation of the widely used Normalized Difference Vegetation Index (NDVI) and is specifically designed to increase the sensitivity to changes in vegetation when the NDVI saturates (Gitelson, 2004; Viña et al., 2004). This index exhibits a linear relationship with the fraction of photosynthetically active radiation absorbed by vegetation (Viña and Gitelson, 2005) and has been used for analyzing the spatio-temporal heterogeneity of tropical forests (Aguilar-Amuchastegui and Henebry, 2006, 2008).

To reduce the effects of temporal autocorrelation in the WDRVI image time series a principal component analysis was applied. A few principal components effectively summarize the dominant modes of the spatio-temporal variation, therefore retaining most of the information contained in the image time series (Benedetti et al., 1994; Eklundh and Singh, 1993; Townshend et al., 1985). The first 20 principal components retained (explaining ca. 70% of the total variance) were used as environmental variables. These variables, together with the locations of the 84 field plots (out of the 540 sampled) with giant panda occurrences (i.e., with presence of tracks, feces, dens, sleeping sites) were used in MaxENT. If at least one field plot with a panda occurrence fell within a MODIS pixel, the entire pixel was considered as habitat, and used for model calibration. This constitutes an approximation since a pixel assigned as panda habitat would not necessarily be 100% habitat on the ground as a result of sub-pixel complexity. However, this procedure is common in many pixel-based imagery classification methods (Lu and Weng, 2007). As all the 84 field plots with giant panda evidences were located in different MODIS pixels, 84 pixels were used for model calibration.

2.2.4. Model validation

To evaluate the accuracy of the habitat model, three validation procedures were performed using an independent validation dataset of 1453 giant panda occurrence locations obtained during the third national panda survey performed between 2000 and 2002 (State Forestry Administration, 2006). As sometimes two or more of these giant panda occurrences fell within a single MODIS pixel, a total of 1257 pixels with at least one giant panda occurrence were used for validation.

The first procedure involves binning the HSI scale and then calculating the frequency of pixels with giant panda occurrences that fall in each of these bins. This observed frequency is then divided by the frequency of pixels belonging to the same bin across the study area (i.e., expected frequency). If the locations used for validation occur at random, this ratio of frequencies (observed/expected) is equal to unity. A Spearman-rank correlation coefficient is then calculated between the ratio of frequencies (observed/expected) in each bin and the bin rank. A model with high accuracy should have a high positive Spearman-rank correlation coefficient (i.e., closer to 1), as more observed giant panda occurrences would continually fall within higher bin ranks (Boyce et al., 2002). The main disadvantage of this procedure is that it is sensitive to the number of bins as well as their boundaries (Boyce et al., 2002). Therefore, a modification (Hirzel et al., 2006) was implemented in which the HSI was divided into 100 bins and an observed/expected frequency was calculated in each shift of a moving window of 10 continuous bins. Through this procedure, a continuous observed/expected frequency curve was obtained and a Spearman-rank correlation coefficient [termed Boyce Index (Hirzel et al., 2006)] was calculated.

The second procedure is the Kappa analysis, which is a chance-corrected measure of agreement (Cohen, 1960). The Kappa statistic ranges between 0 and 1 and model accuracy can be judged as excellent if Kappa > 0.75, good if 0.75 > Kappa > 0.4, or poor if Kappa < 0.4 (Araújo et al., 2005; Landis and Koch, 1977). However, this validation procedure could not be performed in its traditional manner due to the lack of species absence information. Therefore, we distinguished presence from random, rather than presence from absence, using two different randomly selected pixel datasets. The first dataset [named Background (BG)] consisted of 1000 pixels randomly selected across the entire study area (i.e., the six mountain regions inhabited by giant pandas). This was done in order to evaluate the accuracy of the model for separating habitat pixels from background pixels. The second dataset [named Forest (F)] also consisted of 1000 pixels randomly selected across the study area, but only among pixels with more than 10% tree cover in the MODIS-derived vegetation continuous fields tree-cover product (Hansen et al., 2003). This was done in order to evaluate the accuracy of the model for separating habitat pixels from forest pixels, as not all forest pixels constitute giant panda habitat (e.g., forests without understory bamboo). The 10% threshold in the tree-cover product was selected with the assumption that pixels with at least 10% tree cover have the potential to be classified as forest under natural conditions, in order to account for the deforestation that has occurred during the last decades (Liu et al., 2001; Viña et al., 2007). Unfortunately the use of presence/random data will always give lower Kappa values than those obtained by presence/absence data because several randomly selected pixels will fall in areas that have been correctly predicted as suitable habitat by the model, thus artificially increasing commission errors. Therefore, the Kappa values obtained in this study will not be fully comparable with those of other studies.

The third procedure consists of calculating a receiver operating characteristic (ROC) curve (Hanley and Mcneil, 1982). The ROC curve is a plot of the sensitivity values (i.e., true positive fraction) vs. their equivalent 1-specificity values (i.e., false positive fraction) for all possible HSI thresholds. The area under the ROC curve (AUC) is a measure of model accuracy. The AUC ranges from 0 to 1, where a score of 1 indicates perfect discrimination, a score of 0.5 implies a prediction that is not better than random, and lower than 0.5 implies a worse than random prediction. A standard for judging model performance based on AUC values (Araújo et al., 2005; Swets, 1988) is: excellent ($\text{AUC} > 0.9$), good ($0.9 > \text{AUC} > 0.8$), fair ($0.8 > \text{AUC} > 0.7$), poor ($0.7 > \text{AUC} > 0.6$), and failed ($0.6 > \text{AUC} > 0.5$). Although presence/absence data are required for calculating ROC curves, we used the same dataset on presence pixels and the two random pixel datasets (i.e., BG and F) used for performing the Kappa analysis to calculate ROC curves. As with the Kappa analysis, AUC values calculated in this manner tend to be underestimated because some of the random pixels are actually presence pixels (Wiley et al., 2003), but a random prediction will still correspond to an AUC of 0.5 (Phillips et al., 2006).

In order to examine the relative importance of each of the 20 principal components (used as environmental variables) for modeling giant panda habitat we developed a model with each of the principal components in isolation and then calculated the AUC using the validation data described above. The principal component with the highest AUC value constitutes the most informative (in isolation) for separating giant panda habitat.

2.3. Habitat status

To evaluate the amount of habitat area and its connectivity in the different mountain regions comprising the study area, it was necessary to find an optimal HSI cumulative threshold for separating the continuous HSI into habitat and non-habitat areas. We selected the optimal threshold as the one that exhibited the maximum Kappa, when applied to all possible HSI cumulative thresholds, using the 1257 pixels with a giant panda occurrence and the 1000 BG pixels obtained randomly across the study area. For assessing the degree of habitat connectivity, we calculated the clumpiness index using the software FRAGSTATS (McGarigal et al., 2002). This landscape metric is related to habitat aggregation and ranges from zero to one, with values closer to zero indicating a higher degree of fragmentation and values closer to one indicating a high degree of aggregation. The most relevant characteristic of this metric for this study is that it is independent of habitat area (Neel et al., 2004), making it suitable for comparing the degree of habitat connectivity in different mountain regions that differ in the amount of habitat they contain.

Since the different mountain regions have particular topographic conditions, in order to compare the habitat status among them we evaluated the predicted suitable habitat in each mountain region (i.e., as obtained by MaxENT applied to field and MODIS data) against a habitat baseline condition defined as the maximum amount of habitat possible (Viña et al., 2007). For this, a map of the habitat baseline condition was generated using elevation and slope obtained in lattice format from a digital elevation model acquired by the Shuttle Radar Topography Mission, which has been shown to exhibit high elevational accuracy (Berry et al., 2007). Because giant pandas have particular topographic preferences (Hu and Wei, 2004; Liu et al., 1999), pixels with slopes $\leqslant 45^\circ$ and within an elevational range between 1200 and 3800 m [although varying these ranges among different mountain regions as shown by Hu and Wei (2004)] were considered as the topographic baseline. It should be noted that this baseline could have a potential bias towards higher elevations, since the upper elevation limit in the distribution of the species is due to physiological constraints while the lower elevation limit is mainly dictated by human disturbance (Feng et al., 2009; Schaller et al., 1985). However, it is still suitable for comparing the habitat status among different mountain regions. To exclude pixels falling within these topographic criteria but not classified as forest under natural conditions, an additional restriction was included in which pixels with less than 10% tree cover, in the MODIS-derived vegetation continuous fields tree-cover product (Hansen et al., 2003), were excluded from the habitat baseline.

3. Results

The map derived from the giant panda habitat model shows that suitable habitat is located primarily in the central (Qionglai mountain region) and northern (Minshan and Qinling mountain regions) portions of the study area, while the southernmost region (i.e., comprising Liangshan, Greater Xiangling and Lesser Xiangling mountain regions) exhibits comparatively lower amounts of habitat (Fig. 2). This map exhibited high accuracy using three different validation procedures (Fig. 3), which demonstrates that the approaches used have utility for evaluating the habitat distribution of the species. The Boyce Index exhibited a high positive value, representing a monotonic increase in the ratio of frequencies (observed/expected) as more observed giant panda occurrences continually fall within higher HSI bin ranks (Fig. 3A), while the Kappa and AUC values ranged between 0.52 and 0.62 and between 0.83 and 0.89, respectively (Fig. 3B and C). These values show that the model is good, based on standards for judging model performance (Araújo et al., 2005; Landis and Koch, 1977; Swets, 1988), not only for separating habitat pixels from background pixels across the study area, but also for separating habitat pixels from forest pixels. These values are quite high, considering the fact that the use of random pixels reduces the Kappa and AUC due to artificial commission errors. In addition, part of the disagreement between the model output and the occurrence data obtained from the giant panda survey of 2000–2002 (State Forestry Administration, 2006) could be attributable to changes in the habitat suitability between validation and remotely sensed data collection dates.

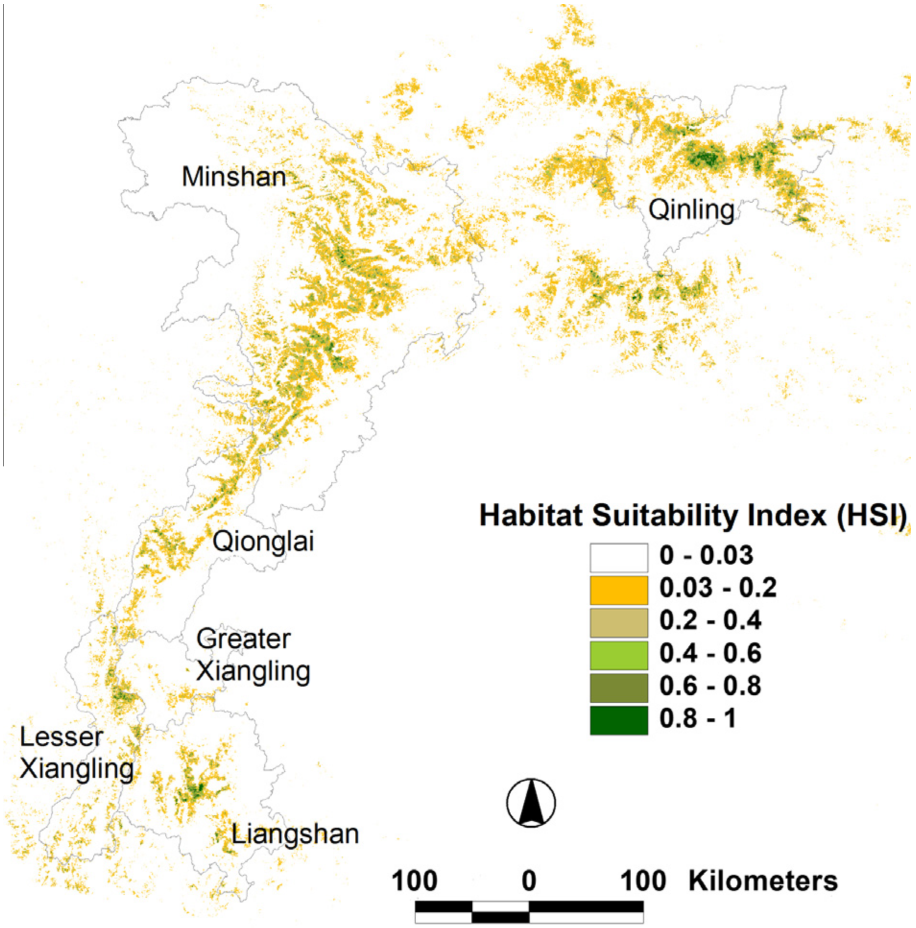

Fig. 2. Spatial distribution of the giant panda habitat suitability index (HSI) values across its entire geographic range obtained through MaxENT using time series of the Wide Dynamic Range Vegetation Index (WDRVI) derived from 8-day surface reflectance data acquired in 2004–2007 by the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor on board the Terra satellite (product MOD09Q1 – Collection 5).

The first principal component, explaining ca. 24.4% of the variance in the time series of MODIS–WDRVI imagery, contains the highest information by itself for discriminating habitat from background pixels (Fig. 4A). The 17th principal component, while explaining only ca. 0.8% of the image time series variance, contains the highest information by itself for discriminating habitat from forest pixels (Fig. 4A). These two components exhibit the highest correlation with spring WDRVI values, as shown by their loadings (Fig. 4B). Therefore, this season seems to be the best time for discriminating giant panda habitat. For comparison purposes, the loadings of the second principal component are also shown in Fig. 4B. This component represents the annual seasonality of the vegetation (i.e., highest loadings occur during summer and winter; Fig. 4B), but while this component explains about 10% of the variance contained in the image time series, it contains little information by itself for discriminating giant panda habitat (Fig. 4A).

A binary habitat/non-habitat map (Fig. 5) was created after finding the optimal HSI cumulative threshold for separating habitat pixels from background pixels (HSI = 0.03), as determined by the Kappa analysis (Fig. 3B). This map shows that the remaining panda habitat inside the six mountain regions currently inhabited by giant pandas covers an area of ca. 21,300 km^2, corresponding to ca. 17% of the entire study area and ca. 27% of the habitat baseline. Although the Minshan mountain region exhibits the largest area of giant panda habitat (around 48% of the entire habitat is located in this mountain region; Table 1), the Qinling mountain region exhibits the highest proportion of giant panda habitat as compared against the habitat baseline (ca. 45% of the habitat baseline; Table 1). Thus, the status of the giant panda habitat seems to be better in Qinling than in any other mountain region. In addition, this mountain region also exhibits the highest values of the clumpiness index (Table 1), suggesting that the habitat present in Qinling exhibits higher connectivity than the one observed in other mountain regions. The mountain regions of the southernmost portion of the giant panda geographic range (i.e., Liangshan, Greater Xiangling and Lesser Xiangling) exhibit not only the lowest absolute and relative amounts of suitable habitat (i.e., compared against the habitat baseline), but also the lowest clumpiness index values (Table 1). Therefore, the status of the habitat in these mountain regions is the poorest in the entire geographic range of the species, in terms of the amount of habitat present and its degree of connectivity.

Around 40% of the suitable giant panda habitat in the six mountain regions is within nature reserves, but differences among mountain regions are evident. For instance, while ca. 2/3 of the habitat in Qinling is inside nature reserves only ca. 17% of the habitat in Lesser Xiangling is inside them (Table 1).

Projecting the model to areas outside the study area (i.e., outside the six mountain regions inhabited by giant pandas), we found that large areas of suitable giant panda habitat occur, particularly in areas located to the northwest, west and south of the Qinling mountain region (Fig. 2). Based on the information obtained in the 34 verification plots (Fig. 1), we determined that some of these predicted habitat areas outside the six mountain regions potentially constitute suitable habitat, because they are forested, with

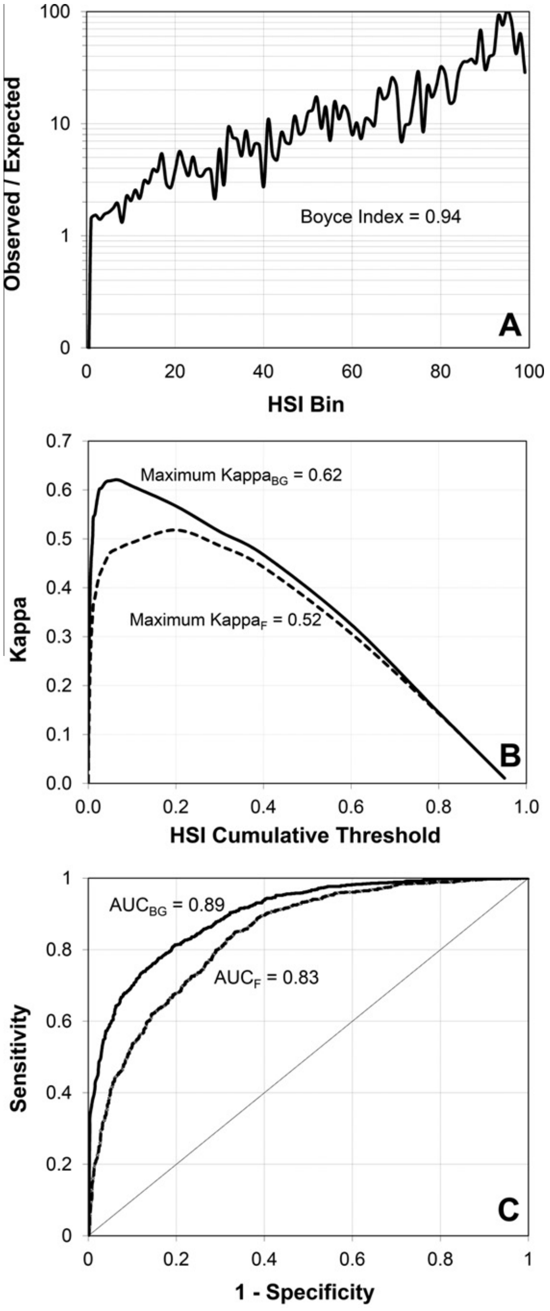

Fig. 3. Results of three validation procedures: (A) Boyce Index, (B) Kappa, and (C) the area under the receiver operating characteristic curve (AUC), calculated using an independent validation dataset of 1453 giant panda occurrence locations obtained from the third national panda survey between 2000 and 2002 (State Forestry Administration, 2006), together with 1000 pixels randomly selected across the study area (BG), and 1000 pixels randomly selected among pixels classified as forest (F) [i.e., with more than 10% tree cover in the MODIS-derived vegetation continuous fields tree-cover product (Hansen et al., 2003)]. Maximum Kappa$_{BG}$ and AUC$_{BG}$ represent the accuracies of the model for separating habitat pixels from background pixels, while maximum Kappa$_F$ and AUC$_F$ represent the accuracies of the model for separating habitat pixels from forest pixels.

gentle slopes and contain understory bamboo species such as *Bashania fargesii* and *Fargesia dracocephala*, which are suitable for the giant panda.

4. Discussion

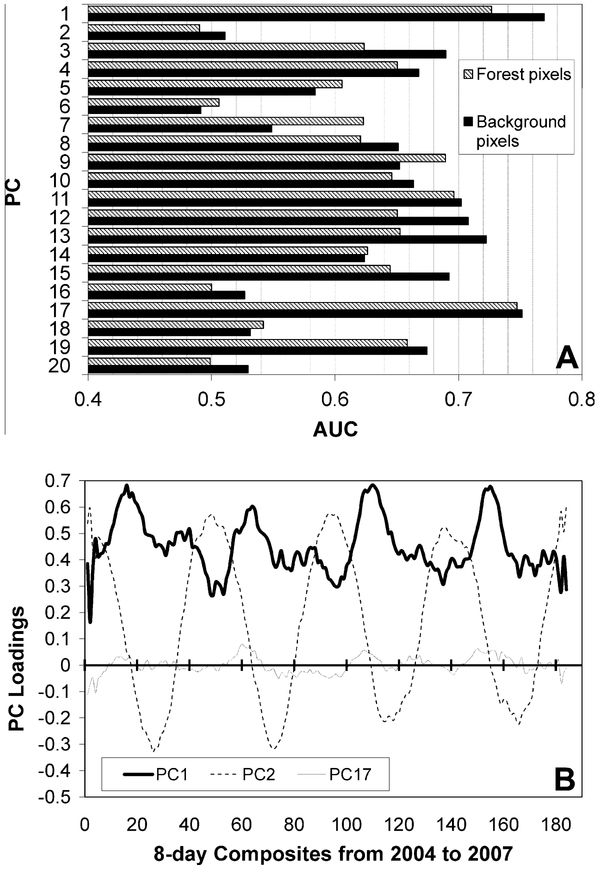

Fig. 4. (A) AUC values (calculated using the same validation data described in Fig. 3) of the giant panda habitat model obtained using each principal component [PC; derived from the MODIS–WDRVI image time series (2004–2007)] in isolation. A higher AUC value indicates that the PC contains more information for discriminating habitat from background (BG) or habitat from forest (F) pixels, respectively. (B) Principal component loadings (which indicate the correlation of each component with members of the original image time series) of the two PC that exhibited the highest AUC values when used in isolation (i.e., PC1 and PC17). Loadings of PC2 are also shown for comparison purposes.

Vegetation phenology, measured through time series of WDRVI derived from MODIS surface reflectance data, proved to be a suitable descriptor of giant panda habitat across its entire geographic range, as shown by the high accuracy of our model predictions. The season in which the time series of WDRVI contains more information for isolating giant panda habitat seems to be the spring. Similar results have been reported in which broadleaf forests with understory bamboo have on average ca. 15.8% higher WDRVI values than broadleaf forests without understory bamboo, particularly during the spring (Viña et al., 2008). Thus, the presence of understory bamboo significantly influences the vegetation phenology in a way that can be exploited for isolating and mapping giant panda habitat. This constitutes an improvement over previous synoptic giant panda habitat evaluations in which the presence of understory bamboo was ignored (Liu et al., 2001; Loucks et al., 2003; Viña et al., 2007) due to the difficulty in isolating its signal from that of overstory canopy (Linderman et al., 2004; Wang et al., 2009). However, it is necessary to emphasize that MODIS data are acquired with a relatively coarse spatial resolution, which is suitable for evaluating the habitat in the entire range of the species, but might not be completely suitable at smaller scales in localized areas. Therefore, while the finer temporal resolution of MODIS data can compensate their disadvantage of coarser spatial resolution (Viña et al., 2008), the results of this study are not directly comparable to those performed with imagery acquired by sensor systems with higher spatial resolutions.

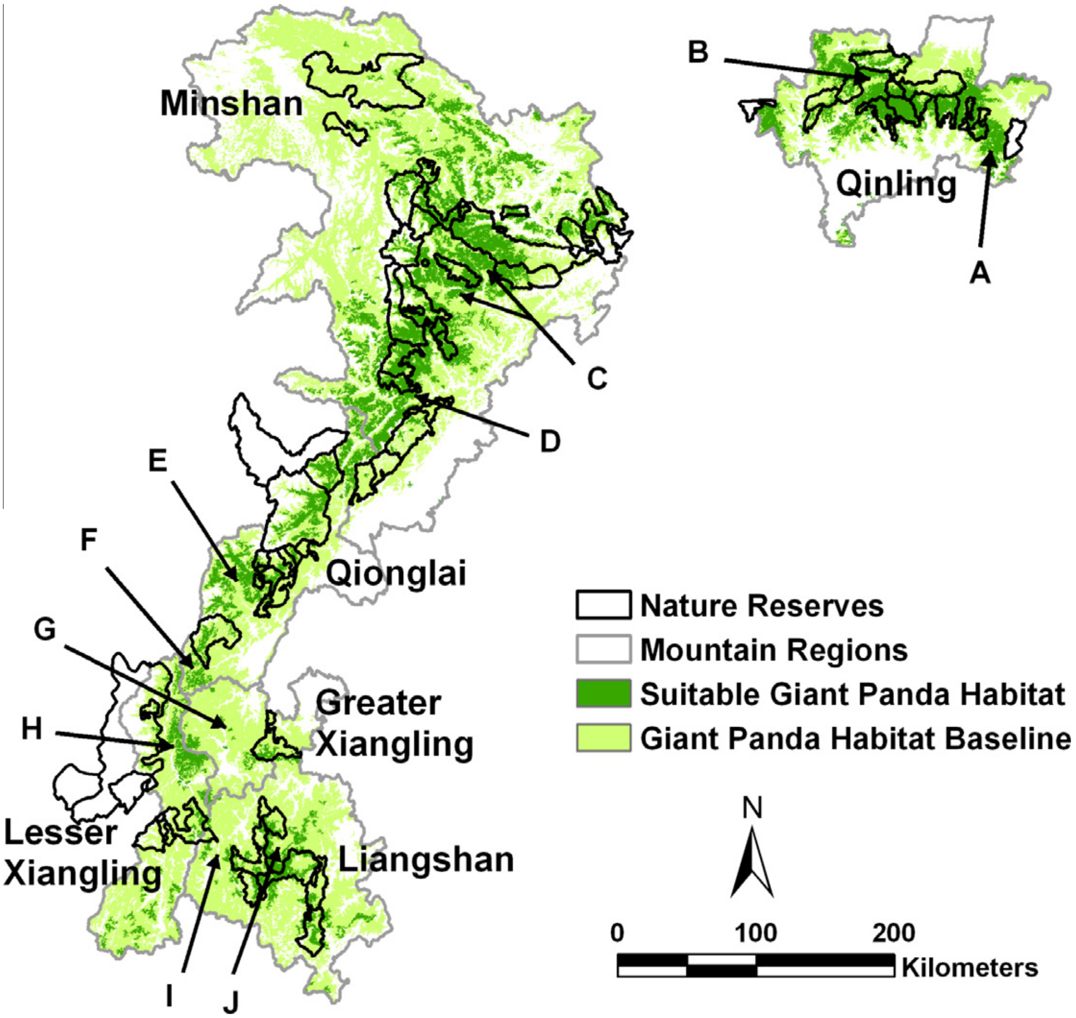

Fig. 5. Predicted distribution of suitable giant panda habitat obtained by thresholding the habitat suitability index (HSI) values from the model developed with the time series of MODIS–WDRVI. The optimal threshold (HSI = 0.03) was selected as the one that exhibited the maximum Kappa$_{BC}$ value (see Fig. 3B). Also shown is the distribution of the habitat baseline, the locations of current nature reserves (as of 2007) and the locations of some areas (A–J) suggested to be included as extensions of current nature reserves, new nature reserves or corridors for the movement of giant panda individuals among nature reserves or among different mountain regions.

Table 1
Absolute and relative amounts of suitable giant panda habitat in each of the six mountain regions comprising the geographic range of the species. The relative amounts represent the proportion of habitat baseline currently occupied by suitable habitat and the amount of suitable habitat inside nature reserves. Also shown is the degree of habitat connectivity in the different mountain regions as measured by the clumpiness index.

Mountain	Area (km^2)	Proportion of baseline habitat area (%)	Proportion inside nature reserves (%)	Clumpiness index
Greater Xiangling	344.8	8.5	30.2	0.818
Lesser Xiangling	1254.8	18.0	16.9	0.806
Liangshan	1849.7	16.5	46.3	0.858
Minshan	10251.1	27.3	43.9	0.864
Qinling	4996.1	45.3	66.4	0.875
Qionglai	2601.8	30.9	22.2	0.846
All mountains	21298.4	26.9	39.9	0.854

As satellite-derived vegetation phenology responds to disturbances of different origins (Eklundh et al., 2009; Koltunov et al., 2009; Morisette et al., 2009; Zhang et al., 2004), it might also be used for evaluating changes in the quality and geographic distribution of the giant panda habitat induced by natural (e.g., bamboo die-offs as a result of mass flowering, earthquake-induced landslides) and/or human (e.g., land use/cover change, agricultural expansion, bamboo harvesting) disturbances (Liu et al., 2001; Mackinnon and De Wulf, 1994; Viña et al., 2007; Wang et al., 2008). We are currently performing further analyses to establish the sensitivity of time series of MODIS–WDRVI to such disturbances.

Since our study analyzed the status of the habitat in the entire geographic range of the species, it has direct management implications for the conservation of the entire giant panda population, particularly regarding initial steps in the design of new panda reserves or adjustments to existing ones (Lindenmayer and Burgman, 2005; Noss, 2003). Our results show that there is still a significant amount of panda habitat outside the current nature reserve system that needs to be considered when planning nature reserve expansions or the creation of new nature reserves. This is particularly true in the Lesser Xiangling and Qionglai mountain regions, which exhibit low proportions of habitat area inside nature reserves. In addition, the current nature reserves are in general small (Mean = 475 km^2 and SD = 586.5 km^2) and isolated from others (Fig. 5) and thus have a limited ability to maintain viable giant panda populations (Loucks et al., 2001). Thus, it is necessary to establish new reserves or corridors to connect isolated habitat patches and nature reserves, a common strategy for species conservation in fragmented landscapes (Beier and Noss, 1998).

The Chinese government has planned to add ca. 180,000 km^2 of land area (2% of China's territory) to China's nature reserve system (Liu and Diamond, 2005; Liu et al., 2003b) between 2010 and 2020. Thus, opportunities exist to create additional nature reserves for numerous species including the giant panda, expand current nature reserves, and create dispersal corridors that increase the connectivity among them. Based on our results, we suggest some areas (A–J in Fig. 5) as candidates to be included in the expansion of China's nature reserve system. While the importance of some of these areas (B–F in Fig. 5) for connecting suitable panda habitat within mountain regions has been identified in previous localized studies (Loucks et al., 2003; Shen et al., 2008; Xu et al., 2006), we found additional areas that have the potential for connecting habitat among different mountain regions. For example, areas F, G and H connect habitat patches among Qionglai, Greater Xiangling and Lesser Xiangling, and area I links habitat between Lesser Xiangling and Liangshan (Fig. 5).

Besides the fragmented distribution of suitable panda habitat and its low ratio to the habitat baseline in all six mountain regions, we also found noticeable differences in the status of the giant panda habitat among mountain regions. These differences suggest that different conservation strategies and allocations of conservation resources are required in different mountain regions. For instance, suitable habitat in the Qinling mountain region corresponds to the highest proportion of habitat baseline and exhibits the highest connectivity (Table 1). This mountain region also exhibits the highest amount of habitat inside nature reserves. Thus, conservation actions in this mountain region can be oriented mainly towards minimizing the impacts of humans in and around nature reserves and alleviate the poverty of the local people in order to reduce their exploitation of forest products (e.g., bamboo culms and shoots, fuelwood and mushroom collection). In contrast, the status of the habitat in the southernmost portion of the giant panda geographic range (i.e., Greater Xiangling, Lesser Xiangling and Liangshan) is in jeopardy, as it comprises the lowest proportions of habitat baseline and exhibits comparatively lower habitat connectivity (Table 1). Giant panda populations in these mountain regions are considered threatened (Hu and Wei, 2004), with only ca. 60 individuals estimated to inhabit them (State Forestry Administration, 2006). Therefore, in addition to establishing conservation actions for minimizing the impacts of humans on these habitat areas, active habitat restoration might also be required in order to link their small and isolated giant panda populations with the larger ones present in other mountain regions. Consequently, while the areas proposed in this study for establishing new reserves or corridors have the potential for linking habitat among Greater Xiangling, Lesser Xiangling and Qionglai (F, G and H in Fig. 5) and between Lesser Xiangling and Liangshan (I in Fig. 5), active habitat restoration (e.g., reforestation and bamboo plantation) might also be necessary in these proposed areas, in order to create suitable habitat corridors. As nation-wide conservation programs have the promise to increase forest cover in China (Liu et al., 2008), we suggest that the managers of these programs in the southernmost mountain regions of the giant panda range consider including active restoration of giant panda habitat in their operations (e.g., planting native tree species as opposed to exotic ones, and planting bamboo species suitable for the giant panda).

The habitat model also predicted large areas of potentially suitable habitat occurring outside the six mountain regions (Fig. 2). Historical reports (Chu and Long, 1983) and Pleistocene fossils (Zhu and Li, 1980) indicate a much wider distribution of the giant pandas in the past, which included these habitat areas predicted outside the six mountain regions. The absence of pandas in these potentially suitable habitat areas could be due to local extinctions and out-migrations as a result of bamboo die-offs after mass flowering (Li and Denich, 2004). Perhaps these areas then became isolated due to the increasing human activities in their surroundings (Li and Denich, 2004; Pan et al., 2001), particularly logging and agricultural expansion. As species reintroductions are regarded as feasible management strategies (Richardson et al., 2009), the suitability of these areas to support giant panda populations should be evaluated in panda reintroduction viability assessments (Guo, 2007; Li and Denich, 2004). Due to the successful breeding of giant pandas in captivity, the Chinese government has been making earnest efforts to reintroduce them to the wild (Guo, 2007). The range-wide analysis performed in this study provides a foundation for identifying potential suitable areas for such panda reintroductions.

The procedures performed in this study are of special significance for establishing an overall view of the status of the entire giant panda habitat and could potentially be used for analyzing its changes through time. This allows identifying different conservation strategies to be implemented in different parts of the giant panda geographic range. As the habitat of this species comprises several types of forest ecosystems (Reid and Hu, 1991; Taylor and Qin, 1993) which are also home to thousands of other animal and plant species, these conservation strategies will also promote the conservation of other endangered species such as the golden monkey (*Rhinopithecus roxellanae*), the takin (*Budorcas taxicolor*), the red panda (*Ailurus fulgens*), the forest musk deer (*Moschus berezovskii*), and the Asiatic black bear (*Ursus thibetanus*). However, it is important to underline that further analyses in the field are required before any management actions are taken.

Range-wide habitat analyses such as the one described in this study might provide similar pertinent information for establishing conservation strategies and identifying conservation priorities in different locations of the geographic range of many other endangered species around the world. Although the final selection of areas for conservation needs to explicitly consider human factors (e.g., land use, land tenure, infrastructure) and treat them as coupled human-natural systems in order to achieve both socioeconomic and ecological sustainability (Liu et al., 2007), the results from range-wide evaluations provide the biophysical foundation to help delineate areas for future socioeconomic feasibility assessments.

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