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The effects of understory bamboo on broad-scale estimates of giant panda habitat

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Abstract

Understory vegetation is an important habitat component for many wildlife species. Previous broad-scale studies on biodiversity and wildlife habitat have suffered from a lack of detailed information about understory distribution. Consequently, it is unclear how understory distribution influences the analysis of habitat quantity and spatial distribution. To address this problem, we compared estimates of giant panda (*Ailuropoda melanoleuca*) habitat with and without understory bamboo. The results show that the spatial distribution of bamboo has a substantial effect on the quantity and spatial arrangement of panda habitat. Total amount of estimated habitat decreased by 29–52% and decreased connectivity was notable after bamboo information was incorporated into the analyses. The decreases in the quantity and quality of panda habitat resulted in a decrease of 41% in the estimated carrying capacity. Our results suggest that it is necessary to incorporate understory vegetation into large-scale wildlife habitat research and management to avoid overestimation of habitat and improve broad-scale analyses of species distributions and biodiversity estimates in general.

Keywords: Habitat modeling; Fragmentation; Landscape; Remote sensing; Understory vegetation

1. Introduction

Understory vegetation is a significant component of wildlife habitat. It is widely recognized that detailed knowledge of vertical structure and horizontal distribution of understory flora is often necessary to accurately predict wildlife-habitat relationships (MacArthur and MacArthur, 1961; James, 1971; Lindzey and Meslow, 1977; Dueser and Shugart, 1978; Ernest, 1989; Estades and Temple, 1999). While understory vegetation has often been incorporated in fine-scale (limited extent and high-resolution) analyses and structural information has been incorporated in some broad-scale (large extent and lower resolution) habitat studies (e.g. Aspinall and Veitch, 1993; Hill, 1999; Lindenmayer et al., 1999; Coops and Catling, 2002), few broad-scale studies have incorporated understory vegetation into habitat analyses (Roughgarden et al., 1991). Not considering the influence of understory vegetation, vertical vegetation structure, and other difficult to measure factors in broad-scale studies has likely limited the reconciliation of fine-scale work and broad-scale estimates (Levin, 1992) and reduced the utility of remote sensing for accurate conservation and management planning.

This is likely the case for estimates of giant panda habitat in the past. Previous efforts to map giant panda habitat based only on available broad-scale data have probably overestimated available habitat and underestimated habitat fragmentation and isolation. Behavioral studies have shown that giant panda (*Ailuropoda melanoleuca*) habitat is a function of forest cover, slope, elevation, and understory bamboo (Schaller et al., 1985; Liu et al., 2001). Prior efforts to collect information on the availability and spatial distribution of understory

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bamboo, however, have been confined to coarse estimates over large areas or more refined maps at fine scales (Schaller et al., 1985; Johnson et al., 1988). Therefore, detailed information on the spatial distribution of bamboo over large areas has not been available and past studies on giant pandas have not been able to incorporate bamboo data in analyses of the spatial distribution of habitat (De Wulf et al., 1988; Liu et al., 2001). As a result, these studies might have led to conservative estimates of human impacts on remaining giant panda habitat.

To illustrate this challenge, we measured the influence of understory bamboo on estimates of giant panda habitat and carrying capacity. Based on extensive ground sampling, remote sensing data, and an artificial neural network, we recently developed a high-resolution (30 m) classification of the spatial distribution of understory bamboo at a large scale (Linderman et al., 2004). This new classification of bamboo distribution enabled us to compare the outcomes of estimating panda habitat and carrying capacity with and without bamboo. The comparative analysis quantified the degree to which panda habitat might be over- or under-estimated and highlights the need to gather and incorporate forest structural information into broad-scale habitat analyses.

2. Methods

To assess the impact of understory bamboo on the quantity and spatial distribution of giant panda habitat, we compared the outcomes of habitat classifications with and without understory bamboo information within a nature reserve in southwestern China. Comparisons were made to a previous multi-temporal analysis of giant panda habitat. Our previous analysis (Liu et al., 2001) provided a good baseline for comparison as it used common approaches to broad-scale habitat analyses, but due to the lack of historical data, it was not able to incorporate information on the distribution of understory bamboo. For the study presented here, the land cover, slope, and aspect data used to derive the 1997 time-series habitat classification in Liu et al. (2001) were combined with recently developed bamboo data to reclassify habitat suitability. The resulting habitat classifications were then compared to the original habitat classification without bamboo information.

2.1. Study area

The study was conducted in Wolong Nature Reserve, in the Qionglai Mountains of Sichuan Province, China (located between 102°52′ and 103°24′ E, and 30°45′ and 31°25′ N). Wolong is one of the largest reserves (approximately 200,000 ha) dedicated to giant panda conservation, and is estimated to contain ~10% of the remaining wild panda population (c. 1000 individuals; Zhang et al., 1997). In the past several decades, human activity has been a major force behind forest loss and degradation of panda habitat (Liu et al., 1999, 2001). Grazing and agricultural use have effectively removed forest cover and bamboo from some areas. Other areas have been clear-cut, leaving a mixed midstory shrub layer and, consequently, less bamboo. Finally, selective logging in other areas has changed the species composition in the overstory and reduced canopy cover. Throughout Wolong and most of the panda range, bamboo is found predominantly as understory species and predicting the spatial distribution of bamboo has not been possible due to a lack of any significant relationship between overstory and abiotic variables and the presence or absence of bamboo (Linderman et al., 2004).

2.2. Comparison study

Classification of habitat suitability for the Liu et al. (2001) study was based on previous giant panda biological research. For example, the vast majority of giant panda activity is in areas containing forest cover (Schaller et al., 1985). In addition, studies have shown that the main elevation range of the panda is between 2700 and 3200 m, but extends down to 2000 m and occasionally up to 3500 m (Schaller et al., 1985; Ouyang et al., 1996). Pandas prefer gently sloping regions, restricting their activity to slopes less than 45° and preferring areas with less than 15° slope (Ouyang et al., 1996). Furthermore, forest understory vegetation plays a particularly vital role. Bamboo comprises ~99% of the panda diet, and pandas spend up to 14 h per day foraging, due to bamboo's low nutrient and energy content (Schaller et al., 1985). Because of pandas' obligate relationship with bamboo, panda habitat is strongly influenced by bamboo availability and distribution (Johnson et al., 1988; Reid et al., 1989).

To analyze the spatio-temporal trends of giant panda habitat in Wolong Nature Reserve, Liu et al. (2001) derived habitat models from satellite images and topographic maps based on previous research of panda behavior. Detailed information on the spatial distribution of bamboo prior to 1997, however, was not available. To be consistent over time and to provide a more conservative estimate of habitat loss, bamboo information was not included in this previous analysis. Therefore, habitat suitability was determined as a multiplicative combination of the three factors (forest cover, elevation, and slope) available for the 32-year time span. Since non-forested areas are considered unsuitable habitat for the panda, forest and non-forest classifications were multiplicative factors of 1 and 0, respectively. Slope and elevation multiplicative factors were proportional to observed use by pandas. The final habitat classification was a categorized suitability measure of four classes termed highly suitable, suitable, marginally suitable, and unsuitable (Liu et al., 2001).

2.3. Bamboo classification

Remote sensing can provide considerable cost and time savings when mapping the distribution of land cover over large areas. However, methods to map the extent of understory vegetation like bamboo, even employing aerial photography, have not been successful (Morain, 1986; De Wulf et al., 1988; Porwall and Roy, 1991). The primary difficulty in classifying bamboo from remote-sensing data is that bamboo within most of the panda range occurs as understory species. The overstory is composed of varying degrees of evergreen deciduous, deciduous, and coniferous cover that typically limits spectral information from understory bamboo, thus restricting traditional remote sensing classification approaches.

We used an artificial neural network to classify the presence/absence of understory bamboo based on Landsat Thematic Mapper (TM) data (30-m resolution) and approximately 120 co-registered field samples (Linderman et al., 2004). A back-propagating neural network was trained based on the field data and corresponding TM data. Once trained, the remaining TM data were fed through the neural network to provide a 30-m classification of the presence/absence of bamboo throughout the reserve. Based on 60 reserved field samples, the neural network achieved a reserve-wide classification accuracy of 80% despite a leaf-on canopy cover (Linderman et al., 2004).

2.4. Incorporating bamboo information into habitat analysis

To relate the bamboo data to reported panda use, account for possible classification errors, and provide a range of classification estimates, the bamboo data were incorporated into the habitat analyses in three forms: unfiltered data, a majority filter, and a proportion filter. The unfiltered data were incorporated as a binary coverage (presence = 1 and absence = 0) at 30-m resolution derived from remote sensing imagery. To take into account panda behavior, the bamboo data were also filtered using moving-window filters to reclassify the center pixel of a square window based on the conditions of other pixels within the window. The two filters (proportion filter and majority filter) were used to reclassify the bamboo data to reflect pandas' use of bamboo area, use of non-bamboo area, and the scale at which pandas interact with bamboo.

As with previous studies on other wildlife species (e.g., Pearson et al., 1996), knowledge of how pandas interact with understory bamboo was necessary to accurately incorporate data on the distribution of bamboo at a 30-m pixel resolution into habitat estimates. Foraging behavior and daily movement patterns suggest pandas are likely to interact with understory bamboo over distances ranging from less than 100 m to over 500 m. For example, typical distances traveled each day are around 300 m and up to 500 m. Radio-tracking studies by Schaller et al. (1985) showed between-patch foraging distances were typically up to 100 m. Furthermore, while most activity is largely restricted to regions with significant amounts of bamboo, pandas also use areas not containing bamboo, mainly for movement between bamboo patches, territorial marking (primarily males) and travel to other places (Schaller et al., 1985). Therefore, filter window size was chosen based on known panda behavior and window size effects on habitat estimates. Window sizes ranging from 3×3 to 21×21 were tested. It was determined that a window size of 11×11 pixels (330×330 m) most closely represents the panda interactions with understory bamboo and provides the most conservative estimate of habitat area and fragmentation.

In the proportion filter method, the center pixel of the 11×11 window was reassigned a value of the proportion of pixels with bamboo within the window. The proportion filter data were then categorized to reflect the overall inter- and intra-patch availability of bamboo. The pixels were divided into three classes: highly suitable (>50%), suitable (25–50%), and unsuitable (<25%). In other words, if more than half of the pixels within a filter window contained bamboo, the center pixel was classified as highly suitable. If less than one-quarter of the pixels contained bamboo, we reclassified the center pixel as unsuitable. Otherwise, the pixel was classified as suitable. We based this classification on previous panda behavior research, bamboo availability as measured by areas within Wolong known to sustain high densities of pandas, and measured travel distance between patches (Schaller et al., 1985).

To provide an alternative estimate of the impact of bamboo on habitat availability and fragmentation, a majority filter was also examined. The majority filter reclassified the bamboo data into just two classes, highly suitable and unsuitable, omitting the suitable class of the proportion filter. In the majority filter the value of the center pixel was reclassified to reflect the condition of the majority of the pixels within the window. For example, if a majority of pixels in the 11×11 window were classified as bamboo, the center pixel was re-classified as bamboo regardless of its original classification. Therefore, compared to the proportion filter, the majority filter mapped only the areas of high-quality bamboo as measured by the proportion filter.

Classifications of overall habitat suitability were generated like those in Liu et al. (2001) with the inclusion of the additional multiplicative factor of bamboo suitability derived from the bamboo data. This resulted in the same four categories of habitat suitability as defined in Liu et al. (2001): highly suitable, suitable, marginally suitable, and unsuitable. Highly suitable bamboo areas (multiplicative factor of 1) resulted in no change to the original habitat classifications. Unsuitable bamboo areas changed all previous habitat classifications to unsuitable. Depending on the quality of the other three factors used in the multiplicative index, suitable bamboo areas from the proportion filter could degrade original habitat classifications by as much as one suitability category.

2.5. Habitat measures

We based comparisons of habitat estimates on three measures: habitat quantity, fragmentation, and carrying capacity. Habitat quantity included not only the total amount of habitat, but also the amount of each suitability class (highly suitable, suitable, and marginally suitable). Fragmentation measures the degree of discontinuity of habitat and is represented by mean patch size and number of patches. We estimated the potential carrying capacity from total quantity of core habitat areas and density of pandas in the core habitat areas. A core habitat area was designated as a habitat patch large enough to support at least one panda. Pandas' home range varies from 3.0 to 6.0 km^2 (Schaller et al., 1985). However, significant overlap occurs between home ranges. Schaller et al. (1985) suggest that prime habitat (equivalent to highly suitable habitat in this study) has an average density of 1 panda per 1.7 km^2. Therefore, to reduce the chance of underestimating total core habitat, we defined core habitat as any habitat (any combination of marginally suitable, suitable, or highly suitable habitat) forming a contiguous patch of at least 1.7 km^2. Based on the frequency of observed use in different categories of habitat (Ouyang et al., 1996), we used density estimates of 1 panda per 3.4 and 5.1 km^2 (2 and 3× less population density than in highly suitable habitat) for suitable and marginally suitable classes, respectively. Total area of each habitat suitability class was then used to determine overall carrying capacity based on estimated population densities for each habitat class.

3. Results

3.1. Habitat comparisons

Not incorporating bamboo yielded a total of 71,050 ha of habitat in the reserve. Compared to the original classification, incorporating unfiltered bamboo data into the habitat estimate resulted in a 52% decrease in total habitat. The habitat classification derived using the majority filter also resulted in a decrease in total habitat area of 52%. Similar decreases (48–54%) occurred in each of the three habitat classes when incorporating unfiltered or majority filtered bamboo data (Table 1). Using the proportion filter, total habitat decreased by approximately 29% relative to the original classification. Predicted high-quality and suitable habitat were reduced by 34% and 44%, respectively. Marginally suitable habitat increased by 58% (Table 1).

The unfiltered bamboo data resulted in a marked increase in fragmentation compared to the original classification. Patch sizes of habitat derived when incorporating the unfiltered bamboo data were 9–29× smaller than the original habitat classification (Table 2). Incorporating the proportion and majority filtered bamboo data resulted in more contiguous patches relative to the unfiltered method. Mean patch sizes of suitable and highly suitable patches when incorporating majority filtered data were 48% and 16% smaller than those using the original data (Table 2). However, majority patches were still 7–15× larger than those derived from the unfiltered data. Mean patch sizes when incorporating proportion filtered data were comparable to the original classification and 11–27× larger than the unfiltered habitat patches (Table 2). Similarly, the number of patches after incorporating unfiltered data was markedly higher than the original classification, 4–13× more patches. However, after incorporating the majority and proportion filtered data the total number of patches either decreased or patches degraded in quality. The number of patches of the highly suitable and suitable proportion classes was consistently lower than the original classification by as much as 50%. The number of marginally suitable patches within the proportion filtered classification was higher than the original classification (Table 2).

Table 1
Estimated habitat area based on classifications using only forest cover, slope, and aspect (no bamboo) and forest cover, slope, aspect and bamboo data (unfiltered bamboo, majority filter, and proportion filter)

Classification methods	Habitat class area (ha)			
	Marginally suitable	Suitable	Highly suitable	Total
No bamboo	9911	49,329	11,811	71,051
Unfiltered bamboo	4542	23,543	5764	33,849
Majority filter	4679	23,234	6162	34,075
Proportion filter	15,617	27,447	7078	50,142

Habitat classes reflect habitat suitability based on the respective factors.

Table 2
Number and mean patch size of habitat classified without (no bamboo) and with (unfiltered bamboo, majority filter, and proportion filter) bamboo per habitat class

Classification methods	Number of patches			Mean patch size (ha)		
	Marginally suitable	Suitable	Highly suitable	Marginally suitable	Suitable	Highly suitable
No bamboo	1871	4158	4301	5.30	11.86	2.75
Unfiltered bamboo	12,970	57,033	18,106	0.35	0.41	0.32
Majority filter	1251	3744	2655	3.74	6.21	2.32
Proportion filter	2747	2436	1959	5.68	11.26	3.61

The spatial patterns of the habitat with the proportion and majority filtered bamboo information differed considerably from habitat distributions based on the original classification (Fig. 1). Marked decreases in the overall amount of habitat were evident. However, an increase in fragmentation and isolation of habitat was also apparent. Habitat in the original classification (without bamboo) was essentially contiguous. In contrast, habitat including bamboo information was distributed in much smaller pockets and connectivity between large areas of quality habitat was reduced. Three relatively isolated main pockets of habitat can be seen in the north, central, and southwest portions of the map (Fig. 1).

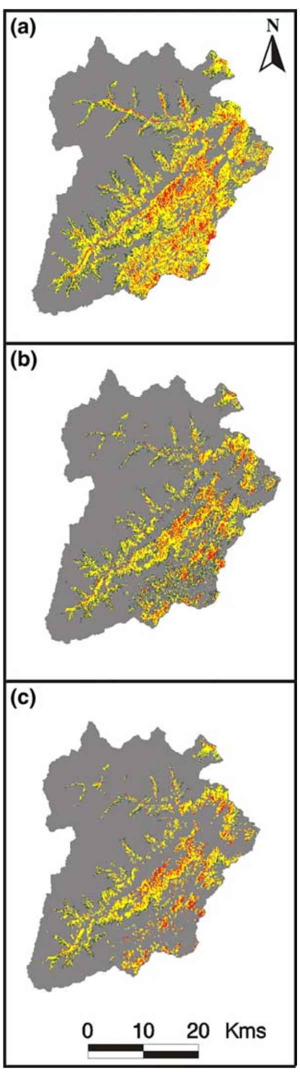

Fig. 1. Habitat distribution throughout Wolong based on classifications without bamboo (a), and with bamboo (proportion filter, (b); majority filter, (c)). Highly suitable, suitable, and marginally suitable habitats are shown in white, light gray, and black, respectively. Unsuitable habitat is shown in gray.

3.2. Carrying capacity

Clear decreases in estimated core habitat (all habitat contained within patches >1.7 km^2) can be seen in Fig. 2. Total core habitat was estimated to be 66,488 ha when not including bamboo information. The increased fragmentation when incorporating unfiltered bamboo data into the habitat classification resulted in only 7813 ha of core habitat. From classifications including majority and proportion filtered bamboo data, total core habitat ranged from 25,744 to 41,139 ha (Table 3). This is 38% and 61% less core habitat than estimated when excluding bamboo. Notable decreases occurred in suitable habitat from the classification incorporating the majority filtered data and the marginally suitable habitat from the proportion filtered method. These classes decreased by 25% and 31%, respectively. This is likely the result of the increased isolation of edge habitat when including bamboo.

Estimates of the carrying capacity based on analyses with and without bamboo information offer further insight into the additional information provided by including bamboo. In the 1970s, panda population surveys estimated there were 145 pandas within Wolong (Giant Panda Expedition, 1974). Subsequent surveys indicated that the panda population size declined to 72 in the early 1980s (China's Ministry of Forestry and WWF, 1989). However, based on the original classification of habitat without bamboo, potential carrying capacity was estimated to be 220 individuals (Table 3). This number far exceeds the survey estimates of panda numbers. Including bamboo in these analyses substantially lowered the estimated carrying capacity of the

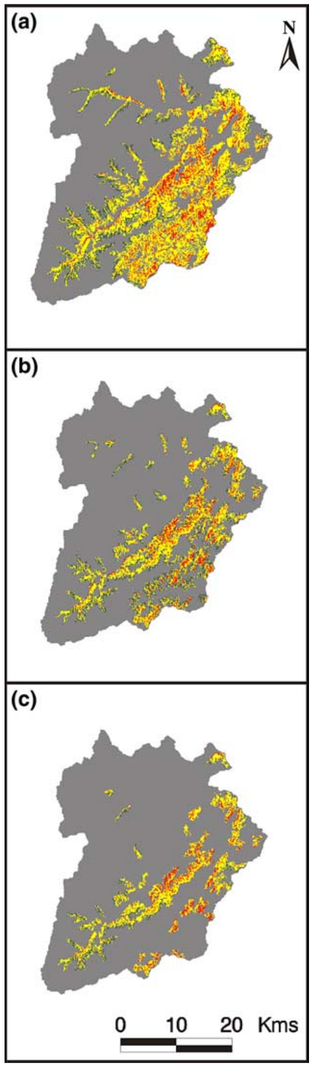

Fig. 2. Maps of core habitat patches (> 1.7 km^2) based on classifications without bamboo (a) and with bamboo (proportion filter, (b); majority filter, (c)). Highly suitable, suitable, and marginally suitable habitats are shown in white, light gray, and black, respectively. Unsuitable habitat is shown in gray.

current habitat in Wolong. The majority and proportion filter habitat classifications resulted in estimates of 88 and 130 pandas, respectively (Table 3). These estimates fall within the historical population range of Wolong (72–145). The proportion estimate is slightly lower than the population estimate from 30 years prior and may reflect the decrease in habitat over that time (Liu et al., 2001). The more restrictive majority filter resulted in a carrying capacity similar to lower estimates of the number of pandas within Wolong and highlights areas of high-quality bamboo habitat.

4. Conclusions and discussion

The range of estimates highlights the influence of different methods of incorporating bamboo into habitat classifications. Incorporating information about understory vegetation into habitat analyses of Wolong Nature Reserve resulted in 30–50% decreases in the estimate of panda habitat and extreme ranges in fragmentation of habitat. Knowledge on the biological relevance of each estimate is essential to interpret and utilize these results. The proportion filter in all probability offers the most meaningful information relative to pandas' use of bamboo. We therefore believe the current best estimate of total potential habitat within Wolong is approximately 50,000 ha. However, the carrying capacity derived from the majority filter method most closely matches low-end estimates of panda numbers. This suggests the panda population size was likely far below the potential carrying capacity and concentrated in areas of high-quality bamboo habitat. Further research is required to determine whether habitat with less suitable bamboo is underused due to the low number of pandas in the wild today or if the increased isolation from bamboo distribution makes patches of habitat unavailable to pandas.

This study has important implications for conservation. De Wulf et al. (1988) reported that total distribution area of giant pandas without bamboo information was approximately 13,000 km^2 (including Wolong, other reserves, and non-reserves). If overestimation due to the lack of detailed information on the spatial distribution of bamboo is consistent across the entire panda range, the total amount of panda habitat is at least 3900 km^2 less than reported by De Wulf et al. (1988). In addition, notable isolation occurs between large habitat patches when bamboo information is included (Fig. 2). Pandas are extreme K-strategists, have

Table 3
Estimated core habitat (all habitat contained within patches >1.7 km^2) without (no bamboo) and with (proportion, majority, and unfiltered) bamboo per habitat class

Classification methods	Core habitat (ha)			
	Marginally suitable	Suitable	Highly suitable	Carrying capacity
No bamboo	8900	46,253	11,335	220
Proportion	6636	23,656	10,847	130
Majority	5182	17,512	3050	88
Unfiltered	1768	5258	787	27

Carrying capacity was calculated based on the quantity and quality of core habitat.

low reproductive success, and are currently at very low numbers (about 1000). Sub-population isolation and inbreeding are already a concern for this endangered species (Lu et al., 2001). This study suggests that carrying capacity is sharply lower (by at least 40%) and isolation of habitat is more prevalent than previously measured. Given the unrealized fragmentation and isolation, studies that continue to rely on generalized data are at risk for not only overestimating the total habitat available, but also overstating the connectivity of viable habitat and developing management plans that do not address true conservation priorities.

The marked decrease in the estimated area available to pandas and the fragmentation of remaining habitat implies that spatial analyses based on previous models of habitat do not correspond to current habitat conditions. The failure to incorporate detailed information in broad-scale analyses may explain one of the difficulties in reconciling local-scale biological studies with broad-scale spatial analyses (Levin, 1992). While broad-scale information will likely never be able to provide all relevant information for all studies, current and increasingly detailed biophysical data may provide a means to improve future habitat estimates.

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