



Temporal transferability of wildlife habitat models: implications for habitat monitoring

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ABSTRACT

Aim Temporal transferability is an important issue when habitat models are used beyond the time frame corresponding to model development, but has not received enough attention, particularly in the context of habitat monitoring. While the combination of remote sensing technology and habitat modelling provides a useful tool for habitat monitoring, the effect of incorporating remotely sensed data on model transferability is unclear. Therefore, our objectives were to assess how different satellite-derived variables affect temporal transferability of habitat models and their usefulness for habitat monitoring.

Location Wolong Nature Reserve, Sichuan Province, China.

Methods We modelled giant panda habitat with the maximum entropy algorithm using panda presence data collected in two time periods and four different sets of predictor variables representing land surface phenology. Each predictor variable set contained either a time series of smoothed wide dynamic range vegetation index (WDRVI) or 11 phenology metrics, both derived from single-year or multi-year (i.e. 3-year) remotely sensed imagery acquired by the Moderate Resolution Imaging Spectroradiometer (MODIS). We evaluated the ability of models obtained with these four variable sets to predict giant panda habitat within and across time periods by using threshold-independent and threshold-dependent evaluation methods and five indices of temporal transferability.

Results Our results showed that models developed with the four variable sets were all useful for characterizing and monitoring giant panda habitat. However, the models developed using multi-year data exhibited significantly higher temporal transferability than those developed using single-year data. In addition, models developed with phenology metrics, especially when using multi-year data, exhibited significantly higher temporal transferability than those developed with the time series.

Main conclusions The integration of land surface phenology, captured by high temporal resolution remotely sensed imagery, with habitat modelling constitutes a suitable tool for characterizing wildlife habitat and monitoring its temporal dynamics. Using multi-year phenology metrics reduces model complexity, multicollinearity among predictor variables and variability caused by inter-annual climatic fluctuations, thereby increasing the temporal transferability of models. This study provides useful guidance for habitat monitoring through the integration of remote sensing technology and habitat modelling, which may be useful for the conservation of the giant panda and many other species.

Keywords

Ailuropoda melanoleuca, China, land surface phenology, model transferability, MODIS, remote sensing, species distribution model, WDRVI, wildlife habitat monitoring, Wolong Nature Reserve.

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INTRODUCTION

Habitat loss and degradation due to human activities and human-induced climate change have had an impact on, and will continue to affect, many animal and plant species (Sala *et al.*, 2000). To minimize negative impacts and threats, there have been increased efforts to protect species habitats. Monitoring the spatio-temporal dynamics of species habitats is therefore essential, not only for improving current conservation efforts but also for guiding future conservation strategies (Balmford *et al.*, 2003; Pereira & Cooper, 2006; Lengyel *et al.*, 2008).

Although routine field surveys can detect fine-scale changes in species habitat, they seldom provide complete spatial coverage of the areas of interest. While empirical habitat models are a useful tool for generalizing field information (Guisan & Zimmermann, 2000), remote sensing technology provides synoptic information about the land surface, in some instances with a high temporal resolution (Turner *et al.*, 2003). Therefore, the combination of remotely sensed data, field survey data and habitat modelling makes it possible to map species habitats and monitor their temporal changes across large areas.

Seasonal variability in the biophysical characteristics (e.g. biomass) of vegetation as portrayed by multi-temporal remotely sensed data, i.e. land surface phenology (Friedl *et al.*, 2006), is an important feature of the land surface for characterizing species habitat. Land surface phenology reflects different land-cover types as well as different characteristics of vegetation (Reed *et al.*, 1994; DeFries *et al.*, 1995), and thus has been used for mapping changes in land use (de Beurs & Henebry, 2004) and for monitoring vegetation dynamics (Beck *et al.*, 2006; Koltunov *et al.*, 2009). In addition, several variables representing land surface phenology have been used in habitat models for mapping both plant and animal habitats at a single point in time (Morissette *et al.*, 2006; Viña *et al.*, 2008; Tuanmu *et al.*, 2010). However, the usefulness of land surface phenology for monitoring the temporal dynamics of species habitats has not been assessed.

When habitat models are intended to be used beyond the areas and time periods over which they were originally developed, one critical characteristic is their transferability, i.e. the ability of a model developed in one area or time period to be reliably applied to different areas or time periods. While spatial transferability has drawn increasing attention (e.g. Randin *et al.*, 2006; Peterson *et al.*, 2007; Zanini *et al.*, 2009), the issue of temporal transferability has received comparatively less attention (but see Thuiller *et al.*, 2004; Varela *et al.*, 2009; Zharikov *et al.*, 2009), particularly in the context of habitat monitoring. As diverse characteristics of the land surface portrayed by remotely sensed data have become increasingly available for habitat modelling (Kerr & Ostrovsky, 2003; Turner *et al.*, 2003), it is essential to assess how different uses of remotely sensed data may affect model transferability.

The goal of this study was to evaluate the utility of different land surface phenology variables for monitoring the temporal dynamics of wildlife habitat, particularly addressing their

effects on model transferability. Using the giant panda, *Ailuropoda melanoleuca* (David, 1869), as a case study, our objectives were: (1) to evaluate the predictive power and temporal transferability of habitat models derived from different land surface phenology variables; (2) to identify the best land surface phenology variable set for modelling, and hence for monitoring giant panda habitat; (3) to explore potential factors affecting model transferability; and (4) to examine implications for monitoring the temporal dynamics of wildlife habitat with the integration of habitat modelling and remotely sensed data.

MATERIALS AND METHODS

Study area

Wolong Nature Reserve, Sichuan Province, China (Fig. 1) is located between the Sichuan Basin and the Tibetan highlands; it exhibits elevational variation in climate and soils that result in a diverse flora and fauna. As one of the largest nature reserves (c. 2000 km²) established for giant panda conservation, Wolong Nature Reserve is home to c. 10% of the entire wild giant panda population (State Forestry Administration, 2006). Natural vegetation along the elevational gradient ranges from broadleaf forests at low elevations to mixed forests and subalpine coniferous forests at high elevations. Evergreen bamboo species dominate understorey layers and constitute the staple food for giant pandas (Schaller *et al.*, 1985). Around 50% of the reserve lies above the tree line (c. 3600 m a.s.l.) and is covered with alpine meadows, rocks and permanent snow, which are not suitable for the giant panda (Schaller *et al.*, 1985).

Giant panda presence data

We obtained giant panda presence data from two field datasets. The first dataset was acquired by the Third National Giant Panda Survey (State Forestry Administration, 2006) during the summer of 2001. This survey covered all areas that were known to, or had the potential to, support giant pandas (Fig. 1). The survey area was divided into c. 2 km² sections and each surveyor was assigned one section per day to search for and georeference giant panda signs (including faecal droppings, feeding sites, dens, footprints and visual sightings) using global positioning system (GPS) receivers (Loucks & Wang, 2004; State Forestry Administration, 2006). The second dataset was obtained from wildlife surveys we conducted from August 2006 to February 2008. We followed the same procedure used in the national survey, but concentrated our survey efforts in one of the regions considered to possess the best giant panda habitat in the reserve (Liu *et al.*, 2001; Fig. 1).

Remotely sensed data

We used a time series of the Moderate Resolution Imaging Spectroradiometer (MODIS) imagery (MOD09Q1) acquired

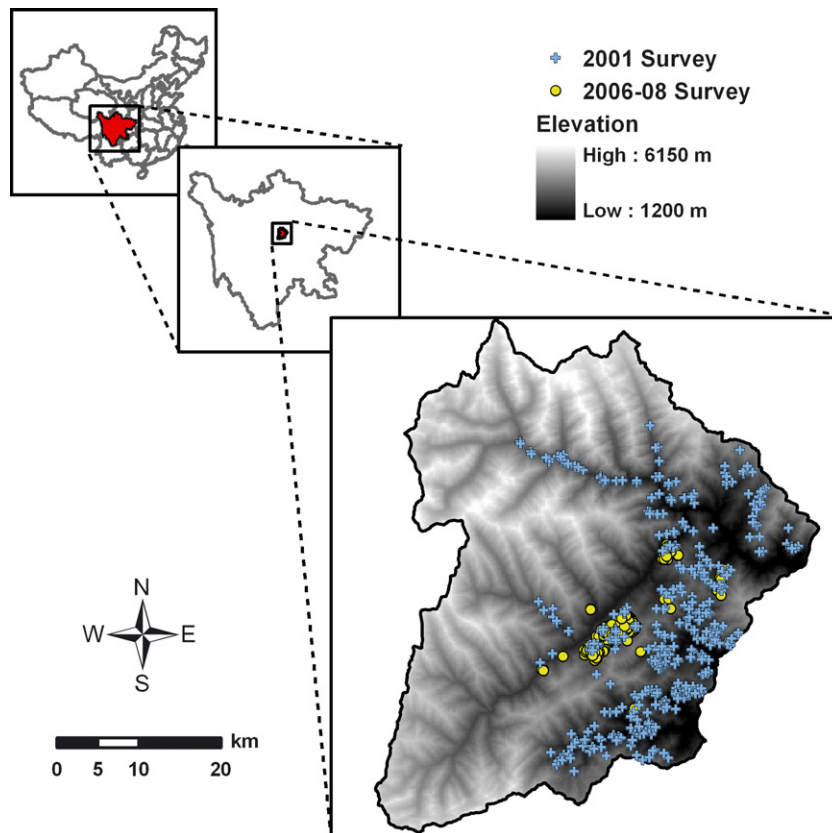


Figure 1 Location and topography of Wolong Nature Reserve, Sichuan Province, China. The locations of giant panda activity signs recorded during the Third National Giant Panda Survey in 2001 and during wildlife surveys from 2006–2008 are also shown.

between May 2000 and April 2008 for portraying the phenological characteristics of vegetation. This image time series is composed of 8-day composite surface reflectance in the red (620–670 nm) and near-infrared (841–876 nm) spectral bands, with a spatial resolution of $c. 250 \times 250 \text{ m pixel}^{-1}$. Using surface reflectance, we calculated the wide dynamic range vegetation index (WDRVI; Gitelson, 2004) for each 8-day composite image. The WDRVI reduces the saturation problem of the widely used normalized difference vegetation index (NDVI) under moderate-to-high biomass conditions (Gitelson, 2004), and thus it is more suitable for detecting vegetation dynamics under high green biomass, such as forests with dense understorey bamboo like those found in our study area. To further reduce the potential effects of cloud cover on the WDRVI values, we generated a time series of 16-day WDRVI composites using the maximum value between two consecutive 8-day periods.

Using TIMESAT 2.3 (Jönsson & Eklundh, 2004), we applied pixel-wise smoothing to the time series of WDRVI composites by means of the adaptive Savitzky–Golay filter (Savitzky & Golay, 1964). We then generated 11 phenology metrics for each of the seven full-year cycles (2001–07) from the time series of smoothed WDRVI values (Fig. 2). These metrics were used to capture the shape and phenological characteristics of the smoothed curve of WDRVI values (Fig. 2), which reflect the seasonal variability of green biomass. Among the 11

phenology metrics, two correspond to the lowest and highest levels of WDRVI values in a cycle (A and B, respectively, in Fig. 2), and a third metric represents the difference between these extremes (C in Fig. 2). Three metrics correspond to the timing of a growing season in a cycle and portray when the season begins, reaches the peak and ends (D, E and F, respectively, in Fig. 2), while another metric portrays season length (G in Fig. 2). Two metrics represent the annual integrated WDRVI and portray total vegetation production and seasonally active vegetation (H and I, respectively, in Fig. 2). Two metrics represent the rates of increase and decrease of WDRVI in the growing season (J and K, respectively, in Fig. 2). Detailed information on the definitions and calculations of the metrics can be found elsewhere (Jönsson & Eklundh, 2004; Tuanmu *et al.*, 2010).

Predictor variables

To assess the effects of different land surface phenology variables on the temporal transferability of habitat models, we created four different variable sets and built panda habitat models for two time frames. Each variable set contained either the time series of smoothed WDRVI composites or the 11 phenology metrics, whose values were derived from single-year or multi-year (i.e. 3-year) MODIS data (Table 1). For the variables derived from multi-year data, the values of each

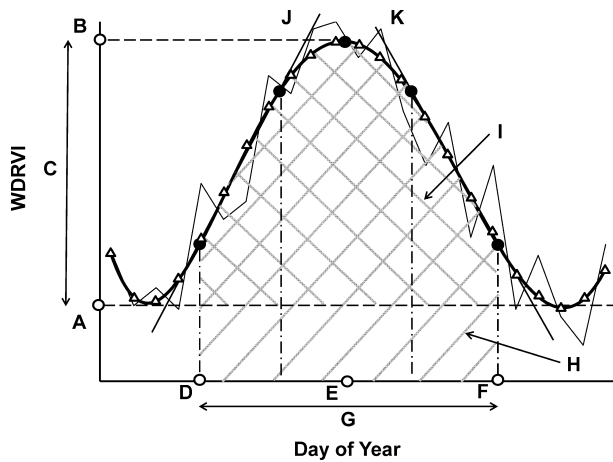


Figure 2 Two types of variables portraying land surface phenology were used for developing giant panda habitat models: smoothed values (triangles) of time series of the wide dynamic range vegetation index (WDRVI) and phenology metrics (A–K) derived from them. A, base level; B, maximum level; C, amplitude; D, date of the start of the season; E, date of the middle of the season; F, date of the end of the season; G, length of the season; H, large integral; I, small integral; J, increase rate; and K, decrease rate. This figure is modified from fig. 2 in Tuanmu *et al.* (2010).

WDRVI composite or phenology metric were averaged over 3 years. Because multi-year averages smoothed out inter-annual variability in variable values, the four variable sets allowed us to assess not only the effects of variable type (i.e. WDRVI or phenology metrics), but also those of inter-annual variability on model transferability.

To represent land surface phenology in the first time frame we used MODIS data acquired in 2001 or 3-year averages of data acquired from 2001 to 2003 (Table 1). For the second time frame we used data acquired in 2007 or 3-year averages of data acquired from 2005 to 2007 (Table 1). For single-year variable sets, phenology metrics could not be calculated for some pixels (5.7% of total pixels for 2001 and 3.4% for 2007) due to either a lack of detectable seasonal cycles or incomplete cycles within a year. We excluded those pixels from further analyses. For multi-year variable sets, we excluded pixels that lacked phenology metrics in ≥ 2 years (0.8% of total pixels for both 2001–03 and 2005–07 time periods) from further analyses.

Using the values of 10,000 randomly selected pixels (c. 26% of total pixels in the study area), we calculated Pearson's correlation coefficients for every pair of variables, and used them as indicators of the degree of multicollinearity among variables. With this procedure, a correlation matrix was obtained for each variable set in each time frame.

Analytical design

The analytical design included three steps: (1) model development, (2) habitat prediction, and (3) model evaluation (Fig. 3). These steps are explained in the following sections.

Model development

We developed panda habitat models using the maximum entropy algorithm (Maxent), a machine-learning approach for making predictions from incomplete information (Phillips *et al.*, 2006; MAXENT software, version 3.3.1). Maxent estimates the probability of species presence by finding the most uniform probability distribution (i.e. with the maximum entropy) as constrained by the data distribution of predictor variables associated with confirmed species locations (Phillips *et al.*, 2006; Phillips & Dudík, 2008). Maxent uses presence-only data, and thus it is especially suitable for mapping the distribution of species when confirmed absence data are difficult to obtain, as is the case for the giant panda.

Maxent contrasts the values of predictor variables associated with species presence locations against the values of the same variables for all available locations (i.e. background). We randomly selected 10,000 pixels as a representation of the entire study area (Phillips & Dudík, 2008), and defined the background by only using pixels where giant pandas could possibly occur following the suggestion of Phillips *et al.* (2009) for single species applications. For this, as giant pandas seldom occur in unforested areas (Schaller *et al.*, 1985), the background was defined by pixels with forest cover according to a binary forest cover map which was derived from a Landsat-5 Thematic Mapper (TM) image acquired on 13 June 2001 (Viña *et al.*, 2007) and resampled to the spatial resolution of the MODIS data (i.e. 250 m).

Maxent derives and uses different forms of input variables (i.e. feature types) to represent nonlinear and interactive effects of predictor variables on species presence probability (Phillips *et al.*, 2006). The contributions of these derived predictors to the model prediction are then evaluated during model development, and only those having significant contributions are retained in a final model (Phillips *et al.*, 2006). We used a combination of linear, quadratic and product feature types, which represent the means, variances and covariances of the predictor variables, respectively (Phillips *et al.*, 2006). The number of terms retained in the final model was used as an indicator of the complexity of model structure.

We developed four habitat models in two different time frames (i.e. Time Frame 1 and Time Frame 2, Fig. 3) using our two panda presence datasets. We considered a 250×250 m pixel as a confirmed presence pixel if it contained at least one panda location according to field surveys. Field datasets contained 399 and 220 presence pixels in 2001 and 2006–08, respectively. For each dataset, we used 70% of the presence pixels for model development and the remaining 30% for model evaluation (see below). In order to reduce the effects of data partitioning on model outputs, we randomly re-partitioned the data and created 20 different data partitions for each field dataset. Twenty variants of each model were then developed using these 20 partitions for each time frame. This number of partitions was used because a

Table 1 Properties of giant panda habitat models developed with four different sets of land surface phenology variables in two time frames.

	WDRVI		Phenology metrics	
	Single-year (SYVI)	Multi-year (MYVI)	Single-year (SYPM)	Multi-year (MYPM)
Variables				
Time Frame 1	A time series of smoothed WDRVI in 2001	A time series of smoothed WDRVI averaged over 2001–03	Phenology metrics in 2001	Phenology metrics averaged over 2001–03
Time Frame 2	A time series of smoothed WDRVI in 2007	A time series of smoothed WDRVI averaged over 2005–07	Phenology metrics in 2007	Phenology metrics averaged over 2005–07
Number of variables (in both time frames)	23	23	11	11
Correlation coefficient between variables*				
Time Frame 1	0.87 ± 0.01	0.90 ± 0.01	0.16 ± 0.12	0.20 ± 0.12
Time Frame 2	0.87 ± 0.01	0.90 ± 0.01	0.21 ± 0.13	0.18 ± 0.13
Number of terms in final models†				
Time Frame 1	103.5 ± 3.3	84.9 ± 2.7	39.4 ± 1.6	34.0 ± 1.4
Time Frame 2	118.8 ± 4.0	96.7 ± 3.1	41.7 ± 2.1	40.7 ± 1.4

*Values were calculated between every pair of variables in the variable set and are shown as mean ± 2 standard errors from the mean.

†Values were calculated from 20 variants of the habitat models and are shown as mean ± 2 standard errors from the mean.

WDRVI, wide dynamic range vegetation index; SYVI, single-year vegetation index; MYVI, multi-year vegetation index; SYPM, single-year phenology metrics; MYPM, multi-year phenology metrics.

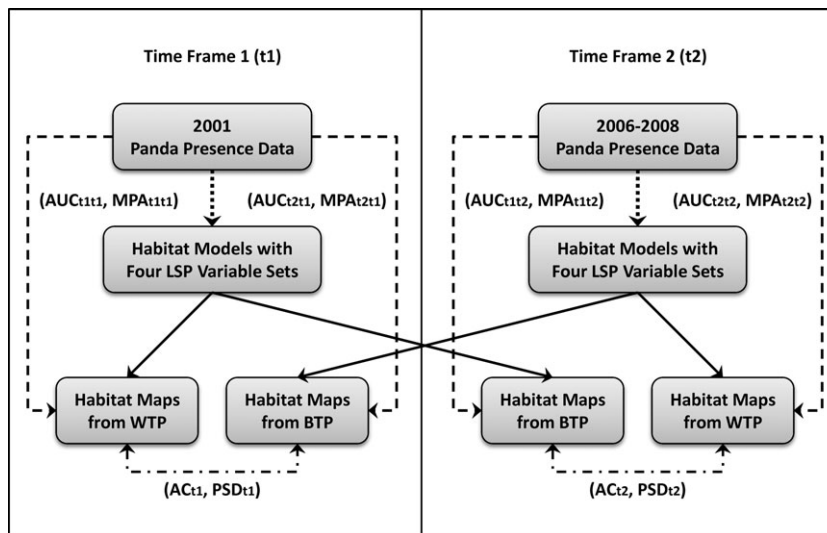


Figure 3 The analytical design included three steps: (1) model development (arrow with dotted line), (2) giant panda habitat prediction (arrow with solid line), and (3) model evaluation (arrow with dashed line). (1) Panda habitat models were developed with four different sets of land surface phenology (LSP) variables in two time frames (t1 and t2) using panda presence data collected in 2001 and 2006–08, respectively. (2) The models were used to predict panda habitat within (WTP) and beyond the time frame (BTP) in which the models were developed. (3) The habitat maps from WTP and BTP were evaluated using the presence data collected in the time frame in which the habitat was predicted. Area under the receiver operating characteristic curve (AUC) and minimal predicted area (MPA) were calculated for the habitat maps from both WTP (AUC_{t1t1}, AUC_{t2t2}, MPA_{t1t1}, MPA_{t2t2}) and BTP (AUC_{t1t2}, AUC_{t2t1}, MPA_{t1t2}, MPA_{t2t1}). The habitat maps from WTP and BTP were compared (arrow with dashed-dotted line) within each time frame, and values of agreement coefficients (AC_{t1} or AC_{t2}) and the proportions of systematic disagreement (PSD_{t1} or PSD_{t2}) were calculated. The AUC, AC and PSD values were then used to evaluate model transferability.

previous study showed that the variation of model outputs decreased with the increase in the number of partitions, but changed negligibly with more than 20 partitions (Tuanmu *et al.*, 2010).

Habitat prediction

For each time frame, 20 variants of each model were used to predict panda habitat within the time frame (i.e. within-time-

frame prediction, WTP) and beyond the time frame (i.e. beyond-time-frame prediction, BTP; Fig. 3). Therefore, in each time frame, 80 panda presence probability maps (i.e. 4 models \times 20 variants) were obtained from the WTP and 80 additional maps were obtained from the BTP (Fig. 3).

Model evaluation

To evaluate the accuracy of model predictions, we used both threshold-independent and threshold-dependent methods. The threshold-independent method consisted of a receiver operating characteristic (ROC) curve analysis, a common method for evaluating the accuracy of classification models (Fielding & Bell, 1997). The area under the ROC curve (AUC) provides a single-value measurement of model accuracy, with a value of 1 indicating a perfect prediction and 0.5 indicating a random prediction (Hanley & McNeil, 1982). In habitat modelling, models with AUC values higher than 0.7 are considered useful (Boyce *et al.*, 2002).

The ROC curve analysis is typically conducted by contrasting presence/absence data. Here, we calculated AUC values by contrasting presence pixels with those randomly selected from the study area (i.e. background pixels) as suggested by Phillips *et al.* (2006) and used in other studies (e.g. Marini *et al.*, 2010). For each time frame, we used 30% of panda presence pixels and the background pixels selected during model development to calculate AUC values for both WTP and BTP (Fig. 3). By contrasting presence to background data in the ROC curve analysis, the maximum achievable AUC value is < 1 and is negatively correlated with the proportion of actual presence pixels in the background pixels, but the value of a random prediction is still equal to 0.5 (Phillips *et al.*, 2006).

Some concerns have been raised about the application of the ROC curve analysis for comparing the accuracy of models using different modelling approaches or among different species, because AUC values are subject to the range of model output values, the reliability of species presence and absence data, and the delineation of a study area, especially when it is used to define the background in presence-only models (Lobo *et al.*, 2008; Peterson *et al.*, 2008). However, comparisons among different AUC values performed in this study are considered to be valid because all models were generated for the same species, by the same modelling algorithm (i.e. Maxent), within the same study area, and were generated and validated with the same presence and background data.

The threshold-dependent evaluation method used was based on the calculation of the minimal predicted area (MPA; Engler *et al.*, 2004). The MPA method evaluates model performance based on the parsimony concept that a good model should predict the smallest habitat area as possible (i.e. minimize commission errors as much as possible), while its omission errors are under control (Engler *et al.*, 2004). Because the MPA depends on the actual proportion of species habitat in a study area, which is almost always unknown, it is only suitable for comparing models generated for the same species in the same area, as is the case in this study. In addition, it is relative

magnitudes of MPA among models, rather than absolute values for individual models, that matter for evaluating model performance. Following Engler *et al.* (2004), we defined a threshold for each panda presence probability map so that 90% of presence locations in the validation dataset were encompassed (i.e. 10% omission error). Instead of using absolute area, we calculated the MPA as the ratio of the number of above-threshold pixels to the total number of pixels.

Model transferability

We evaluated the temporal transferability of panda habitat models based on three criteria adapted from Randin *et al.* (2006). First, a model with good temporal transferability should have similar accuracy between its predictions within and beyond the time frame corresponding to its development. Therefore, for our analytical design (Fig. 3), there should be similar accuracy between WTP in Time Frame 1 (t1) and BTP in Time Frame 2 (t2), as well as between WTP in t2 and BTP in t1. Second, the model should have similar performance no matter which time frame it was developed in. That is, the accuracy of WTP (or BTP) should be similar between t1 and t2 (Fig. 3). This criterion, together with the first criterion, implies that the model should have similar transferability in both transferring directions between the two time frames. Third, besides model accuracy, the spatial patterns of predicted habitat from within- and beyond-time-frame predictions should also be similar. Therefore, the spatial patterns of WTP and BTP in t1 (or t2) should match each other (Fig. 3).

To quantify temporal transferability based on these three criteria, we calculated five indices for each of the four habitat models. We calculated the single-direction ($TI_{t1 \rightarrow t2}$ and $TI_{t2 \rightarrow t1}$) and overall transferability indices (TI_{overall}), which were adapted from Randin *et al.* (2006) as:

$$TI_{t1 \rightarrow t2} = 1 - \frac{|AUC_{t1t1} - AUC_{t1t2}|}{0.5}, \quad (1)$$

$$TI_{t2 \rightarrow t1} = 1 - \frac{|AUC_{t2t2} - AUC_{t2t1}|}{0.5}, \quad (2)$$

$$TI_{\text{overall}} = \frac{0.5 \times (TI_{t1 \rightarrow t2} + TI_{t2 \rightarrow t1})}{1 + |TI_{t1 \rightarrow t2} - TI_{t2 \rightarrow t1}|}, \quad (3)$$

where AUC_{t1t1} and AUC_{t2t2} are AUC values for WTP in t1 and t2, respectively, and AUC_{t2t1} and AUC_{t1t2} are for BTP in the two time frames, respectively (Fig. 3). $TI_{t1 \rightarrow t2}$ and $TI_{t2 \rightarrow t1}$ measure the ability of a model to be transferred from t1 to t2 and vice versa, respectively. They range from 0 to 1 as AUC values are typically between 0.5 and 1, and they are closer to 1 when the AUC values for WTP and BTP are similar (i.e. high transferability based on the first criterion). TI_{overall} measures transferability in both directions and puts a penalty on the difference between two directions. It also ranges from 0 and 1 and is closer to 1 when single-direction transferability indices in both directions are higher and closer to each other (i.e. high transferability based on the second criterion).

We compared the spatial patterns of WTP and BTP in each time frame (Fig. 3), by calculating an agreement coefficient (AC; Ji & Gallo, 2006) for each variant of each habitat model as:

$$AC = 1 - \frac{\sum_{i=1}^n (X_i - Y_i)^2}{\sum_{i=1}^n [(|\bar{X} - \bar{Y}| + |X_i - \bar{X}|) \cdot (|\bar{X} - \bar{Y}| + |Y_i - \bar{Y}|)]}, \quad (4)$$

where X_i and Y_i are pixel values (i.e. estimated panda presence probability) of habitat maps from WTP and BTP, respectively; \bar{X} and \bar{Y} are the mean values of X_i and Y_i , respectively; and n is the total number of pixels. AC is a standardized sum of squared difference between X_i and Y_i , and its maximum value is 1, indicating a perfect agreement in pixel values between two maps (Ji & Gallo, 2006).

Because two maps may have a low AC value even when they show the same spatial patterns with different absolute pixel values, we also calculated the proportion of systematic disagreement (PSD), following Ji & Gallo (2006) as:

$$PSD = 1 - \frac{\sum_{i=1}^n [(|X_i - \hat{X}_i|) \cdot (|Y_i - \hat{Y}_i|)]}{\sum_{i=1}^n (X_i - Y_i)^2}, \quad (5)$$

where \hat{X}_i and \hat{Y}_i are the estimated values of X_i and Y_i , respectively, from a linear regression between X_i and Y_i , based on a geometric mean functional relationship model. The denominator of the main term of equation 5 measures the total disagreement between X_i and Y_i , and the numerator is the sum of residuals from the regression line, which indicates non-systematic or random disagreement. As PSD equals one minus the ratio of non-systematic disagreement to total disagreement, this index measures the proportion of systematic disagreement captured by a linear regression between the pixel values in two maps (Ji & Gallo, 2006). In our case, a higher PSD indicates that a larger proportion of the disagreement between two habitat maps is due to a linear shift of pixel values, and thus the two maps show a more similar spatial pattern of habitat but just with different absolute pixel values.

Model comparisons

We conducted the mixed-design analysis of variance (ANOVA) for comparing AUC and MPA values among habitat models with model variants as a random factor, and used paired *t*-tests for pairwise comparisons. With the same random factor, we used two-way ANOVA to evaluate the effects of land surface phenology variable type and the length of original time-series data used for generating them, as well as their interaction effects on model transferability measured by TI (equations 1–3), AC (equation 4) and PSD (equation 5). We used these parametric statistical tests after verifying the validity of the normality assumption with Shapiro–Wilks tests. All statistical tests were conducted using R 2.10.1 (R Development Core Team, 2009).

RESULTS

Multicollinearity and model complexity

The correlation analysis among land surface phenology variables in each variable set showed that smoothed time

series of WDRVI values, regardless of single- or multi-year data, were highly correlated in both time frames, but phenology metrics were less correlated with each other (Table 1). In both time frames, the models developed with phenology metrics or variables derived from multi-year time-series data tended to have fewer terms, suggesting lower model complexities (Table 1). In addition, each of the four models tended to contain more terms when developed in t2 than in t1 (Table 1).

Model accuracy

According to the threshold-independent evaluation, all habitat models had median AUC values ranging between 0.85 and 0.95 for predicting giant panda habitat within the time frame of model development (i.e. WTP; Fig. 4a,c). In general, accuracy decreased when models were used to predict habitat beyond time frames (i.e. BTP), but all median AUC values were still higher than 0.79, indicating that they constitute useful models (Fig. 4b,d). Significant differences in AUC values were found among the four habitat models in both time frames ($F = 11.96, 267.06, 194.53$ and 489.49 for $AUC_{t1t1}, AUC_{t1t2}, AUC_{t2t2}$ and AUC_{t2t1} , respectively; d.f. = 3, 57 and $P < 10^{-5}$ for all). In t1, the multi-year vegetation index (MYVI) and multi-year phenology metric (MYPM) models had the highest predictive power within the time frame (Fig. 4a), but the MYPM model was significantly better than the MYVI model for beyond-time-frame predicting (Fig. 4b). In t2, the MYVI model was significantly better for both WTP and BTP, although the ranking of the MYPM model improved when it was used for predicting habitat beyond the time frame (Fig. 4c,d).

The threshold-dependent evaluation procedure showed very similar patterns of model accuracy among the four models (Fig. 4e–h; note the reversed *y*-axes). The major difference from the threshold-independent evaluation was found when the models developed in t1 were used for predicting habitat in t2. While the MYPM model was the best in terms of AUC values, the single-year vegetation index (SYVI) and MYVI models were as good as the MYPM model in terms of MPA values (Fig. 4b,f).

Model transferability

Transferability indices

Single-direction and overall transferability indices indicated different transferabilities among the four habitat models. The MYPM model had the highest values of all three transferability indices (Fig. 5), indicating that it was the most transferable among the four models in terms of model accuracy. Results of the two-way ANOVA showed that both the variable type and length of the original time series data had significant effects on model transferability (Table 2). The models developed with phenology metrics were more transferable than those with time-series WDRVI, and the models developed with the

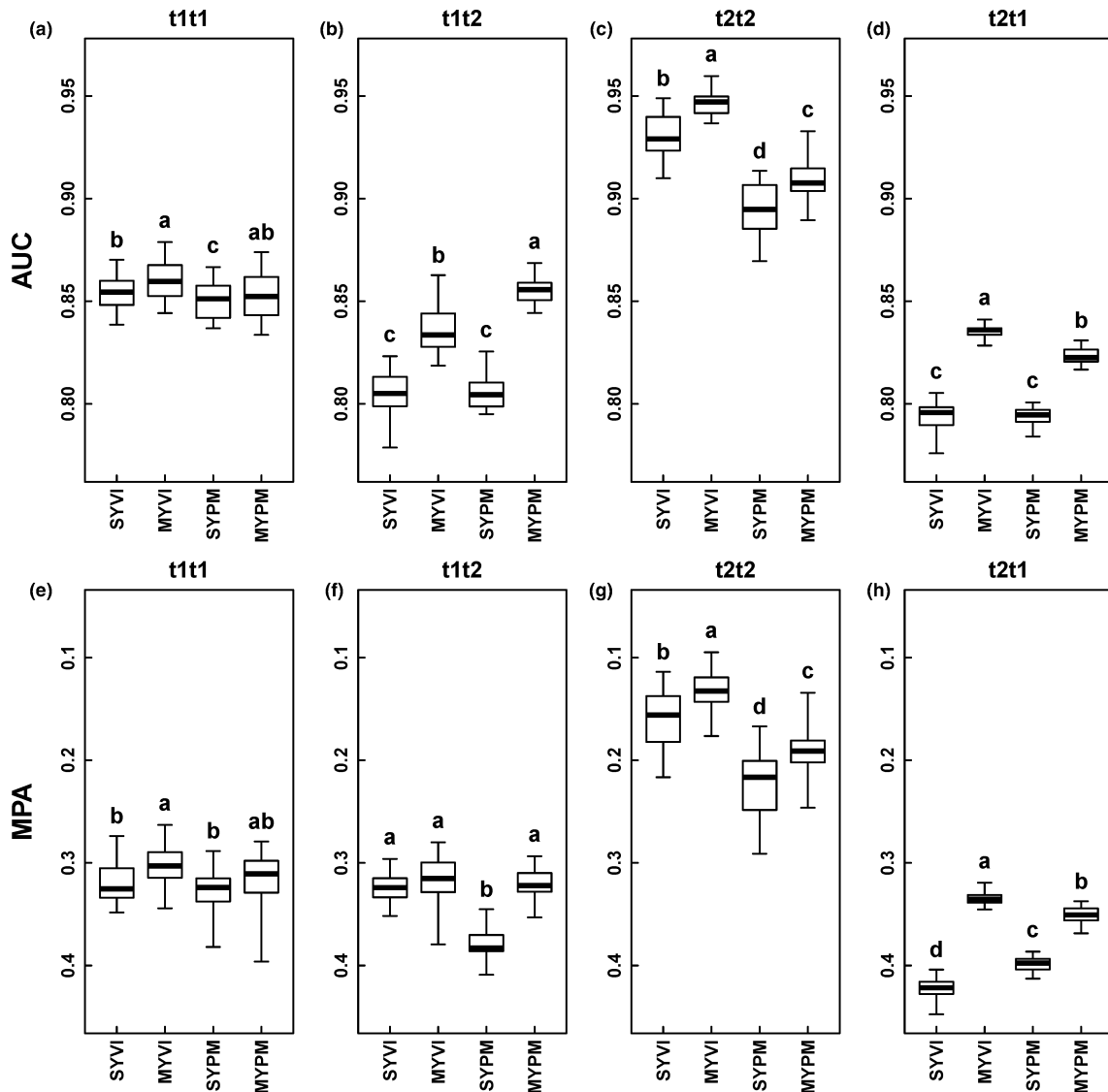


Figure 4 Box plots of the area under the receiver operating characteristic curve (AUC) and the minimal predicted area (MPA) for the giant panda habitat models developed with four different land surface phenology variable sets (SYVI, MYVI, SYPM and MYPM in Table 1) in two time frames (t1 and t2). The AUC and the MPA values were calculated from 20 variants of each habitat model when the model was developed in t1 and used to predict habitat in t1 (a, e) and t2 (b, f), as well as developed in t2 and used to predict habitat in t2 (c, g) and t1 (d, h). Each box plot shows the maximum, 75th percentile, median, 25th percentile and minimum values. Note that y-axes for the MPA are reversed, because lower MPA values indicate higher model accuracies. The letters above box plots indicate the results of pairwise comparisons conducted using paired *t*-tests. The alphabetical order shows the order of model accuracy from high to low. There is no significant difference ($P > 0.05$ after the Holm–Bonferroni adjustment) between two models if they share the same letter.

variables derived from multi-year data had higher transferability than those with the variables from single-year data (Table 2).

Comparing the two single-direction transferability indices indicated that model transferability was also different between transferring directions (Fig. 5a,b). All models were less transferable from t2 to t1 than in the opposite direction (Fig. 5a,b). Although the variable type and data length had the same effects on transferability in both transferring directions, their relative magnitudes were different. While the variable type was more influential on $TI_{t2 \rightarrow t1}$, the data length was more influential on $TI_{t1 \rightarrow t2}$ (Fig. 5a,b).

Agreement coefficient and proportion of systematic disagreement

Regarding the match between spatial patterns of WTP and BTP, significant differences in the ACs and the PSDs were found among models (Fig. 6). For both time frames, the habitat maps produced by the MYPM model showed the most similar spatial patterns, indicated by both the highest agreement in predicted panda presence probabilities (i.e. the highest AC) and the highest proportion of disagreement that can be captured by a linear regression (i.e. the highest PSD; Fig. 6). This indicates that the MYPM was the most transferable

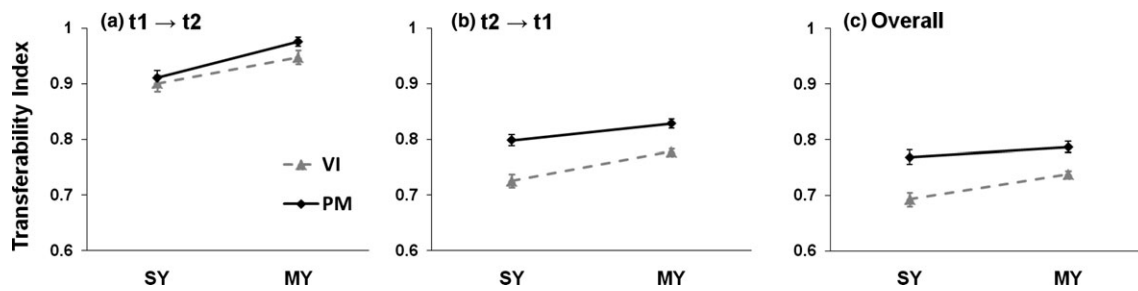


Figure 5 Mean values of the single-direction and overall transferability indices for the four giant panda habitat models. These models were developed with either a time series of wide dynamic range vegetation index (VI) or phenology metrics (PM), which were derived from either single-year (SY) or multi-year (MY) Moderate Resolution Imaging Spectroradiometer (MODIS) data. The indices were calculated from 20 variants of each habitat model for evaluating: (a) the ability of the model developed in Time Frame 1 (t1) to predict panda habitat in Time Frame 2 (t2), (b) the ability of the model developed in t2 to predict habitat in t1, and (c) the overall ability of the model to predict habitat beyond time frames. The error bars indicate 2 standard errors from the mean. The lines connecting two points do not imply any linear relationship, but are provided to aid with the visualization of value differences.

Table 2 Analyses of variance (ANOVA) on the effects of variable type (Type) and the length of original time series data (Length), as well as their interaction effects (Type × Length), on the single-direction and overall transferability indices calculated for the giant panda habitat models developed with different land surface phenology variables.

	TI _{t1→t2} Difference*	F-value	P-value	TI _{t2→t1} Difference*	F-value	P-value	TI _{Overall} Difference*	F-value	P-value
Type	PM > VI	22.3	< 10 ⁻³	PM > VI	313.2	< 10 ⁻¹²	PM > VI	238.7	< 10 ⁻¹¹
Length	MY > SY	113.2	< 10 ⁻⁸	MY > SY	101.0	< 10 ⁻⁸	MY > SY	42.9	< 10 ⁻⁵
Type × Length		2.9	0.11		12.2	0.002		14.0	0.002

*PM, phenology metrics; VI, a time series of wide dynamic range vegetation index (WDRVI) values; MY, multi-year data; SY, single-year data.

among the four models in terms of the spatial patterns of model predictions.

Land surface phenology variable type and length of original time series both had significant effects on AC and PSD values (Table 3). Using the variables derived from multi-year data as predictors increased both AC and PSD values. Significant interaction effects on PSD (Table 3) indicated that the effect of data length was more influential on the models based on phenology metrics (Fig. 6c,d).

The variable type affected AC and PSD differently. While using phenology metrics as predictors increased the agreement in the pixel values of habitat maps (i.e. AC), it reduced the proportions of systematic disagreement in habitat predictions (i.e. PSD; Table 3). However, the significant interaction effects on PSD (Table 3) indicated that the negative effect of phenology metrics was not influential when multi-year data were used to generate the metrics (Fig. 6c,d).

DISCUSSION

Model transferability is an important characteristic of empirical habitat models when they are used beyond the area and time in which they were originally developed. Diverse factors may affect the spatial or temporal transferability of habitat models, such as the environmental variability of species habitat captured by field data (Thuiller *et al.*, 2004; Phillips, 2008; Bamford *et al.*, 2009), the

relevance of predictor variables for describing underlying processes affecting species distribution, especially for those that vary across space or over time (Vanreusel *et al.*, 2007; Zharikov *et al.*, 2009), the ability of modelling methods to capture species–environment relationships (Araújo *et al.*, 2005; Randin *et al.*, 2006) and the consistency of the relationships across space (Zanini *et al.*, 2009) and time (Pearson & Dawson, 2003). By controlling other factors, such as focusing on a single species, using the same field data for model development and validation and using the same modelling algorithm, we showed that the method used to generate predictor variables, in particular from remotely sensed data, has significant effects on model transferability.

Effects of variable type on model transferability

Panda habitat models developed with phenology metrics, especially when they were generated using multi-year data, exhibited higher temporal transferability than those developed with time series of WDRVI in terms of both model accuracy and the spatial match in model predictions. The advantage of using phenology metrics as predictor variables on model transferability may be related to the reduction of (1) model complexity and (2) multicollinearity among variables.

Our results showed that the models developed with time series of WDRVI had a more complex structure than the

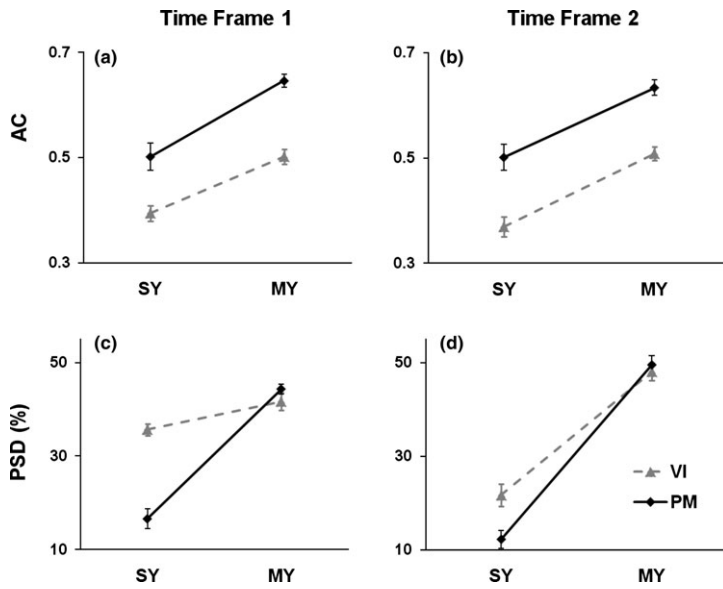


Figure 6 Mean values of agreement coefficients (AC) and the proportions of systematic disagreement (PSD) for the four giant panda habitat models. These models were developed with either a time series of wide dynamic range vegetation index (VI) or phenology metrics (PM), which were derived from either single-year (SY) or multi-year (MY) Moderate Resolution Imaging Spectroradiometer (MODIS) data. The values of AC and PSD were calculated between the maps generated from within- and beyond-time-frame predictions for the panda habitat in Time Frame 1 (a, c, respectively) and in Time Frame 2 (b, d, respectively). The error bars indicate 2 standard errors from the mean. The lines connecting two points do not imply any linear relationship, but are provided to aid with the visualization of value differences.

Table 3 Analyses of variance (ANOVA) on the effects of variable type (Type) and the length of original time series data (Length), as well as their interaction effects (Type × Length), on agreement coefficients (AC) and proportions of systematic disagreement (PSD), which were calculated from within- and beyond-time-frame predictions of giant panda habitat in the two time frames.

	Time Frame 1			Time Frame 2		
	Difference*	F-value	P-value	Difference*	F-value	P-value
AC						
Type	PM > VI	282.5	< 10 ⁻¹²	PM > VI	192.8	< 10 ⁻¹⁰
Length	MY > SY	339.6	< 10 ⁻¹²	MY > SY	218.4	< 10 ⁻¹¹
Type × Length		6.64	0.018		0.14	0.717
PSD						
Type	VI > PM	220.7	< 10 ⁻¹¹	VI > PM	19.2	< 10 ⁻³
Length	MY > SY	365.1	< 10 ⁻¹³	MY > SY	2079.6	< 10 ⁻¹⁶
Type × Length		552.7	< 10 ⁻¹⁴		72.5	< 10 ⁻⁷

*PM, phenology metrics; VI, a time series of wide dynamic range vegetation index (WDRVI) values; MY, multi-year data; SY, single-year data.

models with phenology metrics. More complex models have a higher chance of over-fitting the training data, and thus of losing the ability to capture general relationships between species occurrence and predictor variables thus reducing their transferability (Araújo & Guisan, 2006; Randin *et al.*, 2006). Therefore, the lower risk of over-fitting caused by less complex models is a likely reason for the higher transferability of the models developed with phenology metrics.

Additionally, the models developed in t2 tended to be more complex than t1 models. We also found that temporal transferability was lower and the effects of variable type were stronger when the models were applied from t2 to t1. The lower transferability of t2 models may be due to an incomplete environmental range of panda habitat captured by the field data (Thuiller *et al.*, 2004) because the panda presence data were collected only in high-quality habitat within t2. However, the relationships among higher model complexity, lower transferability, and stronger effects of variable type for t2 models suggest that the lower transferability could also be

attributed to higher over-fitting risks caused by more complex t2 models, and using phenology metrics in a habitat model can reduce these risks and thus increase its transferability.

In regression models, multicollinearity influences the estimation of coefficients and their standard errors, affects significance tests on the coefficients, changes model structure and thus reduces the robustness of the established species–environment relationships in habitat models (Mac Nally, 2000; Graham, 2003). Although no significance tests on coefficients are involved in model development of non-regression-based modelling approaches such as decision trees (Berk, 2006) or Maxent, models developed with these approaches may not be completely free of multicollinearity problems (Mac Nally, 2000). When models are used for predicting species habitats for different areas or time periods, spatially or temporally inconsistent correlations among predictor variables may reduce the predictive ability of the established species–environment relationships, even if they were determined with statistically robust approaches. Therefore, multicollinearity

reduction by using phenology metrics may also be the reason for their positive effects on model transferability.

Although several approaches can be used to reduce over-fitting and multicollinearity, they are not suitable for the habitat models developed with land surface phenology variables. For instance, one common approach is to remove highly correlated variables based on their biological importance for the species of interest (Graham, 2003). However, for a time series of remotely sensed data representing land surface phenology, all variables are highly correlated (e.g. the lowest correlation coefficient was 0.73 in this study). Therefore, even if only two variables are selected from the time series, multicollinearity may still exist. In addition, with the selection of fewer variables, less information on land surface phenology can be represented.

Principal components analyses are also commonly used for solving multicollinearity and over-fitting problems (Graham, 2003; Aguilera *et al.*, 2006), and are useful in models predicting habitat within the same area and time frame corresponding to model development (e.g. Viña *et al.*, 2010). However, the combinations of predictor variables in principal components are data-dependent and thus subject to change through time (Schowengerdt, 2007). As variable values change over time, the inconstancy of principal components may limit their utility for predicting habitat beyond the time frame of model development. Fixed combinations of variables, such as the tasselled-cap transformation commonly used in digital image processing of remotely sensed imagery (Schowengerdt, 2007), may be useful for predicting habitat changes over time. However, finding general and meaningful tasselled-cap components that reflect the underlying processes determining habitat quality and driving its change is quite challenging.

Effects of time-series length on model transferability

Our results showed that length of original time-series data had significant effects on both model accuracy and transferability. The models developed with variables derived from multi-year remotely sensed data had higher accuracy for both within and beyond time-frame predictions and had higher temporal transferability than those with variables derived from single-year data. The major advantage of using multi-year data is in smoothing inter-annual variability of the biophysical and phenological characteristics of the vegetation caused by inter-annual climatic fluctuations (Ichii *et al.*, 2002), which may not reflect real habitat changes. For example, while higher vegetation index values in one year may correspond to higher temperatures (Ichii *et al.*, 2002), this may not indicate long-term changes in the quality of panda habitat. Thus, a habitat model that uses land surface phenology variables derived from single-year data may be affected by the particularities of that year and thus lose its temporal transferability. In addition, different plant species may have different responses to inter-annual fluctuations of climatic conditions, which may cause more non-systematic disagreements in habitat predictions of the models with variables derived from single-year data.

High sensitivity to inter-annual variability of vegetation characteristics is not specific to models developed with land surface phenology variables. Any model using remotely sensed data to reflect vegetation information may have the same problem when used for studying temporal dynamics of species habitat. While average values of climatic variables over several years are commonly used in habitat models to reflect long-term climatic conditions, variables derived from single-year remotely sensed data or even a single image are often used in habitat models (e.g. Zimmermann *et al.*, 2007), mostly due to the limited availability of remotely sensed data. While incorporating remote sensing variables into habitat models can improve model accuracy for the time period corresponding to model development (Zimmermann *et al.*, 2007), predicting species habitat across time frames and using these results to monitor habitat dynamics should be undertaken with caution. As some high-temporal-resolution remotely sensed data (e.g. MODIS data) and multi-temporal data of median spatial resolution [e.g. Landsat TM, Landsat Enhanced Thematic Mapper Plus (ETM+), and Advanced Land Observation Satellite (ALOS)] are becoming increasingly available, variables derived from multi-season and multi-year data appear to be more appropriate for monitoring temporal dynamics of species habitat at broader spatial and longer temporal scales.

The usefulness of land surface phenology for mapping and monitoring species habitats

Our study showed that land surface phenology is useful for characterizing giant panda habitat and also monitoring its temporal dynamics. Forest cover, understorey bamboo, topography and human disturbance are the most important documented determinants of panda habitat (Liu *et al.*, 2001; Bearer *et al.*, 2008). Land surface phenology not only reflects different land-cover types and their dynamics (de Beurs & Henebry, 2004; Beck *et al.*, 2006), but it also reflects the characteristics of understorey bamboo occurring under the forest canopy (Viña *et al.*, 2008; Tuanmu *et al.*, 2010). In addition, human disturbance of panda habitat is usually associated with land cover or vegetation change (Liu *et al.*, 2001; Bearer *et al.*, 2008). Therefore, besides capturing the characteristics of vegetation that is suitable for the giant panda (Viña *et al.*, 2008, 2010), land surface phenology may also capture its temporal dynamics due to human disturbance. While previous studies have found land surface phenology data to be useful for detecting vegetation changes due to human and natural disturbances (Eklundh *et al.*, 2009; Koltunov *et al.*, 2009), this study showed that changes in land surface phenology could be directly linked to changes in wildlife habitat through the use of habitat models.

However, the usefulness of different land surface phenology variables depends on their application. Because the habitat model developed with a time series of WDRVI derived from multi-year MODIS data (i.e. the MYVI model) can produce the most accurate habitat maps in the time frame during which the model was developed, it is a good tool for evaluating the

habitat conditions in that particular time frame (e.g. Viña *et al.*, 2010). Alternatively, the model developed with multi-year phenology metrics (i.e. the MYPM model) reduced the problem of multicollinearity and the risk of over-fitting, and thus it appears to be the best in terms of temporal transferability. Therefore, the MYPM model constitutes a suitable tool for monitoring the temporal dynamics of giant panda habitat and providing essential information for the conservation of the species.

Under changing environments, monitoring the temporal dynamics of species habitats at regional or global scales is essential for reducing biodiversity loss and maintaining sustainable ecosystem services (Balmford *et al.*, 2003; Pereira & Cooper, 2006; Lengyel *et al.*, 2008). Combining remote sensing and habitat modelling provides a practical and efficient tool for monitoring the temporal dynamics of biodiversity and species habitats at different spatial and temporal scales (Pereira & Cooper, 2006; Lengyel *et al.*, 2008). In particular, land surface phenology has been found to be sensitive to vegetation changes due to short-term human and natural disturbances (Eklundh *et al.*, 2009; Koltunov *et al.*, 2009) and long-term climate changes (Zhang *et al.*, 2004; Morissette *et al.*, 2009). Phenology-based models have also been successfully applied to predicting species habitat at different spatial scales (Morissette *et al.*, 2006; Tuanmu *et al.*, 2010; Viña *et al.*, 2010). Therefore, the combination of land surface phenology and habitat modelling constitutes an excellent tool for biodiversity conservation under changing environments.

Although we used giant panda in the Wolong Nature Reserve as a case study, the approaches and conservation implications of this study can go beyond this specific species, geographical area and spatial scale. Previous studies have shown considerable variability in model transferability among species (Randin *et al.*, 2006). However, the direct causes indicated in this study underlying the differences in transferability among models (i.e. model complexity, multicollinearity among variables and relevance of variables to habitat quality and its change) have also been reported in other studies (Mac Nally, 2000; Randin *et al.*, 2006; Peterson *et al.*, 2007; Vanreusel *et al.*, 2007; Zharikov *et al.*, 2009). Therefore, we believe that the suggestions provided for increasing model transferability (i.e. using phenology metrics and multi-year remotely sensed data) can be generally applied for modelling the habitat of many other species in different geographical settings. This is important, as model transferability cannot be directly evaluated for many species, particularly endangered species, due to low availability of field data collected over multiple years. In such cases, habitat models developed using remotely sensed data may still be useful for habitat monitoring if the suggestions provided in this study are taken into consideration.

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BIOSKETCH

Mao-Ning Tuanmu is a PhD candidate in the Department of Fisheries and Wildlife at Michigan State University. This study forms part of his dissertation research focusing on spatio-temporal dynamics of habitat and food resources of the giant panda and underlying anthropogenic and natural processes. It also forms part of long-term research on the interactions in coupled human and natural systems, conducted by a collaborative effort between the Center for Systems Integration and Sustainability (Michigan State University), the State Key Laboratory of Urban and Regional Ecology (Chinese Academy of Sciences) and Wolong Nature Reserve.

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