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MEASURING AND MODELING THE SPATIAL PATTERN OF UNDERSTORY BAMBOO ACROSS LANDSCAPES: IMPLICATIONS FOR GIANT PANDA HABITAT

by

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ABSTRACT

MEASURING AND MODELING THE SPATIAL PATTERN OF UNDERSTORY BAMBOO ACROSS LANDSCAPES: IMPLICATIONS FOR GIANT PANDA HABITAT

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Understory vegetation is a critical component of biodiversity and an essential aspect of habitat for countless wildlife species. However, compared to overstory, information about understory vegetation distribution is scant, available mainly over small areas or through imprecise large area maps from tedious and time-consuming field surveys. As a result, measuring and monitoring wildlife habitat at the landscape level rarely include understory vegetation and has likely led to serious misestimates of wildlife habitat and, consequently, biodiversity. As a case study, we examined an approach to classifying understory bamboo, the staple food of the giant panda (*Ailuropoda melanoleuca*), from remote sensing imagery in the Wolong Nature Reserve, China. We also used these data to estimate the landscape-scale distribution of giant panda habitat, and model the human effects on forest cover and the spatio-temporal dynamics of bamboo and the resulting implications for giant panda habitat.

The spatial distribution of understory bamboo was mapped using an artificial neural network and leaf-on remote sensing data. Training on a limited set of ground truth data and using widely available Landsat TM data as input, a non-linear artificial neural network achieved a classification accuracy of 80% despite the presence of co-occurring mid-story and understory vegetation.

Using information on the spatial distribution of bamboo in Wolong, we compared the results of giant panda habitat analyses with and without bamboo information. Total amount of habitat decreased by 29 – 56% and overall habitat patch size decreased by 16 – 48% after bamboo information was incorporated into the analyses. The decreases in the quantity of panda habitat and increases in habitat fragmentation resulted in decreases of 41 – 60% in carrying capacity.

Using a spatio-temporal model of bamboo dynamics and human activities, we found that local fuelwood collection and household creation will likely reduce secondary habitat relied upon by pandas. Human impacts would likely contribute up to an additional 16% loss of habitat. Furthermore, these impacts primarily occur in the habitat relied upon by giant pandas during past bamboo die-offs. Decreased total area of habitat and increased fragmentation from human activities will likely make giant pandas increasingly sensitive to natural disturbances such as cyclical bamboo die-offs.

Our studies suggest that it is necessary to further examine approaches to monitor understory vegetation and incorporate understory information into wildlife habitat research and management. The success here to map bamboo has important implications for giant panda conservation and provides a good foundation for developing methods to map the spatial distributions of understory plant species. Knowledge of the spatial distribution of bamboo is necessary to accurately measure the quantity and landscape characteristics of giant panda habitat. And integrating more specific habitat information into models of the combined effects of land cover change and natural disturbances allows more accurate assessments of habitat.

To my family

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CHAPTER 1

BACKGROUND AND RESEARCH TOPICS

1.1 Background

There is a long history of studying wildlife/habitat relationships (Leopold 1933; Morrison et al. 1998). While some economically and socially relevant species have been studied in extreme detail, surprisingly little is known of the exact habitat requirements for many species, how their habitat is distributed, how continued human activities will influence the current distribution of habitat, and how the distribution of habitat influences the local and global distribution of species. This is particularly problematic at scales larger than the typical plot or patch scale at which most of the past ecological studies have operated. Broad-scale analyses such as landscape and regional studies have almost always necessarily relied on habitat information available from remote sensing data (Roughgarden et al. 1991). If useful theories are to be developed for a better understanding of wildlife/habitat interactions and to offer viable management options, more detailed information is needed over larger areas. In addition, these data need to be examined relative to species needs. And, the processes and degree to which humans are impacting wildlife habitat need to be better understood.

Habitat loss is a principal threat to the local and global persistence of terrestrial faunal and floral species (Sala et al. 2000). There has been much discussion on the degree of humans have impacted natural areas around the world. Estimates have ranged from 40% of the terrestrial surface having been directly co-opted to 80% directly and indirectly influenced (Vitousek et al. 1997). This large degree of influence on natural areas, and consequently wildlife habitat, necessarily effects the distribution and persistence of almost every species on this planet. Knowing where these impacts are occurring, how they relate to wildlife habitat, and understanding the process related to impacts are needed to mitigate further losses and develop a more sustainable human-environment relationship.

Landscape ecology first emphasized the importance of the spatial arrangement of resources relative to wildlife species and the need of examining habitat at scales relevant to how species interact with the environment (Forman and Godron 1986; Turner 1989). This was one of the first efforts to extend wildlife-habitat relationships to include the influence of the surrounding environment on habitat quality, movement, and population persistence. Expanding ecological analyses from the traditional patch relationships broadened ecological theory, but was very data, and potentially, computationally intensive. Three advancements allowed landscape ecology to include analysis of real heterogeneity found in nature: accessible computational power, remote sensing, and Geographical Information Systems (GIS) (Roughgarden et al. 1991). Increased computational availability allowed increased modeling and quantitative analyses of large amounts of data, remote sensing provided data corresponding to the arrangement of natural features, and GIS provided a system to relate the separate data sources to one another for more intensive and realistic analyses.

Modeling wildlife-habitat relationships is a mainstay of ecology (Turner 1990). Models have ranged from simple linear regressions to complex nonlinear systems analyses. However, intensive modeling has only become increasingly popular with the development of personal computers. Particularly, spatially explicit models have become more commonplace with the availability of computational power and geographically registered data (Dunning et al. 1995). While geographical analyses of socio-economic relationships with the environment have a long history, it has only been the recent availability of detailed geo-referenced data that has allowed coupling theoretical developments with observed distributions of natural resources. Remote sensing data and hand-held Global Positioning System (GPS) devices have led this boom in geo-referenced data. However, many environmental variables found necessary to relate wildlife to habitat at the patch level have not been available from remote sensing sources.

One example of this is past attempts to map giant panda (*Ailuropoda melanoleuca*) habitat. Past analyses have been restricted in their ability to accurately measure panda habitat over large areas by the lack of information on the spatial distribution of bamboo, the principal food source for pandas (Schaller et al. 1985; Morain 1986). Throughout most of the panda range, bamboo is found in the understory. Efforts to map the distribution of bamboo through field surveys have necessitated coarse estimates over large areas or detailed estimates restricted to small areas. Attempts to map bamboo using aerial photography or remote sensing have been unsuccessful in that conventional photo interpretation and digital image analyses have difficulty categorizing understory vegetation (Morain 1986). This lack of understory information, then, is likely leading to overestimates of panda habitat. In addition, as bamboo is not correlated to forest cover or abiotic factors (Linderman, unpublished data), the actual landscape distribution of panda habitat is likely much different than if habitat is only calculated using traditional approaches.

Giant pandas historically extended across much of current China (Schaller et al. 1985). Fossils dating back to the Pleistocene era (approximately 3 million years ago) have been found across China and in neighboring Burma. In the mid-1980's, MacKinnon and DeWulf (1985) estimated that the total available habitat has been reduced to approximately 32,000 km^2. Drastic human population growth and subsequent development and deforestation have led to the loss of much of the panda's former range. It is this extensive loss of habitat and isolation that has resulted in the fragile nature of the current panda populations.

While rugged topography and isolation from humans protected the current available panda habitat and populations, continued growth in human population and development pose increasing risks to the remaining panda habitat. Currently, pandas occupy only a portion of the remaining habitat, found only at the fringe of their former range in Sichuan and Shaanxi provinces. Within the Min, Qionglai and Min mountains, it is estimated that less than 1,000 pandas remain in the wild, existing in isolated populations separated by topography and human development (Zhang et al. 1997). The isolation of distinct populations severely threatens the genetic stability of the species (Lu et al. 2001). However, other threats exist in the form of incidental poaching, decreasing accessibility to quality habitat, and continued development and human impacts of the remaining habitat (Schaller et al. 1985).

For example, between 1974 and 1989 it is estimated that the panda population in Wolong Nature Reserve (one of the largest reserves dedicated to protecting giant panda habitat) plummeted from 140 to approximately 74 individuals (Zhang et al., 1997). Schaller et al. (1985) suggest the loss of habitat and incidental poaching most likely contributed to the attrition of the reserve's population. A more publicized explanation of the decrease of pandas in the reserve was a mass-flowering of bamboo that occurred in 1982 (Schaller et al. 1985). While pandas are obligate grazers of bamboo and the species (*Bashania fangiana*) which mass-flowered was the primary bamboo species for pandas in the reserve, it is unlikely the loss of this species contributed significantly to the loss of any pandas. Schaller et al. (1985) noted that no pandas died of starvation and very few pandas suffered malnutrition. This is in stark contrast to a similar situation in the Min mountains where in 1982 a sudden die-off of several bamboo species resulted in drastic number of pandas dying of starvation. The die-off of the principal bamboo species in Wolong Nature Reserve did not result in similar impacts on pandas because a contiguous secondary bamboo species (*Fargesia robusta*) was accessible. However, continued human impacts threaten habitat throughout Wolong with the most likely areas of development and use located in areas of secondary bamboo. The loss of this habitat could result in drastic consequences for the panda population in Wolong and poses a problem throughout much of the panda range. The current fragmentation of habitat and inaccessibility to alternative bamboo sources seriously threaten the remaining panda populations.

Bamboo is fairly unique in that it is a semelparous grass with a gregarious flowering and subsequent mass die-off (Janzen 1979). Few environmental associates or triggers have been found and few conclusive hypotheses on the cause for flowering are available (Keeley and Bond 1999). The time between flowering (or intermast time) varies considerably depending on the species. Intermast times for bamboo species range from 10 years to over 100 years, but seem to show extremely consistent intermast times within species (Janzen 1979). Taylor et al. (1991) found that environmental variables contributing to stress of the bamboo limits areas of flowering. For example, large tracts of *Bashania fangiana* (common name: Arrow bamboo) flowered in 1983 in Wolong Nature Reserve. Patches of *Bashania* at the extreme upper elevation range, on steep north-facing slopes, or in large canopy gaps (and consequently different local moisture conditions) were less likely to flower than patches not stressed. Reestablishment after mass-flowering is difficult to predict based on environmental conditions. However, slight increases in recruitment were noted in small canopy gaps (Taylor and Qin 1993). Growth in canopied areas was slightly lower than in gaps with an average of 15 years for *Bashania* to return to full cover in most areas (Taylor and Qin 1993). However, even after 15 years, visible signs of the flowering and large tracts devoid of *Bashania* can still be found throughout much of the range of *Bashania* (Linderman, personal observation).

Bamboo's unique life-history poses a significant threat to the current distribution of giant pandas. Where pandas previously were able to move to areas of alternative bamboo species, current habitat fragmentation limits movement and restricts panda's access to areas containing other bamboo species. The dependence of pandas on secondary bamboo species was apparent in Wolong during the recent *Bashania* die-off and the consequences due to the lack of secondary bamboo during the simultaneous die-off of several bamboo species in the Min Mountains. This problem has become increasingly acute as humans appropriate increasing amounts of habitat, but more relevant is that habitat loss is occurring in areas that may have a considerably higher impact on panda populations than total quantity of habitat loss predicts alone. If pandas are excluded from an alternative bamboo resource during the subsequent flowering of Bashania, the current panda population could be seriously impacted. Furthermore, this points to wider problems and needs for effective management of panda habitat and mitigation of human impacts. Current knowledge on the spatial distribution of bamboo is inadequate relative to panda needs, the spatial distribution of bamboo has a significant impact on panda habitat, and human activities are increasingly occurring in areas vital to panda survival.

This situation is not confined to the giant pandas of China. Countless fauna, as well as flora, depend on environmental conditions that exist below canopies. Therefore, past attempts reliant upon remotely sensed data are likely misestimating species distributions and landscape arrangements of habitat. Efforts to derive species-relevant data from remotely sensed images at a scale that species are interacting with the environment are needed to more accurately reflect the spatial distribution of habitat, allow more robust analyses of wildlife/habitat relationships over large areas, and permit the development of more viable policy alternatives.

This dissertation was developed with the principal goals of deriving pertinent giant panda habitat information from remotely sensed data, studying the impact of detailed bamboo information on the distribution of habitat, and projecting future impacts from human activities on giant panda habitat. It was hoped this study would allow a more accurate representation of panda habitat over large areas, increase our understanding of the current habitat conditions, and provide additional information to management officials to insure the protection of this endangered species. To this end, I developed three primary areas of analysis: (1) I developed methods to map the spatial distribution of bamboo from remote sensing data, (2) analyzed the influence of the spatial distribution of bamboo on the landscape distribution of giant panda habitat at the landscape scale, and (3) modeled the spatial trends in human impacts relative to the spatial distribution of bamboo. A review of the principal topics of this dissertation and the three research chapters follows.

1.2 Research Topics

The first goal was to develop a viable method to classify the presence/absence of bamboo from remote sensing. The impetus for this was the lack of detailed information on the spatial distribution of bamboo. Past efforts to map the distribution of bamboo have relied on ground surveys. Due to the cost and effort required, this approach resulted in either coarse maps over large areas (e.g. 1000's of square kilometers) or detailed maps constrained to small areas (e.g. 10's of square kilometers). The detail of the coarse maps, while sufficient for broad estimates of giant panda habitat, were not nearly at the resolution at which pandas interact with bamboo nor sufficient to predict habitat use and resulting influence of bamboo on the spatial distribution of habitat. To achieve the detail as in the small area maps would be very costly and time consuming endeavors. Therefore, I examined the utility of remote sensing data to map the distribution of bamboo. A significant obstacle to the successful classifications of bamboo from remote sensing in the past is that throughout most of panda habitat bamboo is found as an understory species (Morain 1986; Porwall and Roy 1991). Overstory cover reduces the amount of irradiance at the understory, modifies irradiant downwelling light, intercepts reflected light from the understory, and modifies upwelling reflected light from the understory (Lillesand and Kiefer 1994). Therefore, the radiance measured at a distant sensor is a complex integration of reflected energy with the main contribution coming from the overstory features.

Irradiant energy obviously does reach the understory. Direct light from canopy gaps, reflected light from overstory features, and transmitted light (particularly near and shortwave infrared energy) interacts with the understory. The ability of remote sensing then would be a matter of sufficient signal from the understory reaching the remote sensor relative to noise (or a sufficient signal-to-noise ratio). To examine this complex problem, we compared the utility of an artificial neural network to parse the signal and classify the presence or absence of understory bamboo. Using Landsat TM data as input and hundreds of ground samples as training and validation data, we were able to achieve over 80% accuracy in classifying the presence/absence of understory bamboo at a resolution of 30 meters for the entire Wolong Nature Reserve.

A subsequent study used the bamboo presence/absence data to examine the effects of bamboo distribution on panda habitat throughout the reserve. Traditional landscape studies have relied on remotely sensed data to map habitat. However, information on the vertical and horizontal distribution of vegetation beneath canopies is needed to accurately relate wildlife use and environmental conditions (MacArthur and MacArthur 1961; James 1971). Theoretical studies and practical application of landscape ecology then require more detailed environmental information to more accurately predict the influence of the spatial arrangement of habitat on wildlife species. A comparison was made between a reserve-wide analysis on the distribution of habitat that did not use bamboo information (Liu et al. 2001) and reserve-wide analyses including the spatial distribution of bamboo. This has significant implications for future panda habitat monitoring and management. In addition, the comparison suggests data requirements for other landscape-level analyses.

Finally, it has been long recognized that wildlife species require access to specific resources (e.g. watering holes, forage, trees of sufficient diameter, etc.) In more general terms, landscape ecology is based on the principal that the arrangement of resources influences ecosystem processes whether they are fire disturbances, wildlife movement, or human impacts. In particular, it has been noted that certain resources can be vital for wildlife species. The spotted owl controversy centered on the owls' requirement of large areas of old-growth forest. Low-elevation graze areas are critical to elk and large mammals in Yellowstone (Turner et al. 1994). And, the availability of alternative bamboo sources is vital to the survival of giant pandas. Even limited impacts to habitat, then, can have drastic implications for a wildlife species. This is occurring in Wolong Nature Reserve. Local farmers, while only harvesting a small proportion of the total forest area, are concentrating their resource use (e.g., fuelwood collection) on easily accessible forests at lower altitudes corresponding to the current distribution of the secondary bamboo utilized by pandas. Continued impacts in these areas could have drastic consequences during the next die-off of the principal bamboo species in the reserve. In an attempt to understand the driving factors for the spatial distribution of fuelwood collection, predict impacts under different scenarios in the future, and offer possible mitigation strategies, we have modeled human activities in Wolong Nature Reserve. The study suggested that the spatial arrangement of human activities is as important as the sheer quantity of activity when considering possible impacts on native species.

Wolong Nature Reserve is unique in that it is one of only a handful of reserves dedicated to the protection of an extremely high profile species, the giant panda. However, the ecological problems occurring in Wolong are not unique at all. Humans will continue to degrade habitat, more detailed information is needed on specific habitat requirements such as understory vegetation, and more accurate measurements of actual habitat area and spatial distribution are urgently needed for species around the world. The methods outlined in this dissertation hopefully represent possible alternative approaches to developing these data, examining ecological questions, and developing viable alternatives.

CHAPTER 2

USING OPTICAL REMOTE SENSING DATA TO CLASSIFY THE PRESENCE/ABSENCE OF UNDERSTORY BAMBOO IN A GIANT PANDA RESERVE

In collaboration with

Jianguo Liu, Jiaguo Qi, Li An, Zhiyun Ouyang,
Jian Yang, and Yingchun Tan

Abstract

Understory vegetation is a critical component of biodiversity and an essential habitat component for many wildlife species. However, compared to overstory, information about understory vegetation distribution is scant, available mainly over small areas or through imprecise large area maps from tedious and time-consuming field surveys. A practical approach to classifying understory vegetation from remote sensing data is needed for more accurate habitat analyses and biodiversity estimates. As a case study, we mapped the spatial distribution of understory bamboo in Wolong Nature Reserve (southwestern China) using leaf-on remote sensing data. Training on a limited set of ground truth data and using widely available Landsat TM data as input, a non-linear artificial neural network achieved a classification accuracy of 80% despite the presence of co-occurring mid-story and understory vegetation. These results suggest that understory vegetation influences remote sensing data and classifying understory vegetation is feasible. The success here to map bamboo has important implications for giant panda conservation and provides a good foundation for developing methods to map the spatial distributions of understory plant species.

2.1. Introduction

Understory vegetation is a significant component of biological diversity and critical habitat for countless wildlife species (MacArthur and MacArthur 1961, Odum 1971, Schaller et al. 1985). However, monitoring of understory conditions has been restricted to tedious and time-consuming ground surveys due to a lack of alternative methods such as remote sensing. More specifically, whereas significant advances in regional ecology have been made from overstory mapping (Roughgarden et al. 1991), extensive spatial distribution information of understory vegetation has remained unavailable due to the limitations of traditional remote sensing classification techniques. Thus, the development of a practical approach to classify understory vegetation irrespective of canopy cover would significantly increase knowledge of the spatial distribution of understory vegetation and assist in modeling wildlife habitat for species-specific studies and biodiversity estimates.

Classification of vegetation from remote sensing data has typically relied on multispectral optical data as variations in chemical, water and structural composition between vegetation types all influence incident optical radiation allowing differentiation between classes of vegetation (Asrar et al. 1989). In sparse forests or regions with significant canopy gaps, direct reflectance from the understory certainly influences the optical reflectance response as measured by a distant sensor. In fact, in the near-infrared region, understory can dominate the overall reflectance from open-canopy stands (Nemani et al. 1993). Furthermore, several studies have shown that canopy background features have a significant influence on optical radiance measured by remote sensors even under considerable cover (Huete et al. 1985, Ranson et al. 1986, Guyot and Riom 1989, Bausch 1993). In particular, studies on the ability to retrieve Leaf Area Index (LAI) values from optical data have shown that, even in canopies up to 89% closed, understory vegetation characteristics have a measurable effect on the radiance response recorded by a satellite sensor (Nemani et al. 1993, Law and Waring 1994, Spanner et al. 1994, Qi et al. 2000). The influence from background features is due not only to direct reflectance from gaps in the canopy, but also multiscattering between understory and the overstory as well as transmission through the canopy and is therefore a combination of linear and non-linear contributions (Borel and Gerstl 1994). The degrees of linear and non-linear contributions vary relative to the understory and overstory cover, structure, and other variables. Therefore, while understory vegetation and background features influence the response measured at distant sensors, the understory contributions can often result in a complex signal that has not been amendable to traditional classification techniques.

Attempts to use traditional methods to map understory vegetation, even a coniferous understory with a leaf-off deciduous overstory, have had, at best, mixed results (Stenback and Congalton 1990, Porwall and Roy 1991, Ghitter et al. 1995). Traditional approaches to classifying understory vegetation land cover from multispectral data have been based on modeled categorizations of a discrete thematic space using the statistical separability of pixel signatures (Jensen 1996). These approaches are often restricted in their applications and accuracy for classifying complex scenes. Topography, mixed classes and spectral similarities have all been shown to influence traditional classification accuracy (Lillesand and Kiefer 1994). This becomes particularly relevant when considering the complex contributions of understory vegetation. In addition, changes in canopy cover and species composition, and understory species composition and cover from pixel to pixel results in an extremely variable spectral signature, often with varying degrees of non-linear contributions, that is difficult to classify using standard methods.

In order to utilize remote sensing data for classifying understory vegetation, a method to parse the highly variable and complex understory influences (canopy gap and sub-canopy) from the integrated radiance received at the sensor then must be used. Artificial neural networks are essentially non-parametric data transformations that can account for non-linear effects given a sufficiently complex partitioning of the classification space (Atkinson and Tatnall 1997). To classify the presence/absence of the variable spectral influence of understory vegetation, a non-linear approach is almost certainly required as well. Understory contributions to the radiance at the sensor are a mix of decreasing linear contributions from canopy gaps as the overstory becomes increasingly dominant and increasingly non-linear components due to multi-scattering and transmission. Furthermore, whereas traditional classification techniques make assumptions on the underlying model of the data, neural networks are a non-parametric method and are capable of learning the complex trends in data necessary to parse the variable and subtle trends in areas of more canopy (Foody and Arora 1997, Atkinson and Tatnall 1997). Neural networks should therefore be able to more accurately classify sub-canopy gap vegetation while considering non-linear components of understory contributions. In addition, this technique should be more capable of adapting to the variability in the signature due to varying canopy and understory conditions. Therefore, to test the practicality of classifying understory vegetation, we compared the ability of an artificial neural network to predict the presence or absence understory vegetation from optical remote sensing data based on limited ground-truth data relative to traditional techniques.

2.2. Methods

The impetus for this study was the need for a practical method to classify the spatial distribution of understory bamboo irrespective of the canopy conditions over large regions. Bamboo plays a vital role in the survival of the endangered giant panda (*Ailuropoda melanoleuca*) (Schaller et al. 1985, Liu et al. 1999a). The impact of the spatial distribution of bamboo on panda populations has been well-documented (Johnson et al. 1988, Taylor and Qin 1997). However, past panda habitat analyses have been limited in their ability to conduct accurate habitat assessments over large areas due to the lack of bamboo distribution maps with sufficient detail or extent as shown in Figure 2.1. Remote sensing would be a preferable method for data acquisition at larger scales. However, methods to map the extent of bamboo, even employing aerial photography, have not been successful (Morain 1986, De Wulf et al. 1988, Porwall and Roy 1991). The main problem in classifying bamboo in much of the panda range is that it is typically found as an understory species under variable canopy species, percent cover and densities. We required an approach that would be able to classify the presence/absence of presence/absence of understory bamboo irrespective of the overstory. Therefore, to test the applicability of an artificial neural network to this problem, classifications from a neural network and supervised classifications of the bamboo distribution using limited training data were compared.

2.2.1 Study Area

Located between 102°52' and 103°24' E and 30°45' and 31°25' N in the Qionglai Mountains of southwestern China, the reserve is approximately 200,000 ha in size and one of the largest parks dedicated to giant panda preservation (Liu et al. 1999b, Liu et al. 2001). It is estimated that over 10% of the remaining worldwide panda population can be found within this reserve. The topographic nature of Wolong directly relates to habitat preferred by panda. Within Wolong, elevations range from 1200m to 6525m creating several climatic zones and consequently high habitat diversity. This also provides cooler climatic conditions that panda prefer coupled with precipitation levels necessary for bamboo of which panda are obligate grazers. From the lowest elevation to approximately 1600 meters, the canopy consists mainly of evergreen broadleaf. From 1600 to 2000 m there is an increasing mixture of the broadleaf and deciduous. The canopy is dominated by deciduous vegetation from 2000 m to about 3600 m with an increasing mix from conifer at the higher altitudes. Above this elevation, subalpine conifers give way to alpine meadow at an elevation of approximately 4400 m.

Throughout the reserve forest canopies averaged 56% closure and rarely exceed 90%, maintaining significant gap area for light penetration.

Within the reserve, bamboo occurs up to an elevation of 4500 m and is typically an understory species. Up to eleven species of bamboo are found in Wolong. Two species, ***Bashania fangiana*** and ***Fargesia Robusta*** (Figure 2.2), predominate. In forested areas, bamboo is distributed in patches ranging in size from single plants to hundreds of meters across. Where bamboo does occur, it averaged 41% of the ground cover. However, the spatial distribution of bamboo seemingly does not follow any trends relative to overstory or abiotic factors (Reid et al. 1989). Regression relationships based on ground samples of overstory cover, slope, altitude and bamboo ground cover in forested areas are shown in table 2.1 and suggest that the prediction of bamboo presence/absence is independent of within stand characteristics. The lack of correlation of the spatial distribution of bamboo and environmental factors may be partly due to the unique episodic synchronized die-offs of large areas of bamboo (Reid et al. 1989, Keeley and Bond 1999). However, it is precisely this distribution that affects pandas.

The spatial distribution of bamboo is also influenced by human activities and restricted environmentally (e.g. high-altitude permanent rock, alpine meadow). Grazing and agricultural use have effectively removed bamboo from some areas. Other regions have been clear-cut leaving a mixed midstory shrub layer and a lower occurrence of bamboo. Finally, selective logging has changed the species composition of the overstory and reduced canopy cover in some areas. Few forested areas contained large gap areas. Selective logging has been characterized by random thinning. Clear-cuts and other land cover changes have typically been larger than 60 x 60 m. While relatively limited in impact, these human activities are transforming the landscape and introducing additional complexity in classifying the land cover. The complex relationships between land cover and the lack of substantial correlation between the presence of bamboo and canopy conditions made prediction or classification using traditional methods difficult and required a new approach for accurate classification. Knowledge of the distribution of bamboo irrespective of land cover is needed to allow better classifications of the suitability of panda habitat, test the implications of the spatial distribution of habitat on panda populations, and provide recommendations for future restoration and conservation management.

2.2.2 Data

Field data were collected throughout the reserve during the summers of 1998 and 1999 and included vegetation ground sampling plots for algorithm training and validation and Ground Control Points (GCPs) to allow registration of the remote sensing data. Landsat Thematic Mapper (TM) data acquired over Wolong Nature Reserve in September 1997 were used for this study. The Landsat TM scene was registered to UTM WGS-84 coordinates to allow co-registration of the ground truth data. The remote sensing data were registered using the GCPs collected to an RMSE of less than one pixel. To gather representative ground data, stratified sampling of the land covers and understory conditions was conducted.

Ground sample plots were located where access was possible and registered to the remote sensing data through differential Global Positioning System (GPS) using Trimble Pro XRS and Community Base Station receivers. Plots were selected where the vegetation was relatively homogeneous over a 60m x 60m area. A sample area was considered relatively homogeneous where similar percentages of vegetation were distributed evenly throughout the entire sample plot. Therefore, any 30m x 30m subplot would contain the same vegetation percentages regardless where it was situated within the 60m x 60m plot. The 60m x 60m dimensions were chosen as prior knowledge of the GPS position in relation to the remote sensing grid was unknown and ensured one pixel of the Landsat TM data (30-meter resolution) would be fully contained within a sample plot. For each plot, information on the biota such as vegetation types for the overstory, midstory and understory, as well as the corresponding percent cover, were recorded. Percentages of vegetation cover in the overstory, > 5m, midstory, 2 – 5m, and understory, < 2m were estimated visually for the 60m plots.

Training data for the artificial neural network were selected from the vegetation ground truth data where positions were known at a suitable accuracy (field data were filtered for GPS measurements with standard deviations greater than 10 meters) and stratified to include a representative sample of vegetation conditions. On this basis 189 sample plots were chosen. Approximately, two-thirds of these data were used to train the neural network and the remaining third reserved for validation. The data were categorized into presence/absence categories. If bamboo cover was greater than 10%, the training value was assigned a 1 (presence), else if the bamboo cover was less than or equal to 10% within the sample area, the training value was assigned a 0 (absence). Such categorization was done for three reasons. First, sampling methods were limited in assigning absolute ground cover percentages over large sample plots. Therefore, data were binned into 0, 25, 50, 75 and 100% categories. For example, a sample of between 0% and 10% was categorized as 0%. If a sample fell between 15% and 35% it was categorized as 25%, etc. Therefore, samples estimated to have 25, 50, 75 or 100% bamboo ground cover were considered presence. Second, at less than 10%, the cover was extremely insignificant, did not provide any useable biomass for pandas, and was considered to have a very limited influence on the spectral response. And third, it was anticipated that a binary categorization would reduce data transformation complexity.

2.2.3 Application of Artificial Neural Networks

The multi-layer perceptron (MLP) is the most commonly used neural network structure in remote sensing and was used in this study (Atkinson and Tatnall 1997). The basic structure of an MLP is the existence of distinct data layers through which the data are transformed (Figure 2.3). For example, the first layer (input layer) could be represented by a series of nodes consisting of the separate bands of remote sensing data, ancillary data or any combinations of these data. The next layer(s) are referred to as hidden layer(s) as the user does not have access to the values within the nodes of these layers. Each hidden node is a weighted sum of a function of the input vector. The final output layer is the weighted-sum of a function of all hidden nodes. The learning process of the neural network occurs by back-propagation and error minimization according to the training data.

The training data are composed of input data and corresponding known output values. The input data for this study consisted of the single TM pixels fully contained within the sixty-meter ground sample plots. The output data consisted of the corresponding ground sampled bamboo absence/presence values of those plots. Therefore, the output layer consisted of a single node with the expected values of 0 (absence of bamboo) or 1 (presence or bamboo). Typically when training neural networks, the hidden functions are initially set with a random weight value. The input values are then passed through the hidden layers for the first time and the output from the hidden layers (the output layer) is compared to the expected outcomes according to the ground sample training data. Learning algorithms then modify the hidden layer weights to reduce the error between the training values and algorithm outputs. This process is repeated as the individual hidden node weights and biases are modified in an iterative process until acceptable error levels compared to the training data are achieved. This repeated error minimization essentially allows the algorithm to learn the nature of the training data (Atkinson and Tatnall 1997). If the training data are perfectly representative, the algorithm theoretically learns the nature of the full data set. However, it is often very difficult to collect a training set that is completely representative of the whole data set. Consequently, image data not seen by the algorithm or consistent with the training data can result in variations from the expected output values.

For this study, the neural networks were simulated in the Neural Network module of Mathworks MATLAB (The MathWorks Inc. 1999). Several variations of internal network structure, input data, and learning algorithms were tested to determine optimal algorithm characteristics. Different combinations of the Landsat TM (6 bands excluding thermal band) were examined as potential data input. As a result, the input layer consisted of three to six input nodes depending on the layers used. The structure of the hidden layers was also tested to determine the necessary number of hidden layers and number of nodes per layer required. In addition, generalization techniques, methods to reduce overfitting, were analyzed including techniques such as early stopping by adjusting the training Mean Square Error (MSE) goal and automated regularization utilizing the Bayesian Regularization (BR) learning algorithm. Early stopping, as the term suggests, establishes a higher error convergence threshold and thus stops the training process before full convergence occurs. This can be done automatically by comparing an additional reserved data set to determine when error minimization reduces generalization of the full data set. However, since training data were limited, preset early stopping error levels of 1×10^{-05} and 1×10^{-08} were tested relative to a full convergence level, typically around 1×10^{-20} (known from preliminary trials).

Evaluation of individual algorithms was conducted by examining algorithm performance through each of four stages: training, simulation, verification and validation. The algorithms were first presented with training data (i.e. remote sensing pixel values and corresponding ground-truth data presence/absence values). If the algorithm was able to converge on the preset error goal, a 15 x 15km evaluation subset of the remote sensing data was fed through the trained data, or simulated, to output a predicted map of bamboo presence/absence. This output subset was then examined to determine how well the predicted values conformed to the expected output values of 0 or 1. As in many practical applications, it was not possible to collect a completely representative training sample. Therefore, the output values of pixel values not seen in training are expected to vary relative to the expected outputs and were categorized if they did not conform exactly to the expected presence/absence values of 1 or 0. The prediction maps were then verified with the training data and validated using independent data. The optimal algorithm characteristics were chosen based on the validation accuracy and conformance to expected output levels for the entire image. This algorithm was then used to simulate the remaining 17 subsets to produce a full map of the reserve.

2.2.4 *Comparison to Traditional Techniques*

It was hypothesized that the underlying restrictions and assumptions of traditional classification methodologies would not allow accurate classification of understory features. To allow comparison to traditional techniques, supervised classifications of bamboo distribution were conducted on the 15 x 15km validation subset using Erdas Imagine v. 8.3.1 (Erdas 1999). The same training data used to train the neural network within the validation subset were used to gather supervised signatures. These signatures were categorized to allow Maximum Likelihood classifications and retained as single signatures for a Minimum Distance classification. This allowed testing of the effects of classification algorithms and merging of spectral signatures. Each method is a standard supervised classification approach. However, it was anticipated that the extreme topography and overstory variation would require more than one signature to obtain accurate results. Utilizing different combinations of signatures allowed testing of these effects. The resulting output classes from each method were recombined into presence and absence categories. These binary classifications were then compared to the independent validation data to determine classification accuracy.

2.3. **Results**

2.3.1 Evaluation Results

Evaluation and comparison of the simulations were initially conducted on a 15km x 15km evaluation subset. For each algorithm where convergence was achieved, conformance to expected values, verification, and validation results were examined. It was found that the full TM data set (all six bands) was required for adequate convergence. Inputs using fewer bands converged more slowly or not at all. Adequate convergence was also not possible using an algorithm structure containing only one hidden layer. For comparison between algorithm structures using more than one hidden layer, verification and validation results were examined.

Prior to verification and validation analyses, the outputs were categorized into presence and absence values. This was necessary since the training data were not a fully representative sample of all land covers, combinations of land covers, topographic effects, and understory conditions. Therefore, variations in the output value from the expected 1 or 0 were seen. For example, comparison of output values corresponding to training data plots showed value ranges of 0.99-1.00 as classification values for the presence of bamboo and only 0.00 for absence. However, output values for pixels where ground samples were available but not used for training showed a larger spread. In fact, for land covers (clouds, exposed rock, snow) where training data were not available, output values were as high as 2.5. In addition, since complete control even within sampled vegetation types and abiotic factors was not absolute, output values in vegetated areas ranged from 0 – 1.90. Therefore, when the entire image was simulated, output values from the network less than 0.50 or greater than 1.50 were considered absence and values greater than 0.50 and less than 1.50 were considered presence.

Algorithm verification was significantly higher when using at least 24 hidden nodes in the first layer and as high as 100% agreement for all convergence levels tested when using at least 24 nodes in the first layer and 48 nodes in the second hidden layer. The validation data for six algorithm architectures given in table 2.2 show the basic trend in network training. Validation results ranged from less than 50% from networks failing to fully converge (not shown) to 82% for the most optimal method shown. As shown in table 2.2, learning algorithms (e.g.

BFGS quasi-newton (BFG) and Levenberg-Marquardt (LM)) had less influence on the overall accuracy compared to early stopping levels.

Examples of the outputs from the neural network algorithm tests on the 15km x 15km study area are shown in Figure 2.4. Consistent areas of agreement among the outputs can be seen (Figure 2.4 letterboxes) and represent trends in landcover such as major clearings and agriculture areas. The differences are less obvious. In tests run to convergence levels of 1×10^{-8} and 1×10^{-20} (Figures 4b and c), landcovers not represented in the training data are not classified within the expected 0 – 1 range of values and are noted as very bright features. Compared to the 1×10^{-5} trials (Figure 2.4a), the latter image shows more consistent bamboo classification and better conformance to expected trends in output values (0 – 1). In addition, compared to overstory classifications and knowledge of the region, the 1×10^{-5} method seems to retain landuse features (i.e. human appropriated areas, permanent rock, etc.) better. Based on these visual assessments and the validation results shown in table 2.1, the algorithm with 2 hidden layers, 24 and 48 hidden nodes, and convergence level of 1×10^{-5} with classification accuracy for the 15 x 15km study area of 80 – 82% was selected for full reserve analysis.

2.3.2 Supervised Classification

Performing supervised classifications of the validation subset yielded consistently lower classification accuracy than the optimized neural network methods. Merging the individual signatures into two, presence and absence, signatures and then performing a Maximum Likelihood (ML) classification yielded a 71% classification accuracy based on the validation data set. Using each of the individual signatures to perform a Minimum Distance classification resulted in a 69% classification accuracy of the bamboo. Subdividing the ML signatures into spectrally similar categories (i.e. similar aspect, slope, overstory vegetation) produced similar results of 71% accuracy.

2.3.3 Full Reserve Results

Full reserve images of outputs from the neural net stopped at 1×10^{-5} are presented in Figure 2.5. Figure 2.5 shows the mosaick of the 18 outputs. A comparison between the bamboo predictions from the neural network to the field survey map shows an excellent correspondence between the predicted and surveyed distributions (Schaller et al. 1985). Temporal differences of actual distribution between the surveyed and predicted bamboo maps are expected from natural dynamics and human disturbance, but since potential habitat is controlled by abiotic factors such as altitude, precipitation, and slope, overall distribution should be consistent through time. A confusion matrix of the full reserve output validation is presented in Table 2.3. Overall accuracy based on all validation data was 80%. The matrix shows more clearly the correspondence between predicted and ground truth data and those pixels not being correctly categorized. Of particular note is the technique's inaccurate prediction of pixels containing bamboo as having an absence of bamboo, or false negatives. This category represents 75% of the incorrectly assigned pixels.

Further analyses examining factors influencing the errors and these false negatives in particular showed very interesting trends. For example, no relation between the percent of canopy closure and prediction ability was found. In other words, the distribution of canopy closure for the mis-categorized pixels was the same as all the data. It should be noted, however, that complete canopy closure was rare and bamboo was not found under 100% canopy closure. Nor was any relation of mis-categorized pixels to the percent bamboo found. Again, the distribution of mis-categorized pixels was similar to that of all the data. However, significant trends were found in regards to co-occurring midstory and understory vegetation within mis-categorized pixels. In the case of 90% of the false negatives, a midstory, typically 2 – 5m deciduous sub-canopy trees and shrubs, either partially covered and/or intermingled with the bamboo. In every case of the false positives, a grass understory, with similar characteristics as *Bashania*, covered the forest floor. Ground truth plots with co-occurring shrub in the case of false negatives and grass in the case of false positives in all represent 92% of the mis-categorized pixels.

2.4. Conclusions and Discussion

Data and algorithm requirements were found through testing various combinations of input, training data format, and algorithm architecture for successful neural network prediction of understory bamboo presence/absence. The best results were obtained when using all six bands of the TM data as inputs. Infrared wavelengths have a greater canopy penetration compared to shorter wavelengths (Lillesand and Kiefer 1994). The TM sensor records information in three bands in the infrared, one in the near and two in the shortwave infrared. In addition, general application of the trained network was most accurate when stopped from reaching full convergence. Using this information, we were able to derive spatial distributions with significant correspondence to independent data. The results showed as high as 82% correspondence between predicted bamboo distribution and ground truth validation data.

In comparison to the supervised classifications, clear gains were made using the neural network for bamboo classification. Relative to the observed distribution of bamboo, the supervised classifications seem to be more closely related to the general trends in the dominant vegetation. It is possible that the gains in the bamboo classification using the neural network are due to the ability of the neural net to more precisely learn trends in the dominant vegetation to that of the co-existence of bamboo. However, based on field observations (Table 2.1) and classification errors we do not believe this is the case. While not providing conclusive evidence, trends in the classification and the lack of any discernable correlation of overstory vegetation in forested regions to the existence of bamboo lead us to believe that the neural network is more capable of utilizing canopy gap and sub-canopy influences to more accurately classify understory bamboo. The neural network is probably more capable of classifying minority features, adapting to the variable influences of changing canopy conditions, and accounting for the non-linear effects of sub-canopy vegetation. The misclassification trends discussed in the results and shown in table 2.3 lead us to believe that the neural network method is basing the classification, at least in part, on understory vegetation to increase classification accuracy of understory bamboo. We believe, for example, in the case of the false positives the neural network is falsely classifying other understory grasses as bamboo. The grasses may be spectrally similar enough to the bamboo as to cause false positive classifications. In the case of the false negatives, it is possible that the co-occurring shrubs are simply masking understory features. These pixels of co-occurring shrub and bamboo represent about 89% of the false negatives. The neural net may also be training against shrub containing plots as typically shrub dominated areas are devoid of bamboo. To test this, further data are being collected with emphasis on samples where there is co-occurring vegetation.

Canopy cover rarely exceeded 90% in Wolong and was on average around 56%. Neural network classification of canopy gap vegetation is, therefore, very feasible. The increased classification accuracy and correlation between mis-categorized pixels and understory vegetation suggest this is probably occurring here. The degree to which the neural net is capable of incorporating non-linear effects such as multi-scattering and IR transmission due to sub-canopy vegetation is unknown. Further studies are necessary to test this and utilize this information if it is available. For example, to accurately classify the percent cover and density of understory vegetation, important data for many habitat models and mapping studies, the non-linear influences are most likely required. Much of the understory vegetation occurs below the canopy. Determining the fraction of cover will require that the contribution of the sub-canopy vegetation be distinguishable and proportional to the fraction of sub-canopy vegetation. To this end, we are examining the relationship of the percent cover of bamboo to optical remote sensing data using neural networks. However, further theoretical studies and controlled experiments are needed as well.

Data from other types of sensors may also contribute to these analyses and make parameterization of understory conditions more applicable. Significant structural information (e.g. biomass and vertical distribution) can be inferred (and consequently some differentiation between structurally distinct vegetation types) from Synthetic Aperture Radar (SAR) (Luckman et al. 1997, Treuhaft and Siqueira 2000) and lidar (*li*ght *d*etection *a*nd *r*anging) (Lefsky et al. 1999). Classification of sub-canopy vegetation is typically not possible from canopy penetrating SAR or lidar data (e.g. confusion between understory shrub and bamboo). However, we anticipate that the fusion of the increased biomass and structural information with the signature information available from optical sensor data may allow enhanced classifications and biophysical parameterization.

It is widely recognized that the understory contains significant biomass and diversity of vegetation. However, it typically remains unclassified using traditional remote sensing techniques. The use of artificial neural networks to extract the complex information available from optical remote sensing data seems promising as a method to accurately classify understory features. In addition, the neural network's ability to learn the complex trends in the data and to generalize across land covers make this method broadly applicable. Practical approaches to classifying understory vegetation are needed for studies requiring more accurate information of biomass, biodiversity, and habitat conditions, as in the case for the endangered giant panda. We believe the results from this study at least point to a need for further analyses on the influence of understory vegetation on remote sensing data, information available from other data sets, and practical methods to use these data to classify understory vegetation. Research in this area has the potential to provide a practical approach to classifying understory vegetation and developing information on the quantity and spatial distribution of understory vegetation species on a scale previously prohibitive.

Acknowledgements

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Table 2.1: Relationship between overstory species and abiotic factors and understory bamboo.

	Bamboo (%)	Canopy (%)	Slope (deg)	Altitude (m)
Mean	41.2 ± 36.2	55.6 ± 20.8	23.0 ± 10.7	2583 ± 285
R		0.11	0.30	0.14
R^2		0.01	0.09	0.02

Table 2.2: Influences of early stopping and learning algorithms on validation and verification accuracy (percent).

Learning Algorithm	MSE Goal	Accuracy (Verification)	Accuracy (Validation)
LM	$1x10^{-5}$	100.0	80.0
LM	$1x10^{-8}$	100.0	62.2
LM	$1x10^{-20}$	100.0	55.6
BFG	$1x10^{-5}$	100.0	82.2
BFG	$1x10^{-8}$	100.0	75.6
BFG	$1x10^{-20}$	100.0	68.9

Table 2.3. Confusion matrix showing ground truthed values compared to predicted presence/absence from full-reserve analysis based on BFG $1x10^{-5}$ algorithm output using Landsat TM data. Numbers in parentheses represent those absence and presence validation points containing co-occurring *grass and †shrubs, respectively.

		Ground Truth Data		
		Absence of bamboo	Presence of bamboo	Accuracy
ANN Prediction	Absence of bamboo	31	$9(8^{\dagger})$	78%
	Presence of bamboo	3(3*)	17	85%
	Accuracy	91%	65%	Overall 80%

Figure Legends. (Images in this dissertation are presented in color)

Figure 2.1. Examples of past bamboo distribution maps for Wolong Nature Reserve. Figure 2.1a shows the full-reserve map derived from field survey work conducted from 1979-1983 (Schaller et al., 1985). The inset shows the approximate area of the map shown in Figure 2.1b, a higher detail, smaller extent map derived from work done by Johnson et al. (Johnson et al., 1988) in response to a mass die-off of *Bashania fangiana* within the reserve.

Figure 2.2. Examples of (a) *Bashania fangiana* beneath a typical overstory and (b) *Fargesia Robusta* with co-occurring vegetation.

Figure 2.3. Representative schematic of an artificial neural network. The arrows represent a feed-forward process of transforming input data, such as remote sensing imagery, to an output space (e.g. bamboo existence/absence). Networks are trained through *a priori* knowledge of output and input relations (ground-truth data and corresponding remote sensing pixel values) and a reiterative back-propagation of training errors to update the hidden layer weights.

Figure 2.4. Effects of algorithm structure are shown with variations in learning algorithm and error goal. Figure 2.4a is the output map from BFG training algorithm with convergence threshold of MSE = $1x10^{-5}$. Figures 4b and c show output maps from training algorithms with convergence thresholds of MSE = $1x10^{-}$

^{8}, and 1×10^{-20}, respectively. Effects of generalization are apparent between methods using a 1×10^{-5} threshold (a) and LM 1×10^{-8} and 1×10^{-20} outputs (b and c). Better delineation of an agriculture area (inset A) using a 1×10^{-5} threshold and decreased generalization at 1×10^{-8} and 1×10^{-20} shown as brighter areas in 4b and c (inset B) not conforming to expected output values.

Figure 2.5. Full-reserve output maps from optimal algorithm input and structure. Input data were Landsat TM data excluding the thermal band and algorithm characteristics included 2 hidden layers with 24 and 48 nodes. The BFG learning algorithm with a convergence threshold of MSE = 1×10^{-5} were used. Figure 2.5a shows only the bamboo distribution with green areas representing bamboo and gray areas the absence of bamboo. Figure 2.5b shows the good correspondence of the neural network output as it compares to the full-reserve output. Neural network bamboo prediction shown as green overlaying ground survey distribution (legend corresponds to Figure 2.1b).

Figure 2.1


AFTER DIE-OFF
Wuyipeng
Chouchugou
BAMBOO
☐ F. spathacea
■ S. fangiana >3 ha

Figure 2.2

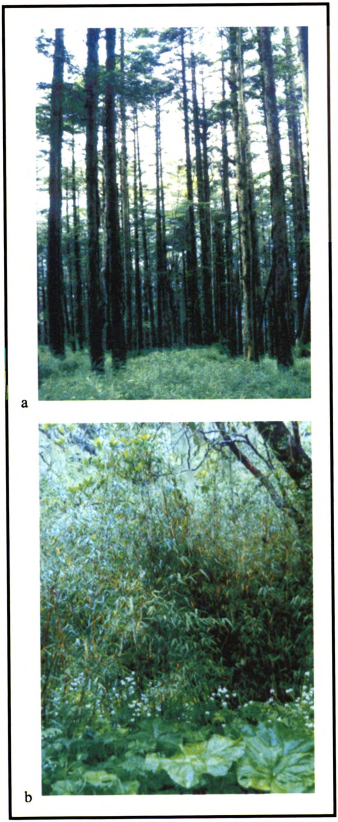


Figure 2.3

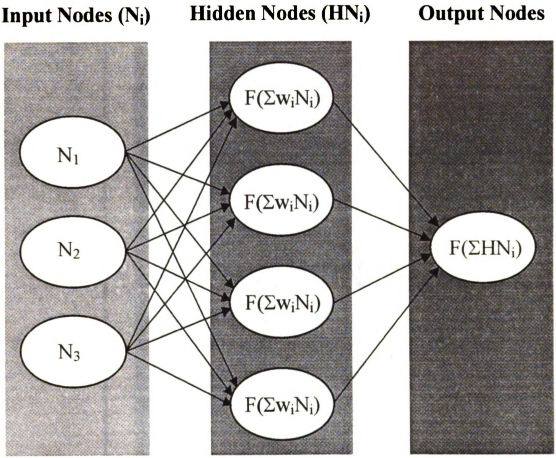

Input Nodes (N_i)
Hidden Nodes (HN_i)
Output Nodes
N1
N2
N3
F(Σw_iN_i)
F(Σw_iN_i)
F(Σw_iN_i)
F(Σw_iN_i)
F(ΣHN_i)

Figure 2.4

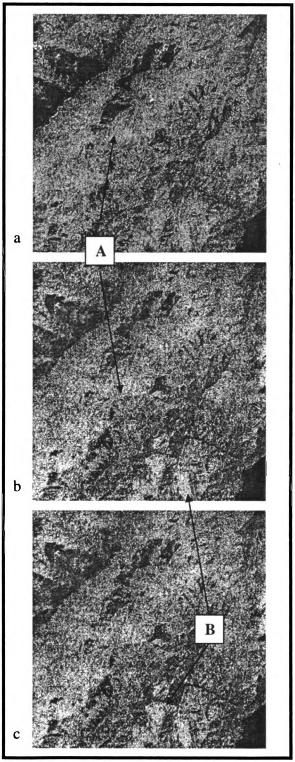
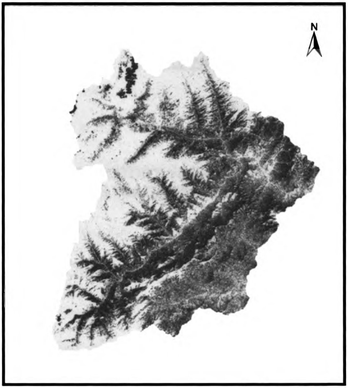


Figure 2.5



CHAPTER 3

THE EFFECTS OF UNDERSTORY VEGETATION ON WILDLIFE HABITAT ACROSS FRAGMENTED LANDSCAPES

In collaboration with

Scott Bearer, Li An, Yingchun Tan,
Zhiyun Ouyang and Jianguo Liu

Abstract

Understory vegetation is an important component of biodiversity and habitat for many wildlife species, but previous large-scale studies on biodiversity and wildlife habitat have suffered from lack of detailed information about understory distribution. Consequently, it is unclear how understory distribution influences the analysis of habitat quantity and fragmentation. To fill this gap, we have recently developed a method of mapping understory bamboo distribution using remote sensing data (Landsat TM) and field data in Wolong Nature Reserve (China), one of the largest reserves designated for conserving giant pandas (*Ailuropoda melanoleuca*). In this paper, we compared the results from panda habitat analyses with and without bamboo information. 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 habitat decreased by 29 – 56% and overall habitat patch size decreased by 16 – 48% after bamboo information was incorporated into the analyses. The decreases in the quantity of panda habitat and increases in habitat fragmentation resulted in decreases of 41 – 60% in carrying capacity. Our study suggests that it is necessary to incorporate understory vegetation into wildlife habitat research and management to avoid overestimation of habitat.

3.1. Introduction

Understory vegetation is a significant component of wildlife habitat in forested landscapes. Understory vegetation provides forage and cover for ground birds (Estades and Temple, 1999), small and large mammals (Lindzey and Meslow, 1977; Dueser and Shugart, 1978), and invertebrate species (Ernest, 1989). For example, lack of understory forage availability can limit white-tailed deer (*Odocoileus virginianus*) ranges (McCaffery et al. 1974), and berry-producing understory shrubs are an essential component of the North American black bear's (*Ursus americanus*) diet (Powell et al. 1997). As a result, it is widely recognized that detailed knowledge of vertical structure and horizontal distribution of understory flora is often necessary to predict wildlife-habitat relationships accurately (MacArthur and MacArthur 1961, James 1971).

While the importance of understory vegetation has long been recognized and often incorporated in fine-scale analyses, the influence of understory vegetation on broad-scale analyses of habitat has not been quantified. We believe incorporating understory information will have considerable implications for many broad-scale theoretical ecological issues and practical applications. For example, behavioral studies have shown that giant panda (*Ailuropoda melanoleuca*) habitat is a function of forest cover, slope, altitude, and understory bamboo (Schaller et al. 1985, Liu et al. 2001). Previous efforts to collect information on the availability and spatial distribution of understory 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. 1989). 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 understory vegetation information in analyses of the spatial distribution of habitat (De Wulf et al. 1989, Liu et al. 2001). As a result, Liu et al. (2001) suggest it is probable these studies are leading to conservative estimates of the loss and fragmentation of giant panda habitat.

However, to what degree understory vegetation influences broad-scale habitat analyses has not been examined. The lack of detailed understory information has forced past studies to base landscape analyses of habitat only on features that can be measured easily over large areas such as obvious land cover and topography. If understory vegetation, vertical vegetation structure, and other difficult to measure factors are limiting or have a different spatial distribution relative to measured features, estimates of total habitat and landscape metrics may not accurately reflect the availability and spatial distribution of habitat. This is likely the case for past analyses of giant panda habitat. Based on extensive ground sampling and a recent classification of the distribution of understory bamboo using remote sensing data and an artificial neural network, we have found that understory bamboo is distributed independently of forest cover. Mapping giant panda habitat based only on overstory and topography is, therefore, likely leading to an overestimation of available habitat and underestimation of habitat fragmentation and isolation.

To illustrate the importance of understory vegetation on the quantity and spatial distribution of wildlife habitat, we examined the influence of understory bamboo on giant panda habitat. Specifically, we compared panda habitat with and without recently developed high-resolution (30-meter) classification of the spatial distribution of understory bamboo over a range of a couple hundred thousand hectares. Given the importance of understory vegetation throughout forested ecosystems around the world, our comparative approach offers an example of the degree to which habitat may be over- or under-estimated and emphasizes the need to incorporate understory vegetation in many broad-scale habitat analyses.

3.2. Methods

To assess the impact of understory vegetation information on the quantity and spatial distribution of giant panda habitat, we compared the landscape characteristics of habitat classifications with and without understory bamboo information within a nature reserve in southwest China. Comparisons were made to a previous multi-temporal analysis of landscape trends in 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 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. were combined with recently developed bamboo data to reclassify habitat suitability. The resulting habitat classifications were then compared to the original habitat classification. Comparisons were made based on habitat quantity, habitat fragmentation, and panda carrying capacity.

3.2.1 Study Area

Our 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. 1,000 individuals; Zhang et al. 1997). Within Wolong, elevations range from 1,200 m to 6,525 m, creating several climatic zones and consequently high habitat diversity.

Throughout Wolong and most of the panda range, bamboo is found predominantly as understory species. The distribution of bamboo species present in Wolong is restricted by elevation. The two predominant species, umbrella bamboo (*Fargesia Robusta)* and arrow bamboo (*Bashania fangiana)* (both utilized by pandas), are typically found between 1,500 and 2,550 m and 2,550 to 3,500 m, respectively. Bamboo is distributed in the understory in patches ranging in size from a single plant to hundreds of meters across. However, predicting the spatial distribution of bamboo within these elevation ranges 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. in review).

The distribution of overstory vegetation in the reserve is also related to the elevation: from approximately 1,200 to 1,600 m, the canopy is composed primarily of evergreen broadleaf (*Quercus*) with broadleaf shrubs and occasional grasses. From 1,600 to 2,000 m there is an increasing mixture of deciduous broadleaf (***Betula*, *Acer***) overstory and understory vegetation. From 2,000 m to about 2,700 m, the canopy is a mixture of deciduous (***Acer*, *Betula***) and evergreen (*Larix,Tsuga*) broadleaf. Above 2,700 subalpine conifers (***Abies***) dominate until about 3,600 m where subalpine conifers, fern, and grass understory grade into alpine thickets and meadow (Reid et al. 1989, Schaller et al. 1985).

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.

3.2.2 Comparison Study

Classification of habitat suitability for the Liu et al. study was based on previous giant panda behavioral research. For example, pandas are rarely seen outside of forested areas. Sick and hungry pandas have been found in non-forested areas and panda droppings have been found in canopy openings, but the vast majority of their activity is in areas containing forest cover (Schaller et al. 1985). In addition, studies have shown that the main altitude range of the panda is between 2,700 m and 3,200 m, but extends down to 2,000 m and occasionally up to 3,500 m (Schaller et al. 1985, Ouyang et al. 1996, Liu et al. 2001). Pandas prefer gently sloping regions, restricting their activity to slopes less than 45 degrees and preferring areas with less than 15 degrees 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 hours 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. 1989, Reid et al. 1989).

To analyze the spatio-temporal trends of giant panda habitat in Wolong Nature Reserve over the past 32 years, Liu et al. derived data corresponding to pandas' habitat preferences on data available from satellite images and topographic maps. Images from 1965 (Corona satellite photographs), 1974 (Landsat MSS imagery), and 1997 (Landsat TM imagery) were used to map the temporal dynamics of the quantity and spatial distribution of forest cover in Wolong. The photographs and imagery were used to derive classifications of forested/non-forested for each time step. Slope and altitude values were derived from a digital elevation model (see Liu et al. 2001 for details).

Detailed information on the spatial distribution of bamboo prior to 1997 was not available. To be consistent over time and to provide a more conservative estimate of habitat loss, bamboo information not was included in this previous analysis. Therefore, habitat suitability was determined as a multiplicative combination of the three factors (forest cover, altitude, 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 altitude multiplicative factors were proportional to the 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).

3.2.3 Bamboo Classification

Remote sensing is a preferable method for mapping the distribution of forest overstory over large extents. 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 main problem in classifying bamboo from remote sensing data is that bamboo occurs as an understory species. The overstory typically limits spectral information from understory bamboo, thus restricting traditional remote sensing classification approaches. To overcome this problem, we developed a new approach for classifying the presence/absence of understory bamboo regardless of overstory canopy (Linderman et al. in review). Using widely available Landsat TM imagery as input and ground samples of understory and overstory conditions for training, a non-linear artificial neural network achieved a bamboo classification accuracy of

80% despite variations in canopy cover and the presence of co-occurring mid-story and understory vegetation (Linderman et al. in review).

3.2.4 Incorporating Bamboo Information into Habitat Analysis

To examine the influence of bamboo information on landscape-level analyses of panda habitat, we incorporated the above-mentioned bamboo data into habitat analyses using the same procedures as those used in Liu et al. (2001). For consistency, we incorporated the bamboo data as an additional multiplicative factor in addition to the three factors (forest cover, slope, and elevation) used in the previous study.

The bamboo information was incorporated into habitat analyses in three forms: unfiltered data and two filtered forms of these data. We incorporated the unfiltered data as a binary coverage (presence = 1 and absence = 0) at the 30-m resolution derived from remote sensing imagery. Like many other species (e.g., Pearson et al. 1996), however, pandas may perceive bamboo availability differently from the patterns of bamboo distribution at the 30-m pixel level. For example, previous behavioral studies (Schaller et al. 1985) have found that pandas spend up to 14 hours/day foraging, with significant daily movement within and between patches of bamboo. Typical distances traveled each day are around 300 m and almost always <500 m. In addition, radio-tracking studies by Schaller et al. (1985) showed between-patch foraging distances were typically < 100 m. These studies suggest that pandas perceive bamboo distribution at a scale of >30 m. Furthermore, while most activity is largely restricted to regions with significant amounts of bamboo, pandas do use areas not containing bamboo, mainly for movement between bamboo patches, territorial marking (primarily males) and travel to other places (Schaller et al. 1985). Thus, we used two filters (proportion filter and majority filter) to reclassify the bamboo data to reflect pandas' perceptions of bamboo distribution, use of non-bamboo area, and the scale at which pandas interact with bamboo. The bamboo data were filtered by reclassifying the center pixel of a square window based on the conditions of other pixels within the window. The window sizes ranged from 3 x 3 pixels (90 x 90 m) to 21 x 21 pixels (630 x 630 m), representing the lower and upper extremes in daily foraging distance by a panda.

In the proportion filter method, the center pixel of a window was reassigned a value of the proportion of pixels with bamboo within the window. This represented an estimate of bamboo availability in the surrounding area as perceived by a panda. The estimates were then categorized 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, the center pixel was reclassified as unsuitable. Otherwise, the pixel was classified as suitable. This classification was based on bamboo availability as measured by approximated panda use throughout the reserve and measured travel distance between patches (Schaller et al. 1985). Areas within Wolong known to historically sustain high densities of pandas were used to represent high-quality bamboo habitat.

The majority filter adjusts the value of the center pixel to reflect the conditions of the majority pixels within the window. For example, if at least 5 of the 9 pixels in a 3 x 3 window were classified as bamboo, the center pixel would be re-classified as bamboo regardless of its original classification. Like the proportion filter, the majority filter maps the same areas of high-quality bamboo areas as measured by the proportion filter. However, the proportion filter retains more potential highly suitable, suitable, and marginally suitable habitat in areas of lower levels of bamboo due to the relative influence of suitable bamboo habitat within the proportion filter. The majority filter highlights only high-quality bamboo areas and provided an alternative estimate of the impact of bamboo on habitat availability and fragmentation.

Classifications of overall habitat suitability were generated as in Liu et al. (2001) with the inclusion of the additional multiplicative factor of bamboo suitability. 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.

3.2.5 Habitat Measures

Panda habitat under different methods of analysis was compared using three measures: habitat quantity, fragmentation, and potential carrying capacity. Habitat quantity included not only the total amount of all habitat classes (highly suitable, suitable, marginally suitable), but also the amount of each suitability class. Fragmentation measures the degree of discontinuity of habitat and is represented by mean patch size. Potential carrying capacity was based on 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 times 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.

3.3. Results

Incorporation of bamboo information into habitat analysis substantially reduced the amounts of panda habitat and drastically changed the spatial distribution of panda habitat (Figure 3.2, Tables 3.1 and 3.2). The impacts varied with filter methods and filter sizes that resulted in different amounts and distribution patterns of bamboo (see examples in Figure 3.1). For instance, using the majority filter, highly suitable bamboo areas decreased by 11.8% to 32.8% for 3 x 3 and 21 x 21 windows, respectively, while mean bamboo patch sizes (3.97 to 17.9 ha) were about 8 to 34 times larger than those from the unfiltered method (0.53 ha). Total amounts of suitable and highly suitable bamboo areas derived from the proportion filter were 59.9% to 92.6% more than those from the unfiltered method, respectively.

Unfiltered bamboo data caused a considerable decrease in habitat quantity and a marked increase in fragmentation (Table 3.1). While the amounts of all habitat classes combined and each habitat class from the unfiltered method were similar to those from the majority filter (Table 3.1), mean patch size from the unfiltered method was considerably lower than the mean patch size based on the two filter methods (Table 3.2). In other words, the filter methods resulted in larger mean patch sizes and more contiguous habitat. As shown in Figure 3.2, the amount of high-quality habitat (highly suitable habitat) was highest using the proportion filter with filter sizes between 7 x 7 and 11 x 11 pixels. The quantity of high-quality habitat using the majority filter was substantially lower for each filter size relative to the proportion filter (Table 3.2). With the majority filter, the number of patches of high-quality habitat decreased and patch size increased asymptotically relative to filter size (Table 3.2). Differences in habitat class area relative to habitat classifications not including bamboo ranged from a decrease of 40.1% for high-quality habitat using the 11 x 11 proportion filter to a decrease of 54.2% for marginally suitable habitat incorporating the unfiltered bamboo data (Table 3.1).

Because results using different filter sizes varied considerably, determining the appropriate filter size was necessary for comparisons of the results from analysis without bamboo. For each filtering method, we chose the filter size of 11 x 11 pixels (330 x 330 m) according to behavioral studies of daily foraging activities of pandas (typical daily travel distance was approximately 300 meters, Schaller et al. 1985). In addition, patch sizes and number of patches derived using a window of 11 x 11 pixels were relatively consistent with those from neighboring filter sizes (e.g. 7x 7 – 15 x 15 pixels).

Using the filter size of 11 x 11 pixels, habitat distribution patterns with and without bamboo information differed considerably (Figure 3.3). Total habitat quantity decreased by approximately 29% under the proportion filter (Table 3.3). More significantly, high-quality habitat was reduced by 34%. Patch size decreased by 41% for suitable habitat and 18% for highly suitable habitat (Table 3.2). The number of highly suitable patches decreased by 28%. Compared to the results from analyses without including bamboo, bamboo information derived from the majority filter (with filter size = 11 x 11 pixels) also produced a smaller quantity of habitat and a higher degree of fragmentation. Specifically, total habitat area decreased by

52% (Table 3.3), and mean patch size decreased by 48% and 16% for suitable and highly suitable patches, respectively (Table 3.2).

Estimates of the carrying capacity based on analyses with and without bamboo information offer further insight into the accuracy of each method. In the 1970s, there were 145 pandas (Giant Panda Expedition 1974). Panda population size declined to 72 in the early 1980s (China's Ministry of Forestry and WWF 1989). A recent population survey of Wolong has suggested that the current number of pandas within Wolong is 74 individuals (Zhang et al. 1997). However, based on habitat analyses without bamboo, carrying capacity (220 individuals) far exceeded the survey estimates of the past and current panda numbers (Table 3.4). Including bamboo in these analyses substantially lowered the estimate of the number of possible pandas the current habitat in Wolong can support. Potential carrying capacity derived from habitat analyses using unfiltered bamboo data was only 27 pandas. However, the majority and proportion filter habitat classifications resulted in estimates of 88 and 130 pandas, respectively (Table 3.4), falling within historical and population range in Wolong (72 – 145). The fact that the carrying capacity resulting from the majority filter method most closely matches current estimates of panda numbers may suggest that pandas are concentrated in high-quality bamboo areas.

3.4. Conclusions and Discussion

Incorporating information about understory vegetation into habitat analyses of Wolong Nature Reserve resulted in substantially lower estimates of panda habitat (at least 30%), lower estimates of habitat patch size (16 – 48%), and lower estimates of carrying capacity (at least 40%). These new estimates have enormous implications for panda conservation. For example, 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 3,900 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 (Figure 3.4). Pandas are extreme K-strategists, have low reproductive success, and are currently at very low numbers (about 1,000). Sub-population isolation and inbreeding are already a concern for this endangered species (Lu et al. 2001).

To accurately estimate habitat distributions at the landscape scale, we have found that data derived from remotely sensed imagery must relate to how species perceive the environment. For this study, information from behavioral research (Schaller et al. 1985, Ouyang et al. 1996) offered insight into pandas' bamboo use and relevant scales of interaction. We chose the most appropriate filter size to reflect pandas' daily movement patterns. The proportion filter offers the most meaningful information relative to pandas' perception of bamboo availability, as it includes areas that have less than optimal bamboo still utilized by pandas. However, the carrying capacity resulting from the majority filter most closely matches the reserve's current panda population size. Because the majority filter highlights highly suitable bamboo area, this suggests current panda population size may be below the potential carrying capacity as estimated by the proportion filter method. Either habitat with less suitable bamboo is underused due to the low number of pandas in the wild today, or some isolated patches of habitat are unavailable to pandas.

The approach and results from this study have important implications not only for panda conservation but also for biodiversity conservation and broad-scale habitat analysis in general, as countless wildlife species depend on sub-canopy structure and flora, which are integral components of biodiversity and forested ecosystems. Fortunately, information on understory structure and species composition of forested ecosystems is becoming increasingly available (Linderman et al. in review). Furthermore, biomass and structural information are being derived from synthetic aperture radar and optical satellite data (Baret and Guyot 1991, Beaudoin et al. 1994). Recently, lidar (*l*aser *i*nduced *d*istance *a*nd *r*anging) has been used to measure vertical structure below canopies (Lefsky et al. 1999). As detailed data of understory vegetation become available from remote sensing images, we believe it is necessary and feasible to examine the impacts these data have on landscape-scale habitat analyses, conservation strategies, and management policies.

Acknowledgements

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Table Legends

Table 3.1. A comparison between not including bamboo and three filtered forms of bamboo information in habitat classifications of giant panda habitat. The differences in quantity of the four classes of habitat are shown based on habitat classifications, including each of the four bamboo classifications (No Bamboo, No Filter, Proportion Filter, and Majority Filter). The influence of filter window size is shown for ten window sizes (3 x 3 – 21 x 21 pixels).

Table 3.2. The influences of bamboo data and classification methodology (No Bamboo, No Filter, Proportion Filter, and Majority Filter) and filter size (3 x 3 – 21 x 21 pixels) are shown for a) the number of habitat patches and b) the mean patch size of habitat classes.

Table 3.3. The resulting quantity of total habitat is shown based on each of the four bamboo classifications (No Bamboo, No Filter, Proportion Filter, and Majority Filter) and ten filter sizes (3 x 3 – 21 x 21 pixels). Differences in total habitat relative to the Liu et al. (2001) classification (No Bamboo) show a loss of 29 – 56% habitat by including bamboo information.

Table 3.4. Influence of filter method on core habitat and carrying capacity. Core habitat is defined as contiguous areas of highly suitable, suitable, or marginally

suitable habitat forming patches > 1.7 km^2. Carrying capacity is a function of the total area of each habitat class and panda densities.

Table 3.1. Influences of bamboo filter methods and filter sizes on habitat quantity.

Filter Methods and Sizes	**Habitat Class Area (ha)**			
	Highly Suitable	**Suitable**	**Marginally Suitable**	**Unsuitable**
No Bamboo	11811	49329	9911	135841
No Filter	5764	23543	4542	173049
Proportion Filter				
3 x 3	6772	27411	12121	161318
5 x 5	6971	27884	14071	158696
7 x 7	7066	27908	14898	157750
9 x 9	7065	27713	15325	157518
11 x 11	7078	27447	15617	157480
13 x 13	7024	27140	15838	157619
15 x 15	6968	26808	15997	157848
17 x 17	6940	26479	16067	158136
19 x 19	6899	26159	16163	158401
21 x 21	6861	25818	16208	158735
Majority Filter				
3 x 3	6198	24404	4858	171429
5 x 5	6277	24209	4884	171522
7 x 7	6265	23931	4840	171856
9 x 9	6218	23608	4769	172296
11 x 11	6162	23234	4679	172817
13 x 13	6097	22825	4561	173409
15 x 15	6034	22384	4435	174039
17 x 17	6004	21982	4302	174604
19 x 19	5946	21585	4156	175205
21 x 21	5890	21206	4003	175792

Table 3.2. Influences of filters on patch number and size.

		Number of Patches			Mean Patch Size		
	Filter Methods and Filter Sizes	**Highly Suitable**	**Suitable**	**Marginally Suitable**	**Highly Suitable**	**Suitable**	**Marginally Suitable**
No bamboo		4301	4158	1871	2.75	11.86	5.30
No filter		18106	57033	12970	0.32	0.41	0.35
Proportion Filter	3 x 3	5680	13380	20765	1.19	2.60	0.73
	5 x 5	4358	7827	9534	1.60	4.74	1.86
	7 x 7	3753	6432	7432	1.87	5.90	2.54
	9 x 9	3316	5791	6208	2.12	6.61	3.14
	11 x 11	3105	5446	5599	2.26	7.05	3.57
	13 x 13	2935	5239	5136	2.38	7.33	3.97
	15 x 15	2785	5086	4850	2.49	7.54	4.27
	17 x 17	2728	4992	4614	2.53	7.66	4.56
	19 x 19	2666	4872	4512	2.58	7.83	4.72
	21 x 21	2624	4769	4348	2.60	7.98	4.96
Majority Filter	3 x 3	5708	13370	3434	1.09	1.83	1.41
	5 x 5	4202	8279	2265	1.49	2.92	2.16
	7 x 7	3455	5850	1763	1.81	4.09	2.75
	9 x 9	2967	4528	1481	2.10	5.21	3.22
	11 x 11	2655	3744	1251	2.32	6.21	3.74
	13 x 13	2444	3226	1115	2.49	7.08	4.09
	15 x 15	2269	2899	1037	2.66	7.72	4.28
	17 x 17	2182	2657	936	2.75	8.27	4.60
	19 x 19	2087	2418	910	2.85	8.93	4.57
	21 x 21	2011	2240	874	2.93	9.47	4.58

Table 3.3. Influences of filter methods and filter size on total habitat.

Filter Methods and Sizes	Total Habitat (ha)	% Change from "No Bamboo"
No bamboo	71050	
No filter	33848	-52.4
Proportion Filter		
3 x 3	46304	-34.8
5 x 5	48925	-31.1
7 x 7	49872	-29.8
9 x 9	50104	-29.5
11 x 11	50141	-29.4
13 x 13	50003	-29.6
15 x 15	49773	-29.9
17 x 17	49485	-30.3
19 x 19	49221	-30.7
21 x 21	48887	-31.2
Majority Filter		
3 x 3	35460	-50.1
5 x 5	35369	-50.2
7 x 7	35036	-50.7
9 x 9	34596	-51.3
11 x 11	34075	-52.0
13 x 13	33483	-52.9
15 x 15	32853	-53.8
17 x 17	32288	-54.6
19 x 19	31687	-55.4
21 x 21	31100	-56.2

Table 3.4. Influence of filter method on core habitat and carrying capacity.

	Core Habitat (ha)			
Filter	**Highly Suitable**	**Suitable**	**Marginally Suitable**	**Carrying Capacity**
No Bamboo	11335.0	46253.4	8900.5	220
No Filter	1767.6	5258.5	786.6	27
Proportion	6636.1	23655.7	10847.4	130
Majority	5182.1	17512.3	3049.6	88

Figure Legends. (Images in this dissertation are presented in color)

Figure 3.1. Classifications of bamboo suitability based on proportion and majority filters. Filter sizes include 3x3, 11x11, and 21x21 for the majority filter (3.1a, c, e, respectively) and for the proportion filter (3.1b, d, f, respectively). White represents areas of high quality bamboo areas and black represents unsuitable areas in each of the images. The gray regions in the proportion filter maps (3.1b, d, f) represent areas of suitable bamboo areas.

Figure 3.2. The effects of filter methods and filter sizes on highly suitable habitat class.

Figure 3.3. Habitat distribution throughout Wolong based on classifications without bamboo (3.3a), with bamboo (proportion filter with filter size = 11 x 11 pixels, 3.3b), and with bamboo (majority filter with filter size = 11 x 11 pixels, 3.3c). Highly suitable, suitable, and marginally suitable habitats are shown in red, yellow, and green, respectively. Unsuitable habitat is shown in gray.

Figure 3.4. Maps of core habitat patches (> 1.7 km^2) based on classifications without bamboo (3.4a), with bamboo (proportion filter with filter size = 11 x 11 pixels, 3.4b), and with bamboo (majority filter with filter size = 11 x 11 pixels, 3.4c). Highly suitable, suitable, and marginally suitable habitats are shown in red, yellow, and green, respectively. Unsuitable habitat is shown in gray.

Figure 3.1

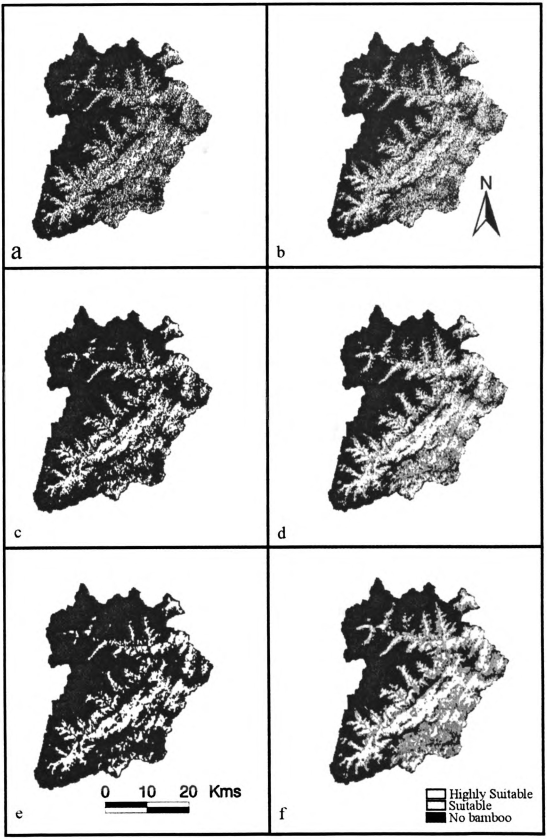
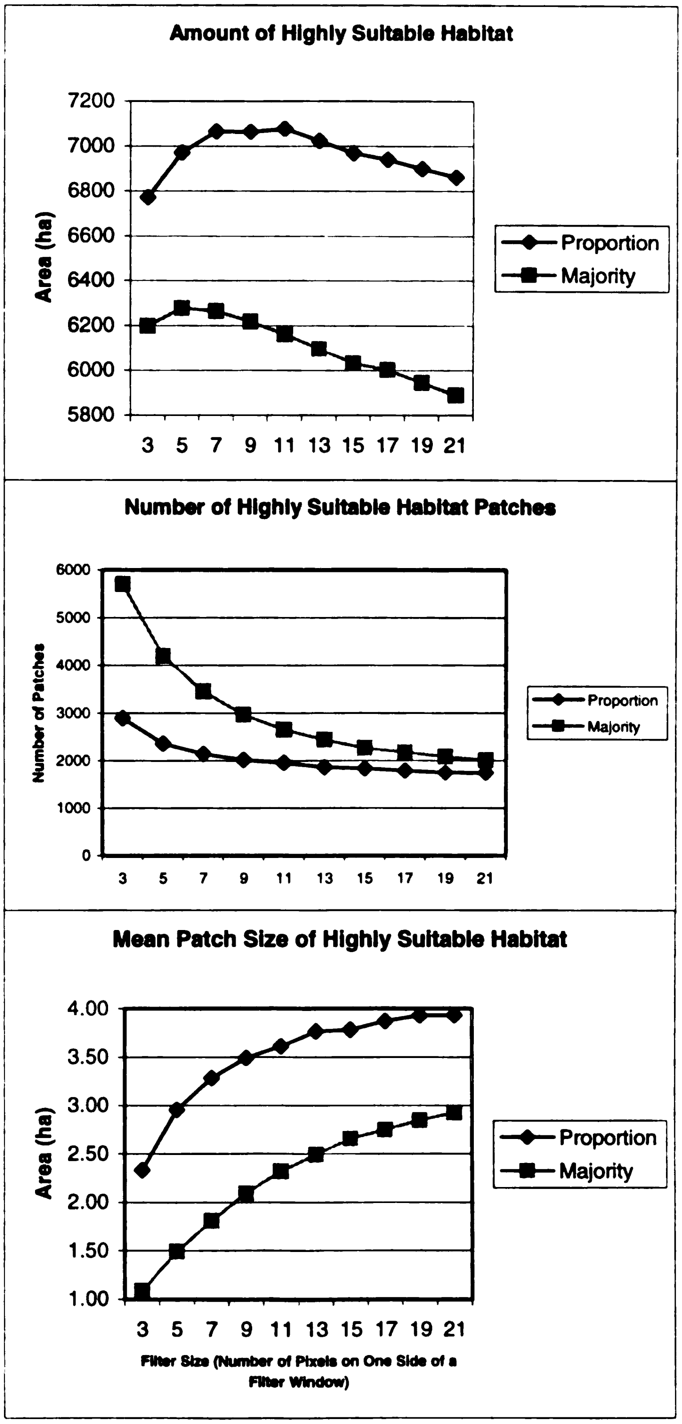


Figure 3.2



Amount of Highly Suitable Habitat

Number of Highly Suitable Habitat Patches

Mean Patch Size of Highly Suitable Habitat

Figure 3.3

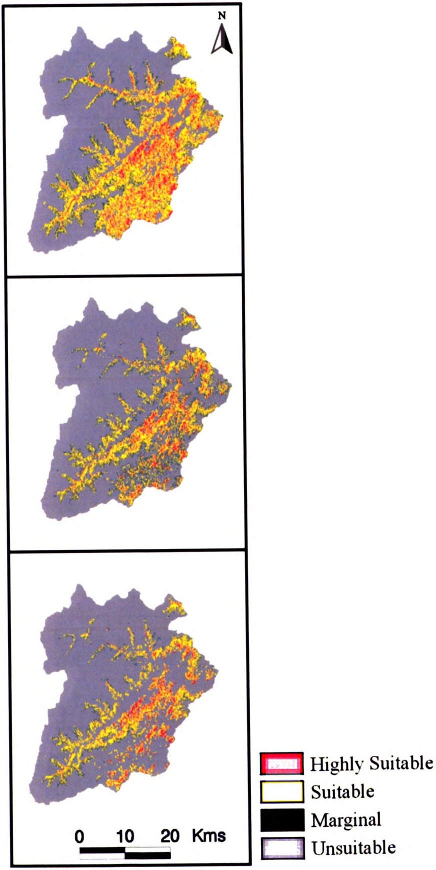
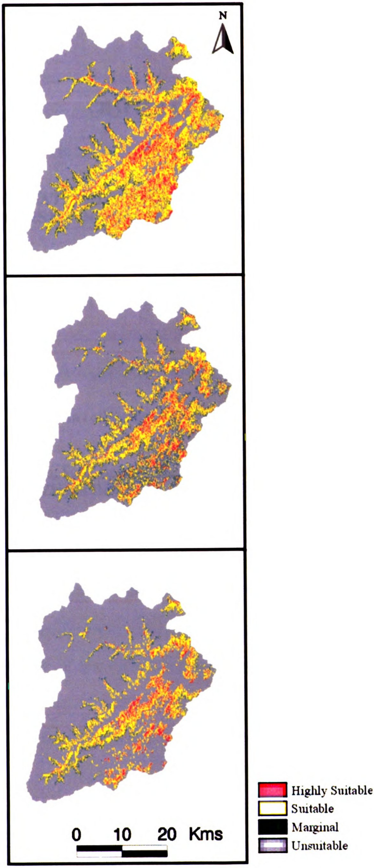


Figure 3.4



CHAPTER 4

IMPACTS OF NATURAL AND HUMAN DISTURBANCES ON FORESTS AND GIANT PANDA HABITAT

In collaboration with

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Abstract

Human modification of land cover has been a leading cause of floral and faunal species extirpation and loss of local and global biodiversity. As natural areas become increasingly scarce, habitat becomes fragmented and animal and plant populations become isolated. Thus, the spatial arrangement of human impacts is of increasing importance. This is particularly evident in systems experiencing regular natural disturbances such as in the mountainous areas of southwest China supporting the remaining population of giant pandas (*Ailuropoda melanoleuca*). Giant panda populations have been restricted to remnants of habitat from extensive past land-cover change. We developed a spatiotemporal model of bamboo dynamics and human activities and their impacts on panda habitat. We found that local fuelwood collection and household creation will likely reduce critical habitat relied upon by pandas during times of bamboo die-offs. Human impacts are projected to result in up to 16% loss of habitat over the next 30 years. In addition, we found that not only was it the accumulation of the loss of habitat, but also the spatial location of the effects of human activities that will have a significant impact on giant pandas. The impacts primarily occur in habitat relied upon by giant pandas during past bamboo die-offs. Therefore, human impacts are leading to decreased total area of habitat and increased fragmentation and are likely making giant pandas increasingly sensitive to natural disturbances such as the cyclical bamboo die-offs.

4.1. Introduction

It is widely recognized that habitat loss is one of the leading causes of local and global species extinction (Ceballos and Ehrlich 2002). Natural (e.g. fire, drought, flooding) and human (e.g. logging, urbanization) disturbances alter the quantity, quality, and spatial arrangement of habitat, and, consequently, affect species distribution and persistence. While many species have adapted to natural disturbance regimes and are often resilient to natural changes in land cover or even rely on them (Romme et al. 1995), human influences on land cover have reduced the total quantity of natural areas, decreased the connectivity between species populations, and destroyed or restricted access to secondary habitats that can be crucial in times of natural disturbances. Increased understanding of the implications of the spatial arrangement of human activities on landscapes relative to the spatial arrangement of habitat are necessary to better predict habitat required by species and allow mitigation of impacts on the remaining ecologically intact areas at the earliest time possible.

Past studies of the impact of natural and human disturbances have examined the total quantity of habitat lost (Sala et al. 2000), the resulting overall fragmentation of habitat (Collins and Barrett, 1997), restrictions in habitat connectivity (Diffendork et al. 1995), and potential influences on meta-population dynamics (Hess 1996). Models have also explored the implications of the spatial arrangement of natural (Berjak and Hearne 2002, Perry and Enright 2002) and human (Liu 1993, Stéphenne and Lambin 2001) disturbances to natural systems.

However, the spatial arrangement of human impacts relative to natural disturbance regimes has received less attention. As a result, species area requirements and the impact of human activities may be considerably underestimated or overestimated. By not considering natural disturbances, past estimates may have misestimated not only the total area necessary for many species, but also the relative importance of habitat until now regarded as marginal or secondary habitat (Fahrig 2001). Further studies on the arrangement of human activities and estimates of the quantity and spatial distribution of critical habitat for population maintenance are needed.

The idea that the spatial arrangement of habitat and/or components of habitat play a crucial role in ecosystem function, habitat suitability, and biodiversity is certainly not new (Leopold 1933, Forman and Godron 1986). Recent studies have expanded on this to also show that the spatial arrangement of disturbances can have a disproportional level of impact when they are concentrated in locations of seasonal, breeding, or other crucial habitats. For example, Turner et al. (1994) found that elk winter survival in Yellowstone National Park after the 1988 fires were sensitive to the precise location and pattern of the burned areas. High-elevation disturbance was less important than the loss of lower-elevation grasslands. In addition, the removal of small wetlands surrounding larger wetlands has been shown to critically impact populations in times of drought and even in non-drought conditions (Takekawa and Beissinger 1989, Naugle et al. 2001)

A similar situation exists for giant pandas in China. Once ranging across most of present-day China, giant pandas are now extremely endangered and restricted to only the western fringe of their former habitat (Schaller et al. 1985).

Loss of habitat and poaching have reduced the panda population to its present level of probably less than 1000 individuals (Zhang et al. 1997). While intentional and incidental poaching have declined, land cover change pressures continue to threaten vital habitat, even in designated protected areas (Liu et al. 2001). Decreasing quantities of habitat are resulting in isolation of sub-populations of giant pandas and may be increasingly restricting access to secondary habitats.

Past behavioral (Schaller et al. 1985) and more recent landscape studies (Linderman et al. in review) have examined how pandas relate to the environment. There is now an increased understanding of the local habitat requirements and the scale at which pandas interact with the landscape. For example, Liu et al. (2001) measured the aggregated landscape effects humans have had in the Wolong Nature Reserve over time. However, little is known of the potential impacts local activities will have in the future in terms of total area or spatial pattern of giant panda habitat (Liu et al. 1999). In particular, little is known of the potential impact humans will have on crucial panda habitat during periodic bamboo die-offs. Current policies have mainly focused on protecting core habitat and have not incorporated the need for secondary habitat in times of bamboo die-offs. Extensive human activity in these areas following a die-off of the main bamboo might limit geographical groups of pandas from required secondary habitat.

Fragmentation of panda habitat has resulted in isolation of sub-populations and decreased genetic fitness of the overall population that will have significant implications for long-term conservation of the panda (Lu et al. 2001). However, continued fragmentation and degradation of habitat may also have more short-term implications. Similar to natural and human disturbances that have resulted in loss of crucial habitat for other species, the combined loss of habitat and the episodic die-offs of bamboo increasingly threaten the panda. For example, in the mid-1970s several species of bamboo in the Min mountains mass-flowered and subsequently died-off. Over 138 pandas died of starvation since secondary bamboo species were not available (Johnson et al. 1988). In 1983, a mass die-off of the primary bamboo species (*Bashania fangiana*) in the Wolong Nature Reserve also resulted in the loss of the main food source for the local populations (Schaller et al. 1985). However, at the time, pandas had access to secondary bamboo sources (*Fargesia robusta*) adjacent to primary habitat and there were no reported starvation deaths of pandas (Schaller 1987). Access to secondary bamboo resources, therefore, appears to be essential to the persistence of panda populations as a result of these large, cyclical die-offs of bamboo species.

Liu et al. (1999) found, however, that human activities continue to have considerable impacts to panda habitat and may have profound consequences in the future. Commercial logging has likely been the main cause of measured losses of giant panda habitat. Household activities have had limited impact on forested areas in areas of preferred giant panda habitat. However, increasing numbers of households, expanding agriculture activity, and increased fuelwood needs have resulted in more extensive impacts of low-elevation forests. These are the same forests relied on by pandas for spring forage of new bamboo shoots and, particularly, during times of massive die-offs of preferred high-altitude bamboo.

Giant pandas have co-existed with bamboo, their primary food source, for at least thousands of years. Bamboo naturally mass-flowers and synchronously dies-off over extremely large areas every 3 – 120 years, depending on the species. In the past, these die-off events were followed by a brief dormancy before the bamboo regenerated to pre-flowering biomass and distribution (Figure 4.1). Pandas typically responded to die-off events by moving to other species of bamboo while the die-off species regenerated. However, human activities are likely increasingly interfering with the natural bamboo cycles and pandas interaction with bamboo. For example, human activities are decreasing the total area of habitat. In addition, it is likely that changes in forest structure and composition are also affecting the ability of bamboo to regenerate to pre-flower conditions (Figure 4.1). This leads to two problems. First, humans are likely causing more loss of habitat than even previously measured. Second, the spatial arrangements of the impacts may be restricting pandas from secondary habitat relied upon during past bamboo die-offs.

In this study, we examined the dynamics of human impacts on forest cover and bamboo distribution within Wolong Nature Reserve in southwest China (Figure 4.2). Similar to many reserves worldwide, local residents continue to rely on natural resources in Wolong. For example, the population of local farmers residing within the reserve has increased from approximately 2500 people in 1975 when the reserve was established at its current size to about 4500 people in 2001. The rapid rise in the number of local residents and an increased tourist industry within Wolong have resulted in increased development and demand for natural resources such as fuelwood, timber, and traditional medicinal plants. The combination of past commercial logging and fuelwood collection has resulted in decreased quantity and quality of panda habitat. Specifically, Liu et al. (2001) found that fuelwood collection occurs primarily at low elevation areas in the general proximity of households resulting in significant loss of habitat pandas relied on in the 1980s during the last die-off of the primary bamboo species. In addition, as fuelwood is exhausted at low elevations, impacts are increasingly occurring at higher elevations and core habitat areas.

Our model combines the spatiotemporal effects of household fuelwood collection, new household creation, forest regrowth, and bamboo on giant panda habitat. The objectives of this research were to (1) examine the relationship of households to the environment, (2) examine the landscape effects of fine-scale household activities on giant panda habitat, and (3) predict future impacts of different scenarios of household activities, combined with the dynamics of bamboo, on giant panda habitat.

Using this model we examined the driving factors influencing the spatial distribution of human activities including fuelwood collection and household creation. Sub-models of household activities were then coupled with the spatiotemporal distribution of forest cover and understory bamboo die-off models to determine the potential impacts to panda habitat. Specifically, we focused on the loss of habitat from bamboo die-offs, the spatial arrangement of human impacts, and the potential implications for giant panda habitat.

4.2. Methods

4.2.1 Study Area

The study was conducted in Wolong Nature Reserve, which is located between 102°52' and 103°24' E and 30°45' and 31°25' N covering approximately 200,000 ha (Figure 4.2). Wolong is one of the largest reserves dedicated to giant panda conservation and is estimated to contain about 10% of the remaining wild panda population (Zhang et al. 1997).

Approximately 40% of the reserve is currently forested (Linderman, unpublished data). Elevations range from 1200 m to 6525 m creating several climatic zones and consequently high biological diversity. The distribution of overstory vegetation in the reserve is related to the elevation: from approximately 1,200 to 1,600 m, the canopy is composed primarily of evergreen broadleaf (*Quercus*) with broadleaf shrubs and occasional grasses. From 1,600 to 2,000 m there is an increasing mixture of deciduous broadleaf (*Betula, Acer*) overstory and understory vegetation. From 2,000 m to about 2,700 m, the canopy is a mixture of deciduous (*Acer, Betula*) and evergreen (*Larix,Tsuga*) broadleaf. Above 2,700 subalpine conifers (*Abies*) dominate until about 3,600 m where subalpine conifers, fern, and grass understory grade into alpine thickets and meadow (Schaller et al. 1985, Reid et al.1989). Most forests in the reserve were logged (either clear cut or selectively-cut) from 1916 until the reserve was established in 1975, reaching peak intensity between 1961 and 1975 (Schaller et al. 1985).

Commercial logging typically resulted in relatively large clearcuts distributed throughout the reserve. Logging has been officially banned in the reserve since 1975; however, to varying degrees illicit logging does continue (M. Linderman, personal observation). Other human activities have also been a major contribution to forest loss and, consequently, the spatial distribution of habitat (Liu et al. 1999, 2001). In 2001, 4,440 local residents in 1098 households resided within the reserve. The majority of these residents are farmers with the primary economic activities consisting of farming maize and vegetables, raising livestock such as pigs and yaks, and collecting wild herbs. A household usually relies on fuelwood for heating, cooking, and livestock feed preparation using 8 – 30 m^3 of wood each year (An et al. 2001). Selective logging for fuelwood collection typically changes the species composition in the overstory and reduces canopy cover until all overstory vegetation is removed. In some areas, forest cover is also removed by grazing and agricultural use. Land tenure is through assignment by the local government and typically limits agriculture to 0.5 – 1.0 hectares per household. Grazing areas are seemingly local commons and are maintained by heavy grazing activity.

Wolong also contains up to 4000 plant species including up to 11 species of bamboo, two of which constitute the significant portion of the total biomass, *Fargesia robusta* and *Bashania fangiana*. *F. robusta* grows to a height of 4 – 6 meters often in dense clumps spread through the elevational range of 1500 – 2600 meters. Pandas often migrate down the mountains in late spring to eat the new shoots and were shown to rely on *F. robusta* during times of mast-seeding of the primary bamboo, *B. fangiana*. *B. fangiana* is a smaller, thinner bamboo growing to heights of 1 – 1.5 meters. However, it often grows as large carpets of dense growth as large as several hectares area at elevations of 2600 – 3600 m.

Most bamboo species in China are semelparous and are characterized by a synchronized mast-seeding occurring every 3 – 120 years, depending on the species (Janzen 1976). Mast-seedings of *B. fangiana* are estimated to occur every 45 years. In 1983, *a B. fangiana* mast-seeding and corresponding mass die-off occurred over an extensive area within the reserve. Pandas in Wolong continued to utilize small patches that did not flower and old stems, but were forced to migrate to lower elevations in the winter of 1986 to forage on *F. robusta*. It is estimated that another mast-seeding of *B. fangiana* will occur between 2025 – 2030. The intervals between mast-seedings of *F. robusta* are unknown, but estimated at 60 – 80 years (Schaller et al. 1985). The last mast-seeding of *F. robusta* is believed to have occurred in 1949 (Wolong Administration, personal communication).

4.2.2 Model Description

The model was developed in the SELES (Spatially Explicit Landscape Event Simulator) framework (Fall and Fall 2001, Fall et al. 2001). SELES is a high-level programming language that facilitates modeling of the temporal and spatial dynamics of gridded landscapes. SELES also allows the incorporation of georeferenced raster data, the design of sub-systems that interact on the landscape, and temporal and spatial dynamics.

This model is intended to provide insight into the landscape-level interaction between forest, humans, and understory bamboo. It seeks to balance parsimony and realistic landscape driving factors for each aspect of the model and to examine the influence of each of the model processes. The model included four sub-models: household fuelwood activities, household creation, forest regrowth, and bamboo growth and die-offs. The resulting impacts of the distribution of human activities and bamboo spatiotemporal dynamics are integrated directly into giant panda habitat suitability models and allow model predictions to be measured in terms of changes to landscape indices of panda habitat. The four sub-models and their interactions are shown in Figure 4.3. Each of the human activities influences the spatial distribution of forest cover. Forest regrowth allows for forest re-establishment and annual growth of non-climax forests. The spatial distribution of forest cover influences the spatiotemporal dynamics of bamboo regrowth and die-off. The suitability of giant panda habitat is then determined from forest cover along with abiotic factors. Bamboo is incorporated into habitat models as presence/absence of bamboo and, consequently, giant panda habitat.

The probability of a landscape event (e.g. fuelwood collection) occurring at each cell is determined by the current state of the pixel (e.g. slope, aspect, forest cover) and proximity to cells of a specific state (e.g. pixel containing a household). The number of landscape events is determined by the sub-model characteristics (e.g. total number of households) with the location of the event stochastically determined relative to the cell probability. The event probabilities for each cell (depending on the specific landscape event) could be determined by forest cover (%

pixel), slope and aspect (degrees), elevation (meters), agriculture cover (% pixel), distance to households or roads. The modeling framework also allows for landscape events to spread to neighboring cells (e.g. if a cell does not contain sufficient fuelwood for the annual collection of a household fuelwood needs, fuelwood collection can spread to a neighboring cell to meet the annual needs of the household).

The four sub-models and habitat suitability model are described below along with examples of probability functions:

- ***Fuelwood Collection*** – It was assumed that households collect fuelwood based on availability, accessibility, and previous fuelwood collection activity. Typically, fuelwood is collected around the household. As these areas are diminished, foraging extends to the neighboring areas characterized by easy accessibility (Liu et al. 2001). Many households have been forced to travel several kilometers to collect annual stocks of fuelwood (An et al. 2001). Accessibility is characterized in this model by the distance to collection site, slope, and elevation and is summarized as a cost function relative to the distance to roads and main paths and topographic variability (i.e. slope and elevation difference along path to the pixel). The probability function was a linearly decreasing function of increasing cost:

$$P(\text{fuelwood} \mid \text{cost}) = (1 - (\text{cost}/\text{maximum cost}))$$

Pixel forest cover and average yield per hectare determined availability. Households are also more likely to return to the same pixel, if sufficient forest volume exists (An, unpublished data), or neighboring cells of previous fuelwood extraction. Therefore, a higher probability of collection was assigned to cells previously harvested and neighboring cells. The overall probability of fuelwood extraction for each forested pixel is then a multiplicative combination of these factors.

- ***Household Creation*** – Since 1965 new households were established as children moved out of their parents' home or through immigration into the reserve. Immigration is now restricted to new spouses of current residents. Each new household is presumed to also establish its own agriculture land, clearing the forest area or occupying previously deforested area. New household establishment is based on suitable agriculture land and proximity to transportation routes and other households (An, unpublished data). The precise X,Y location of the actual residence is not included in this model. Rather, households including the physical residence, agriculture land, garden area, and surrounding edge are presumed to occupy cells of the landscape. Suitable agriculture areas were based on abiotic factors: slope, aspect and elevation. While agriculture activity occurs on slopes up to 40 degrees, low slope areas are preferred. Preference for low elevation areas was also noted. For example, relative probabilities for household placement based on elevation were empirically measured as:

$$
\begin{array}{ll}
 & \{\ 0.00\ (h > 2500)\ \} \\
P(\text{household} \mid h)\ = & \{\ 0.08\ (2250 < h \leq 2500)\ \} \\
 & \{\ 0.82\ (1750 < h \leq 2250)\ \} \\
 & \{\ 1.00\ (h \leq 1750)\ \}
\end{array}
$$

In areas of higher elevation, preference is given to south-facing slopes to maximize sunlight. Households were also more likely to develop land adjacent to previously established houses within short distances (typically less than 2 kms) to major transportation routes.

- ***Forest Regrowth*** – Four forest types (Figure 4.4) were identified throughout the reserve based on elevation and species distribution (Schaller et al. 1985). Regrowth models were derived for each of the predominant species within each elevational zone from published and empirical data (Yang and Li 1992). Initial stand volume was estimated for each elevational zone based on approximate time and intensity of commercial logging activity. Regrowth is calculated based on succession age and logistic regrowth of total volume.
- ***Bamboo*** – The spatial distribution of bamboo was derived from 1997 remote sensing data and extensive field surveys conducted from 1998 – 2000 (Linderman et al. in review). Regrowth and spatial and temporal die-off characteristics were obtained from the literature (Janzen 1976, Schaller et al. 1985, Reid et al. 1991, Taylor et al. 1991, Taylor and Qin, 1993). For example, Taylor and Qin (1993) noted that while small forest gaps have higher recruitment and growth rates, it is unlikely that bamboo will recover

from a mast-seeding in clearcuts (likely due to microclimate differences). Reid et al. (1991) found that bamboo in the middle of its altitudinal range had faster growth rates. This was included as a normal probability distribution function defined by the middle of the known altitudinal range and known altitudinal range. And, Taylor et al. (1991) found correlations between the spatial distribution of *B. fangiana* die-off and environmental conditions such as elevation, aspect and forest cover. For example, due to the additional stress of steep, north-facing slopes bamboo was ten times less likely to flower during mass die-offs:

$$\mathrm{P(dieoff \mid aspect,slope)} = \begin{array}{l} \{0.1\ (\mathrm{aspect} \geq 330\ \&\ \mathrm{slope} > 40)\} \\ \{0.1\ (\mathrm{aspect} \leq 30\ \&\ \mathrm{slope} > 40)\} \\ \{1.0\ (30 < \mathrm{aspect} < 330\ \&\ \mathrm{slope} \leq 40)\} \end{array}$$

- ***Habitat Suitability*** –The final habitat classification was a categorized suitability measure of four classes termed highly suitable, suitable, marginally suitable, and unsuitable (Liu et al. 2001). The impacts from human activities are reflected in the habitat suitability model as impacts from fuelwood activity and agriculture development. Bamboo was incorporated by measuring habitat containing bamboo. Measures of habitat quantity and suitability allow analysis of the temporal and spatial dynamics in terms of giant pandas, the influence of household characteristics, and possible future scenarios on the likely landscape implications for giant panda habitat.

Landscape events occurred on an annual time frame. The first landscape event each year is the establishment of new households and associated agricultural development. Each household then collects its annual fuelwood volume. At the end of the year, forest regrowth occurs for each forested cell and the suitability of panda habitat updated.

4.2.3 Data and Parameterization

Several sources of data were used to parameterize, for input, and to validate the model. Satellite data and topographic maps were used to describe the landscape distribution of human activities, vegetation, and abiotic features throughout the reserve. Socio-economic and demographic data were collected from local government agencies and a household survey that was conducted from 1998 – 2001 (An et al. 2001). Literature on panda habitat and bamboo (particularly relating to the 1983 *B. fangiana* die-off) were used for further parameterization of sub-models.

Georeferenced data used for this model included remote sensing measurements of forest cover, topographic maps, and remote and ground surveyed household distributions within Wolong. Additional layers were created by the model relative to the initial layers such as distance to households. Each of these layers was updated as the model progressed (e.g. forest cover was modified) where applicable based on landscape events. Information on the landscape-level distribution of forest was obtained from classification of four dates of remote sensing data, 1965, 1974, 1987, and 1997. The 1965 data are Corona stereo-pair photographs acquired as part of the Corona photo-reconnaissance satellite project (USGS Eros Data Center, Sioux Falls, South Dakota). The 1974 data are Landsat MSS images and the 1987 and 1997 data are Landsat TM images. To account for the spectral and spatial differences between the data, each image was visually interpreted into forest and non-forest areas (for classification details see Liu et al. 2001). Topographic data were derived from a Digital Elevation Model (DEM). Examples of these data are shown in Figure 4.4. The 1997 digital classification of the forest cover is a supervised classification of the Landsat TM data based on over 300 ground samples. The bamboo distribution was derived from field surveys conducted from 1998 – 2000 and 1997 Landsat TM data (Linderman et al., in review).

Location of each household was measured through the use of field measurements and Ikonos 1-m resolution satellite imagery. Ikonos imagery acquired in 2000 by SpaceImaging was georeferenced using ground control points measured using a Global Positioning System with sub-meter accuracy (Trimble Pathfinder Pro XRS receiver and Community Base Station). Households were then identified in the images and the location recorded. All households created on or before 1965 were used to create the initial distribution of households corresponding to the initial forest cover information. New households have been added to the reserve at a steadily decreasing rate each year between 1965 and 1997. Approximately twenty-four new households were created each year.

A household survey was conducted from 1998 – 2001 and included each of the households within Wolong (An et al. 2001). Households were queried on fuelwood use, fuelwood collection, agricultural activity, household creation, and other associated socioeconomic and demographic information. Additional socioeconomic and demographic information was obtained from local government records. Census information was obtained from each township within the reserve. Local governments also maintain information on land allocated to each household. From these data it was found that each household maintains on average 0.7 ha of agricultural land. Including the area of the physical house, garden area, and surrounding edge, the typical total area is approximately 0.8 hectares. Therefore, the scale of the model was chosen to be 90 x 90 meters (0.81 hectares).

Fuelwood use was determined by surveying over 50 households and physical measurements of daily use (An et al. 2001). The volume of wood varied between 8 and 30 m^3 and averaged 15 m^3. An annual volume of wood used by each household in the model was then 15 m^3. Preference for fuelwood collection and household creation sites was derived from comparing DEM and slope coverages, and house locations and fuelwood sites. Distance to fuelwood collection sites varied from 50 meters to over 5 kilometers. The average distance for 100 households surveyed was 500 meters (Li An, unpublished data). Households preferred to collect fuelwood in flat areas (< 20° slope) and had a decreasing probability relative to elevation.

Uncertainty in the 1965 stand volume of the various forest types posed the most difficult parameterization problem. While basic coverage information was available from satellite photographs, data on the average volume throughout the reserve were scant. Quantitative information dating back 35 years is difficult to obtain or non-existent. Schaller et al. (1985) suggest that much of the reserve was commercially logged from the 1916 until 1975. Measurements taken in the late 1990's found much of the lower altitude forests to be well below old-growth volumes. Average volumes for broadleaf forests below 2600 m were approximately 80 m^3/ha (Ouyang et al., unpublished data). It is likely that these forests were the first to be harvested in the first half of the century and have regrown to current volume levels. Based on regrowth data for the broadleaf forests in Wolong, we estimated the average volume for 1965 to be approximately 45 m^3/ha. Stand volume for subalpine conifers was on average approximately 300 m^3/ha (Ouyang et al., unpublished data). Subalpine stand volume was high enough such that variations in estimates would not significantly influence the model.

Forest regrowth was included in the model to allow for previously logged regions to regenerate and the addition of biomass and regrowth in selectively logged cells. Separate logistic regrowth models were developed for each forest type based on species composition, stand age, and altitudinal zone (Figure 4.4b). Model parameters were derived from over 30 plots distributed throughout the reserve (Liu et al. 1999) and species regrowth and yield models derived by the Sichuan Department of Forestry (Yang and Li 1992).

The spatiotemporal trends of the two dominant bamboo species in Wolong, *B. fangiana* and *F. robusta*, were included in models running from 1997 to 2030. Bamboo was not included in models begun in 1965 as data on the distribution of bamboo are not available prior to 1997. The initial spatial distribution of the presence or absence of bamboo in 1997 was derived from remote sensing data and extensive ground surveys (Linderman et al. in review). Species delineation was based on altitudinal range and field surveys (Schaller et al. 1985). *B. fangiana* and *F. robusta* make up approximately 80% of the total bamboo within the reserve and are the primary food sources for pandas in the reserve. Therefore, three classes of bamboo are included in the model: *B. fangiana*, *F. robusta*, and all others (Figure 4.5b). However, because detailed life-history information of other species is unavailable and to provide a conservative estimate of habitat impacts from bamboo dynamics, die-offs for only the two main bamboo species were included in the model.

Growth functions of each bamboo species and environmental influences on regrowth and die-off characteristics were gathered from the literature (e.g. Taylor et al. 1994). In 1983, approximately 85% of *B. fangiana* throughout the study area died after flowering. The areas of die-off were non-randomly distributed across the landscape with bamboo patches experiencing environmental stress (altitudinal limits, steep north facing slopes, and in large clearings) were more likely to not flower. Analyses of *B. fangiana* recovery after a mass-flowering showed that typical patches require 15-20 years to regenerate with an initial dormancy of 0 – 5 years. In addition, Taylor and Qin (1993) found lower seedling establishment and poor overall regeneration in large forest clearcuts.

Behavioral studies have shown that panda habitat is a function of forest cover, slope, altitude, and understory bamboo (Schaller et al. 1985, Ouyang et al.

1996). Ultimately, then, pandas are constrained by canopy cover while understory bamboo strongly influences the quantity, quality, and distribution of habitat within forested areas (Johnson et al. 1989, Reid et al. 1989). While both overstory and understory forest components are known constraints, past estimates of the availability and distribution of panda habitat over large extents have been based solely on overstory features and abiotic factors, not on understory bamboo distribution (De Wulf et al. 1988, Liu et al. 2001). Therefore, we determined habitat suitability using a multiplicative combination of the three factors (forest cover, altitude, and slope) available for the 30-year time span per Liu et al. (2001). Because non-forested areas are considered unsuitable habitat for the giant panda, forest/non-forest classifications were multiplicative factors of 1 or 0, respectively. Slope and altitude multiplicative factors were proportional to the observed use by pandas. For model scenarios run from 1997 – 2030, bamboo presence or absence was included as an additional multiplicative factor of 1 or 0, respectively.

4.2.4 Model Validation and Sensitivity Analyses

Variations in individual parameters such as the rate of new household creation, fuelwood use, and forest characteristics were made to test the validity of each parameter and the sensitivity of impacts to each individual parameter. Exact correspondence between the model predictions and the measured distributions was not expected as the model is stochastic with the probability of a landscape event (e.g. fuelwood collection, bamboo die-off) occurring in a cell based on the biophysical parameters of the cell. Based on the variability of initial tests, the model was run 20 times for each scenario to account for the stochastic processes.

To examine the influence of various parameters on the model predictions, parameters from each of the sub-models were tested to examine the relative influence on the related landscape event for model runs from 1965 - 1997. The overall influence of each component of household submodel (abiotic, proximity, and cost function) was examined by comparing various model scenarios (e.g. model predictions excluding multiplicative factors) and the actual household distribution. This was done to show the overall influence each function had on the model selection of new households and as some functions could not be varied systematically (e.g. abiotic influences were based on conditional probabilities). Accuracy and landscape metrics were calculated based on the average accuracy and indices of the final output from each of the 20 simulations. Systematic analyses of parameter sensitivity of individual parameters were also conducted for the fuelwood model such as the propensity to return to previous fuelwood collection sites and distance to fuelwood collection sites. Since parameterization of stand volumes for broadleaf forests below 2600 meters contained relatively large uncertainty, several average stand volumes for the broadleaf forests were tested including 30, 45, 60, 75, and 90 m^3/ha. Accuracy assessments and landscape measures of fuelwood activities were based on forest cover within the 5 km buffer.

The model was validated based on simulations started in 1965 with the initial distribution of forest based on the classification of forest/nonforest categories from these photos. The original distribution of households was based on all households established prior to or in 1965. Validation simulations were run for 32 years to correspond to the latest remote sensing data available. Two validation methods were used. First, predicted fuelwood impacts on forest cover were compared to visual delineations of forest cover from 1974, 1987, and 1997 satellite imagery (Liu et al. 2001). Visual delineation of the four time steps provided a consistent methodology for forest classification relative to the forest classification used for the 1965 Corona photographs. The 1974, 1987, and 1997 data were used for visual comparison of the multitemporal trends in predicted versus the measured forest changes. Second, measurements of the distribution of households and digital classifications of forest cover as measured in 1997 were compared to final outputs from the model. Digital classification of the 1997 forest cover was possible with extensive ground sample data and provided a more detailed snapshot of the current distribution of forest cover. Household locations as measured in 1997 were compared to locations of predicted households at the end of the 32-year simulations.

Comparisons between the simulated landscapes and measured landscapes included a direct comparison between predicted change areas and measured change. In addition, comparisons were made in the differences in the quantity of forest area and disturbed areas and landscape metrics such as patch size, shape, and complexity. Timber logging activities continued after the establishment of the reserve in 1975 and there is little information available on the total quantity or area affected. To minimize the effect of natural and external influences on the accuracy assessments, analyses were constrained to regions within 5 kms of the current household distribution. This distance corresponds to the maximum distance households travel to collect fuelwood. The accuracy of the model is reported as the percentage of predicted pixels that correspond to measured pixels (e.g. predicted non-forest vs. measured non-forest pixels). This ignores possible omission errors and was used because of the difficulty in distinguishing natural variability in and external impacts on forest cover from household activities even within 5 kms of the households. Visual comparisons of model predictions and measured forest cover change are shown for comparison between commission and omission errors.

Given the difficulty distinguishing between timber logging, fuelwood collection, and natural variability in forest cover, accuracy assessments of the model predictions relative to measured landscape trends (particularly those from the detailed classification) do not provide a complete picture. Additional measures and indices are used to compare the outputs of the model to measured impacts. The impacts measured from projection simulations are reported as the landscape indices relative to the impact of interest (e.g. household distribution and forest cover). Indices were chosen relative to Riitters et al. (1995) and included total number of patches, mean patch size, corrected perimeter to area (p/a) ratio (Baker and Cai 1992), connectivity between patch centroids (Forman and Godron, 1986), and the aggregation index (He et al. 2000).

4.2.5 Household Impacts

To examine the relative influences of different household scenarios on the landscape, a variety of scenarios were run from 1965 until 2030 with 1965 baseline parameters and 1965 land-cover and household data used until 1997. Model parameters were then varied for 1997 to 2030 to examine possible changes in household characteristics. These scenarios represent situations where new policies are introduced after 1997. Parameters examined included fuelwood consumption per household and the household growth rate (or immigration/emigration rate). Varying household characteristics was done to examine the effects of household parameters on model outputs in the absence of natural and external (e.g. commercial logging) variability. This allowed relative comparisons between models and to highlight scenarios of interest to be run in the 1997 – 2030 scenarios described below. Model scenarios were compared based on impacts to giant panda habitat as deforestation for fuelwood and household construction removed habitat and forest regrowth returned land to potential habitat.

Several levels of fuelwood consumption (30, 15, 10, 5, and 0 m3/yr) and household growth (36, 24, 12, 0, -12, and –24 new houses created or removed each year) were examined. Several combinations of these parameters were also examined (Table 4.3). These levels were chosen to reflect possible future household characteristics resulting from new policies and management efforts such as subsidies, forest restrictions, and/or increased accessibility to electricity. For example, efforts to eliminate fuelwood collection and reclaim agriculture land were initiated in 2000. Subsidies have been offered in exchange for managing forests. However, it is unlikely that fuelwood collection will completely cease. As economic opportunities increase and demand for meat products increases, farmers may increase the production of livestock and, consequently, actually increase fuelwood consumption. Electricity prices are also currently unaffordable for most local farmers, particularly for energy consumptive needs such as heating and cooking. In addition, efforts to encourage emigration out of the reserve are being instituted. However, an increasing preference by younger adults to establish new households and in response to subsidy opportunities, new households have increased at higher rates than in past years. To reflect the possible range of values, fuelwood consumption levels were chosen based on the current maximum known household consumption (to reflect increased livestock production) to no fuelwood use. Household creation rates ranging from increases in household establishment to a net emigration were examined to reflect the possible policy influences on household activities.

4.2.6 Integrated effects of household activities and bamboo dynamics

Projection scenarios were run for 33 more years (1997 – 2030) to examine the combined effects of human activities and potential bamboo die-offs. The model was run for 33 years starting from 1997 with the latest available household and forest cover data. These models were coupled with the spatiotemporal trends of understory bamboo (information on the spatial distribution of bamboo is available only from 1997). This coupled model was used to predict actual impacts on forest cover, possible bamboo dynamics and associated interactions with forest cover, and possible implications for giant panda habitat.

The latest household and forest data as measured from satellite imagery and collected in the field were used to develop the final model. Figure 4.5a shows the measured forest cover based on digital classifications of Landsat TM data acquired in 1997. Figure 4.5b shows the measured distribution of bamboo in 1997. These data, as well as measured household locations, were used in the scenario runs from 1997 – 2030 to examine potential impacts on giant panda habitat from the coupled human activities and bamboo dynamics.

Four scenarios of household creation and fuelwood consumption were chosen from the scenarios tested above. These included household creation rates of 24, 12, -24 and 0 houses per year. Fuelwood consumption levels of 15, 10, and 0 m^3/year were also used. The scenario of 0 houses/year and fuelwood consumption of 0 m^3/year was used as a baseline for comparison. The other scenarios were chosen to represent the responses found in section 3.2 above and represent ranges in predicted future possibilities under business as usual and management actions to reduce fuelwood use and household creation. The parameters of 12 houses/year and 10 m^3/year, representing efforts to encourage emigration and decreased reliance on fuelwood, were used as the most likely conditions for the next 30 years.

Three bamboo scenarios are presented. First, habitat availability is measured if neither *B. fangiana* nor *F. robusta* die-off during the model run. *B. fangiana* has a fairly well known intermast period of 45 years with the next die-off predicted to occur approximately in 2027. Therefore, two die-off times of *F. robusta* in addition to a *B. fangiana* die-off occurring in 2027 were coupled with the above mentioned household parameters, a *B. fangiana* die-off occurring twenty years prior to the *B. fangiana* and a simultaneous die-off. Twenty years was chosen as recovery time as studies of past die-offs in the reserve suggest 15 – 20 years until complete reestablishment. However, as forest cover affects the probability of reestablishment of bamboo, the dynamic interaction between human activities and bamboo flowering may affect the reestablishment of bamboo to its former distribution.

4.3. Results

4.3.1 Model Validation and Sensitivity

Figure 4.6 shows a multitemporal comparison of the predicted 32-year simulation of household activity and the measured forest cover within 5 km of all households. There appears to be a good correspondence between the model outputs and measured forest distribution. The basic trends in forest cover are comparable between measured and predicted distribution of forest cover though some differences from extraneous activities are apparent. In addition, the 1997 modeled household distribution, based only on the initial 1965 distribution of households, is very similar to that of the measured distribution from ground surveys and satellite imagery for 1998 – 2000 (Figure 4.7a).

Various model scenarios resulted in distinct differences in the distribution of household locations. Considering all household factors resulted in a slight increase in the number of patches and p/a ratio, a 44% larger mean patch size, and slightly higher connectivity and aggregation indices (Table 4.1). Not including topographic preferences resulted in 71% more patches of households (Table 4.1) and in house placement in regions of distinct topographic relief (e.g. areas of extreme slope) (Figure 4.7b). Excluding the distance and topographic variation from main transportation routes resulted in a wide distribution of households (Figure 4.7c). The number of patches was more than three times the measured distribution. Mean patch size and p/a ratio were both considerably lower (Table 4.1). And, the lack of a proximity factor results in decreased clumping of households (low connectivity and aggregation indices), smaller patch size and an increase in the number of patches relative (Table 4.1) to the measured distribution of households (Figure 4.7d).

Accuracy in terms of predicted household locations agreeing precisely with measured locations of household distribution varied from 20 – 27% (Table 4.2). Precise prediction of the 90 x 90 meter plot was not the intention of this model. Foremost, this is not saturated system. This leads to quality areas not being occupied and complex edges that are difficult to predict empirically. In addition, the model has a stochastic decision process and also does not include household-level influences on household placement. However, as the spatial arrangement of households may have an impact on habitat, particularly crucial secondary habitat, we examined the percent of predicted households falling in close proximity (1, 2, and 3 pixels) of measured households. Over 88% of the predicted households from the complete model were within three pixels of the measured locations (Table 4.2). This suggests that the model was predicting households essentially within the same areas as those measured to also contain households. Not including the distance function resulted in the lowest accuracy of 63% for predicted households within 3 pixels of measured households. Not including a preference to create new households next to existing households resulted in an accuracy of 80%. Excluding the selection based on abiotic factors (i.e. slope and elevation) resulted in an accuracy of 81%. The complete sub-model had an accuracy of 27, 68, 82, and 88% for predicted households within 0, 1, 2, and 3 pixels from measured households (Table 4.2).

Analyses conducted for each of the fuelwood parameters showed expected influences from variations in the distance and proximity factors (Table 4.3). Relaxing the tendency for households to collect fuelwood from previously cleared areas resulted in more fragmented impacts and is reflected in the landscape metrics. Variation of the proximity factor three times more or less likely to return to previous sites resulted in 35% fewer and 52% more patches and 54% larger and 34% smaller patch sizes, respectively (Table 4.3). In addition, perimeter and connectivity indices show increasing clustering as the proximity factor is increased. Accuracy of predicting impact areas, however, only varies by less than two percent. Varying the cost factor by 20% resulted in similarly expected results. Easing the influence of the distance factor resulted in more dispersed impact occurring in smaller patches. This is seen in the patch characteristics with more and smaller patches and decreased p/a ratios and decreased connectivity (Table 4.3). Increased probability of using near areas conversely increased patch size, decreased patch number, and increased connectivity between patches. Patch size varied by 17.9% to

33.7% and patch number varied by 24.1% and 20.5% for a twenty percent decrease and increase in the cost factor, respectively (Table 4.3).

Expected trends in deforestation relative to initial stand volume were decreasing area of impact and decreased fragmentation since more volume was available in preferred collection areas (Table 4.3). While the outputs using each of the above mentioned initial volumes shown in Figure 4.8 do seemingly conform largely to these expectations, increased peripheral impacts occur at both increased initial volumes and decreased volumes. Landscape metrics and overall model accuracy also show this trend in the model (Table 4.3). The lowest number of patches was at initial forest stand volumes of 45 m^3/ha. Decreasing stand volume resulted in larger overall impact patch size, particularly the core area nearest to households; however, smaller peripheral impacts were more common. As initial stand volume was increased, the overall impact decreased, however small pockets of impact emerged where more continuous impacts previously existed. These trends are clearly shown in the decreasing patch perimeter and mean patch size. The accuracy of predicted impact sites relative to measured impact also reflects more concentrated impacts as initial volume is increased (Figure 4.8). As fuelwood activity is focused on core areas near households, model accuracy increases. At an initial stand volume of 30 m^3/ha, the overall prediction accuracy is approximately 55%. As the volume is increased, model accuracy increased to 64% when using 90m^3/ha (Table 4.3). The increase in accuracy is largely a result of smaller areas being affected only near households and decreased influence of stochasticity in choosing distant fuelwood sites.

4.3.2 Household Impacts

Projected household impacts on panda habitat are shown in Table 4.4. Current levels of household creation and fuelwood consumption resulted in nearly 10% more habitat loss below 2600 meters. An increase in fuelwood consumption (30 m^3/yr) could impact up to 16% of the low-elevation forest. Reducing fuelwood consumption by two-thirds reduced habitat loss by 59% compared to current trends. However, to maintain levels of habitat as measured in 1997, the removal of households at a rate of at least 50% the current level of creation or complete cessation in fuelwood collection is required. However, as seen from a 50% increase in household creation with no fuelwood collection, increased population and resulting household creation contributed little to habitat loss because considerable areas around households are already cleared of forest cover. Most likely estimates (due to recent policy and management changes) for future new household creation and fuelwood consumption (12 households/year and 10 m^3/year) resulted in approximately 30% less forest loss than current levels of new household creation and fuelwood consumption.

4.3.3 Combined effects of household activities and bamboo dynamics

Human impacts on available giant panda habitat are shown in Figure 4.9a. Increased impacts around households and near main transportation routes are evident. The magnitude of these impacts for the four scenarios is shown in Table

4.5. Decreased area of impact relative to the 1965 to 1997 time period is expected as forests recover biomass. However, up to 6.5% of all habitat is still predicted to be lost relative to the current forest conditions in the near future from fuelwood collection. And, these losses take place in a relatively small area of the reserve with over 95% of the impacts occurring below 2600 meters of elevation. A disproportion percent of habitat below 2600 meters will be impacted with up to 17% of low elevation habitat being lost (Table 4.6). Particularly worrisome is that up to 15% of highly suitable habitat is impacted.

The total area of habitat containing bamboo if no die-offs occur is approximately 30,000 ha. Up to 52% of this habitat may be lost during a simultaneous die-off of *B. fangiana* and *F. robusta* (Table 4.7, Figure 4.9b). Human impacts on habitat are relatively small compared to the loss from bamboo die-offs. However, the total habitat available when considering possible bamboo die-offs is only 14,000 – 16,500 ha. Human impacts are predicted to result in up to 1500 ha of loss of bamboo habitat representing approximately 10% of the remaining habitat below 2600 meters (Table 4.8). In addition, mean patch sizes were considerably lower after bamboo die-offs compared to the landscape without bamboo die-offs (Table 4.9). In addition, the cumulative long-term effects of human activities on habitat (the relatively permanent land-cover changes and spatial location of these changes) now make pandas increasingly vulnerable to bamboo dynamics. Human impacts have further reduced the size of the mean patches of habitat suggesting that timing of bamboo die-off and human activities will influence access to habitat (Table 4.9). As human impacts are focused in areas of *F. robusta* habitat, areas relied on by pandas during the 1983 mass-flowering of *B. fangiana*, loss of access to these habitats may have considerable impact on local panda populations. The model predicts that up to over half of the initial bamboo habitat will be lost given the coupled impacts of human activities and a simultaneous bamboo flowering. Even if *F. robusta* flowers with a sufficient time for recovery (~20 years) prior to *B. fangiana* flowering, total habitat remaining is only about half the original habitat. Figure 4.10 shows the distribution of these impacts. Even with conservative estimates of flowering rate of *F. robusta*, total habitat in certain areas is severely reduced. This is particularly noticeable in the north and west edges of the extent of habitat in the reserve (Figure 4.10).

4.4. Conclusions and Discussion

The landscape approach to modeling the human and biological dynamics of Wolong Nature Reserve provided considerable insight into the historical trends and conditions of the reserve, the driving factors of human causes of land cover change, and the potential consequences of human alterations of land cover and bamboo dynamics on panda habitat. In addition, this particular model can be used to predict conflicts between human activities and species' habitat requirements and more specifically suggests human modification of secondary habitat can have considerable ecological consequences.

A lack of detailed historical information for Wolong posed problems for accurately modeling the human interface with the environment. Except for the

Corona photographs used for this study, very little information on the state of the forest in 1965 was available. However, by comparing projections of household activities from 1965 to a time where we have more detailed information permitted a more detailed estimate of forest conditions and insight into factors contributing to habitat loss. Comparisons of predicted forest loss from 1965 to 1997 to measured forest conditions in 1997 for several scenarios of the average starting volume of low-elevation forest confirmed that these forests were already at relatively low volumes and magnified human impacts since 1965. It is possible that large-scale logging ocurred concurrently with household fuelwood collection from 1965 until 1975 or later. While timber activities almost certainly continued after 1975, no large-scale logging was noted by researchers present in the reserve from 1983 to the 1990's. Forest loss after 1975 until 1997 are likely due to a combination of households and finer-scale timber activities and exacerbated by already low average stand volumes from previous large-scale activity. As these forests are increasingly lost, fuelwood activities move to higher elevation forests with increasing losses of core habitat.

The model is relatively parsimonious. The placement of new households is explained by only four factors: distance to roads, proximity to other households, slope, and elevation. Using only these four factors, however, the model accurately predicts household creation nearly 90% of the time within 3 pixels of the measured distribution of households. Fuelwood collection also is only based on a few landscape variables: distance to roads, previous fuelwood collection locations, slope, and elevation. Again, the model captures the trend in household reductions in forest cover. This simplicity and success of the model suggests basic landscape-level factors have considerable influences on the spatial distribution of human activities. Households were present in the reserve prior to the establishment of the current transportation routes. These roads and the introduction of mechanized transportation have likely led to increased agricultural activity along these routes and increased access to forests near the roads. In addition, as the reserve is situated in a relatively mountainous area, topography plays a significant role in shaping the spatial distribution of household activities. Agricultural activity requires relatively flat land and easy access to transportation. While fuelwood collection is less dependent on the collection site qualities than the cost factor of the distance to roads, the slope, elevation change, and overall accessibility influence the location of collection sites.

This model also provided means to examine the role of household characteristics on possible future impacts to giant panda habitat. Most notably, considerable changes in fuelwood consumption and/or household creation rates were required to maintain the current area of forest. While an increase in household creation itself led to only small decreases in forest area, even limited fuelwood consumption resulted in relatively large losses in habitat. This is likely because areas around existing households have already been deforested. Therefore, the placement of new households is likely not to result in further loss of forest. However, even small amounts of fuelwood required for the large number of households already in the reserve results in increased impacts on forest cover. A decrease in the number of current households such as through emigration does limit the loss of forest from agricultural activity. However, very large decreases in the number of households or simultaneous decreases in average household consumption rates are needed to retain the current forests. These results are similar to estimates as measured by Liu et al. (1999) who showed that relatively high rates of emigration were necessary to restore habitat and suggest that most efforts should focus on reducing fuelwood collection and providing alternative energy sources for the current households while providing viable means and incentives to encourage emigration.

In this study, we further examined the landscape-level factors governing the spatial distribution of human impacts on forests and its implications for giant panda habitat in light of episodic die-offs of bamboo. The continued removal of low-elevation forests considered less important than core habitat areas may seriously restrict current sub-populations of giant pandas within Wolong from necessary secondary habitat when the next *B. fangiana* die-off occurs. Simultaneous or near-simultaneous flowerings of *B. fangiana* and *F. robusta* will be detrimental to panda populations. Even with a sufficient interval between flowerings to allow biomass recovery (15 – 20 years for both species (Taylor and Qin, 1993)), decreasing access to *F. robusta* in the future may have similar consequences for the remaining pandas in Wolong. In 1983, pandas had direct access to significant amounts of *F. robusta*. Pandas eventually shifted to secondary food sources after the last *B. fangiana* die-off. The availability of *F. robusta* during the mast-seeding of *B. fangiana* in 1983 likely buffered the studied populations from the mass-starvations faced by pandas in the Min Mountains. Landscape models are useful in describing the basic driving factors control events occurring at the landscape level. Abiotic, transportation, and biophysical variables can strongly control the location and distribution of human activities. However, by coupling the multitemporal spatial dynamics of bamboo with human activities, the implications of even limited impacts to critical habitat can be seen.

The success of the model to predict similar distributions of households and local land-cover change suggest basic landscape features such as topography and accessibility can play a large role in shaping the spatial distribution of human activities. The limitations of the model point to areas where further study is needed. Most decisions such as consumption level, propensity to use alternative energy sources, emigration rates and new household formations are made at the household-level and are not included in this landscape model. Furthermore, more detailed information on the biophysical characteristics such as total available biomass, growth rates, and efficiency of conversion of biomass to fuelwood are needed.

Even with these limitations, however, the model does provide insight into the causes and driving factors leading to past habitat loss, future impacts, and the spatial arrangement of these impacts. Past studies have identified the impacts of broad-scale logging and household fuelwood collection on giant panda habitat (Schaller et al. 1985, Mackinnon and DeWulf 1989), however, few studies have noted the combined influences of these activities. We found that broad-scale logging is likely providing conditions that exacerbated impacts from households to low-elevation forests. Regrowth following clearcutting of these forests provided trees preferred for fuelwood consumption.

In addition, lower volumes resulting from logging activity led to larger areas required to meet household demands. Similar to past studies (Liu et al. 2001), this study found that access to giant panda habitat increases the likelihood and quantity of losses of habitat. However this study also points out that access clearly plays a role in determining the spatial distribution of household activities. Households require access to roads to transport cash crops to local cities and the ease of access to preferred fuelwood also seemingly shapes fuelwood collection decisions. The distribution of roads had a considerable impact on the past distribution of households and associated activities. Future development of and providing additional access to Wolong and other reserves will likely make these areas vulnerable to similar impacts. Lastly, found as previous studies (Liu et al. 1999) that extensive changes in household characteristics are needed to maintain habitat. The model suggests that the number of new households and the average volume of fuelwood consumed by each household has a strong influence on the quantity of future impacts. Decreases on the order of 150% in new households or a complete cessation of fuelwood collection are needed to preserve habitat at current levels. Providing viable energy alternatives to the local population will likely considerably decrease impacts, particularly the fringe habitat adjacent to primary habitat.

Bamboo die-offs will occur in Wolong every 40 – 60 years. These die-offs reduce total habitat available to pandas until regrowth. We found that even though human impacts on forests in Wolong are relatively small compared to losses of habitat from bamboo die-offs, losses of habitat from bamboo are temporary and have not historically significantly affected the overall panda population. The current extent and spatial distribution of human impacts may, however, have considerable consequences on panda populations, particularly during these temporary losses of bamboo. In addition, human reductions in forest cover reduce the likelihood of bamboo regeneration to previous levels. This model offers insight into the importance the spatial arrangement of even limited human impacts can have on giant panda habitat. Worldwide, human impacts may be underestimated as the combined effects of human and natural disturbances have not frequently been considered. Simultaneous examination of natural and human disturbances may be necessary to assess total habitat area requirements for species persistence. Examining the spatial distribution of human activities in conjunction with natural disturbances further highlights the relevance of examining the consequences of human activities in other areas and the implications for species persistence.

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Table 4.1. Landscape characteristics of the measured households in 1997 (Households 1997) compared to model scenarios. Landscape indices include the perimeter to area ratio (P/A Ratio), centroid connectivity index (Connectivity) and aggregation index (Aggregation).

	No. of Patches	Mean Patch Size (ha)	P/A Ratio	Connectivity	Aggregation
Households 1997	94.00	40931	1.49	0.046	0.423
All Parameters	110.35	59101	1.50	0.053	0.513
No Proximity Factor	261.00	24905	1.41	0.015	0.271
No Abiotic Factor	161.90	40229	1.46	0.034	0.426
No Cost Factor	280.60	23152	1.29	0.009	0.337

Table 4.2. Accuracy of the predicted household locations for the model scenarios relative to the measured households in 1997 (Households 1997). Accuracy as predicted household locations occurring at measured household locations (titled 0) and predicted locations within 1, 2, and 3 pixels (labeled 1, 2, and 3, respectively) of measured household locations. Uncertainties represent one standard error of the accuracies of the 20 simulations conducted for each scenario.

	Accuracy (%)			
	0	1	2	3
No Cost Factor	20.6 ± 1.3	47.3 ± 2.4	57.1 ± 2.6	63.0 ± 2.4
No Proximity Factor	21.2 ± 1.1	54.3 ± 1.7	70.6 ± 1.3	79.8 ± 1.4
No Abiotic Factor	22.4 ± 1.4	55.8 ± 2.4	71.8 ± 2.0	81.2 ± 2.3
All Parameters	27.4 ± 0.7	67.9 ± 1.5	82.5 ± 1.9	88.3 ± 1.9

Table 4.3. Comparison of the influence of variations in individual parameters for each multiplicative factor used within the fuelwood sub-model. Landscape characteristics of the model results are also given for various levels of initial volume per hectare for low-elevation forests.

	Parameter	Number of Patches	Mean Patch Size (ha)	P/A Ratio	Connectivity Index	Aggregation Index
Proximity Factor	0.33	125.2	75.8	1.668	0.719	0.858
	1	192.2	49.2	1.606	0.336	0.829
	3	291.5	32.7	1.538	0.170	0.794
Distance Factor	0.8	145.8	65.8	1.630	0.546	0.848
	1	192.2	49.2	1.606	0.336	0.829
	1.2	231.6	40.4	1.587	0.277	0.816
Initial Volume (m^3/ha)	30	211.4	51.9	1.567	0.365	0.830
	45	192.2	49.2	1.606	0.336	0.829
	60	258.7	33.6	1.540	0.212	0.812
	75	265.9	30.3	1.502	0.161	0.805
	90	246.3	30.5	1.502	0.167	0.802

Table 4.4. The influence of household characteristics on habitat over 65 years (1965 – 2030) relative to a baseline scenario of 0 new households per year and 0 m^3/yr of fuelwood consumed after 1997.

House Growth Rate (houses/yr)	Fuelwood Consumption (m^3/yr)	Total Habitat (%)	Habitat < 2600 m (%)
24	0	-0.06	-0.18
24	5	-1.34	-3.79
24	10	-2.61	-7.36
24	15	-3.32	-9.33
24	30	-6.06	-15.84
0	15	-2.77	-7.74
12	15	-3.21	-8.99
24	15	-3.32	-9.33
36	15	-4.31	-11.74
0	0	0.00	0.00
-12	15	0.01	0.03
-24	15	0.05	0.13
12	10	-2.26	-6.41
36	0	-0.11	-0.45

Table 4.5. The influences of household characteristics on habitat for models run from 1997 to 2030 based on digital classifications and measured household locations.

Parameter	Fuelwood (m^3/yr)	0	10	15	15
	Household (households/yr)	0	12	24	-24
Total Habitat (ha)	Marginal	7669. 9	7662.5	7657.1	7663.9
	Suitable	41863.2	40227.8	38881.8	40606.4
	Highly	9659.3	9199.1	8780.3	9309.9
	Total	59192.4	57089.4	55319.2	57580.2

Table 4.6. The influences of household characteristics on habitat below 2600 meters of elevation for model runs from 1997 to 2030 based on digital classifications and measured household locations.

Parameter	Fuelwood (m^3/yr)	0	10	15	15
	Households (households/yr)	0	12	24	-24
Habitat (ha)	Marginal	72.1	65.0	59.3	66.1
	Suitable	16523.2	14929.4	13636. 7	15296.3
	Highly	5391.4	4958.3	4580.2	5063.9
	Total	21986.6	19952.8	18276.1	20426.3

Table 4.7. The combined influences of bamboo die-offs and household impacts. *B. fangiana* die-offs are held constant at 2027 while *F. robusta* die-offs are varied between 2007 and 2027.

Parameter	Fuelwood (m^3/yr)	0	0	0	10	10	15	15	15	15
	Households (households/ yr)	0	0	0	12	12	24	24	-24	-24
	F. robusta (die-off year)	N/A	2007	2027	2007	2027	2007	2027	2007	2027
	B. fangiana (die-off year)	2027	2027	2027	2027	2027	2027	2027	2027	2027
Habitat (ha)	Marginal	3564.8	3299.6	3335.9	3322.9	3263.3	3346.3	3330.7	3310.0	3322.9
	Suitable	20502.7	10290.2	8864.6	9598.2	8639.1	9180.9	8190.7	9865.2	8722.1
	Highly	4981.5	2975.6	2669.8	2781.2	2576.4	2651.6	2444.3	2835.6	2573.9
	Total	29049.0	16565.5	14870.3	15702.3	14478.9	15178.8	13965.7	16010.8	14618.9

Table 4.8. The combined influences of bamboo die-offs and household impacts on habitat below 2600 meters of elevation. *B. fangiana* die-offs are held constant at 2027 while *F. robusta* die-offs are varied between 2007 and 2027.

Parameter	Fuelwood (m^3/yr)	0	0	0	10	10	15	15	15	15
	Households (households/ yr)	0	0	0	12	12	24	24	-24	-24
	F. robusta (die-off year)	N/A	2007	2027	2007	2027	2007	2027	2007	2027
	B. fangiana (die-off year)	2027	2027	2027	2027	2027	2027	2027	2027	2027
Habitat (ha)	Marginal	2.43	3.2	3.2	3.4	3.3	3.2	3.0	3.2	3.0
	Suitable	6960.3	5962.1	4662.8	5480.5	4379.7	5048.6	4072.8	5612.1	4459.1
	Highly	2587.9	2374.8	2087.5	2217.1	1964.3	2069.8	1847.3	2265.3	1996.8
	Total	9550.7	8340.2	6753.5	7701.1	6347.2	7121.5	5923.1	7880.6	6458.9

Table 4.9. The combined influences of bamboo die-offs and household impacts on habitat fragmentation.

Parameter	Fuelwood (m3/yr)	0	0	0	24	24
	Household (households/yr)	0	0	0	15	15
	F. robusta (die-off year)	N/A	2007	2027	2007	2027
	B. fangiana (die-off year)	N/A	2027	2027	2027	2027
Mean Patch Size (ha)	Marginal	2.85	2.47	2.49	2.48	2.47
	Suitable	4.16	1.96	1.80	1.89	1.73
	Highly	2.33	1.88	1.81	1.80	1.72
	All	6.88	3.06	2.86	2.93	2.71

Figure Legends. (Images in this dissertation are presented in color)

Figure 4.1. A conceptual depiction of previous bamboo dynamics effects on habitat (solid line) and the combined bamboo and land-use effects on habitat (dashed line) based on model predictions and projected continued effects.

Figure 4.2. Wolong Nature Reserve lies in the Qionglai Mountains between the Tibetan plateau and Sichuan basin.

Figure 4.3. A conceptual flow schematic diagram of the model.

Figure 4.4. Figure 4.4a shows the digital elevation model (DEM) and Figure 4.4b shows the distribution of forest types.

Figure 4.5. Examples of spatial data used for post-1997 simulations. Figure 4.5a is the digital classification of forest cover from 1997 Landsat TM data and Figure 4.5b shows the classification of presence/absence of bamboo throughout the reserve. Species delineation of bamboo is based on elevational differences and ground surveys.

Figure 4.6. Comparisons between visual classifications of satellite data from 1965, 1974, 1987, and 1997 and predicted forest cover due to household activities of corresponding years.

Figure 4.7. Comparisons of the influence of the three multiplicative factors contained within the household sub-model. Accuracy of each scenario is shown relative to the measured households with corresponding predicted households and measured households shown in black, incorrectly predicted households are shown in dark gray, actual households where no households were predicted are shown in white. Figure 4.7a shows the predicted household distribution in 1997 relative to the actual distribution. Figure 4.7b is without abiotic preferences, Figure 4.7c without cost factors, and Figure 4.7d without proximity influences.

Figure 4.8. Predicted forest cover due to fuelwood collection compared to the digital classification at various starting volumes for low-elevation forests. Figure 4.8a – e are with starting volumes of 30, 45, 60, 75, and 90 m^3/ha, respectively.

Figure 4.9. Impacts from household activities and bamboo dynamics. Figure 4.8a shows impacts from household growth of 24 houses per year and an annual fuelwood consumption of 15 m3/yr. Figure 4.8b shows the remaining habitat after a simultaneous die-off of *F. robusta* and *B. fangiana* while other bamboo species remain.

Figure 4.10. The impacts of household activities and bamboo die-offs to habitat below 2600 meters are shown. Figure 4.10a shows the impacts from households alone while Figure 4.10b includes loss of habitat from bamboo die-offs.

Figure 4.1

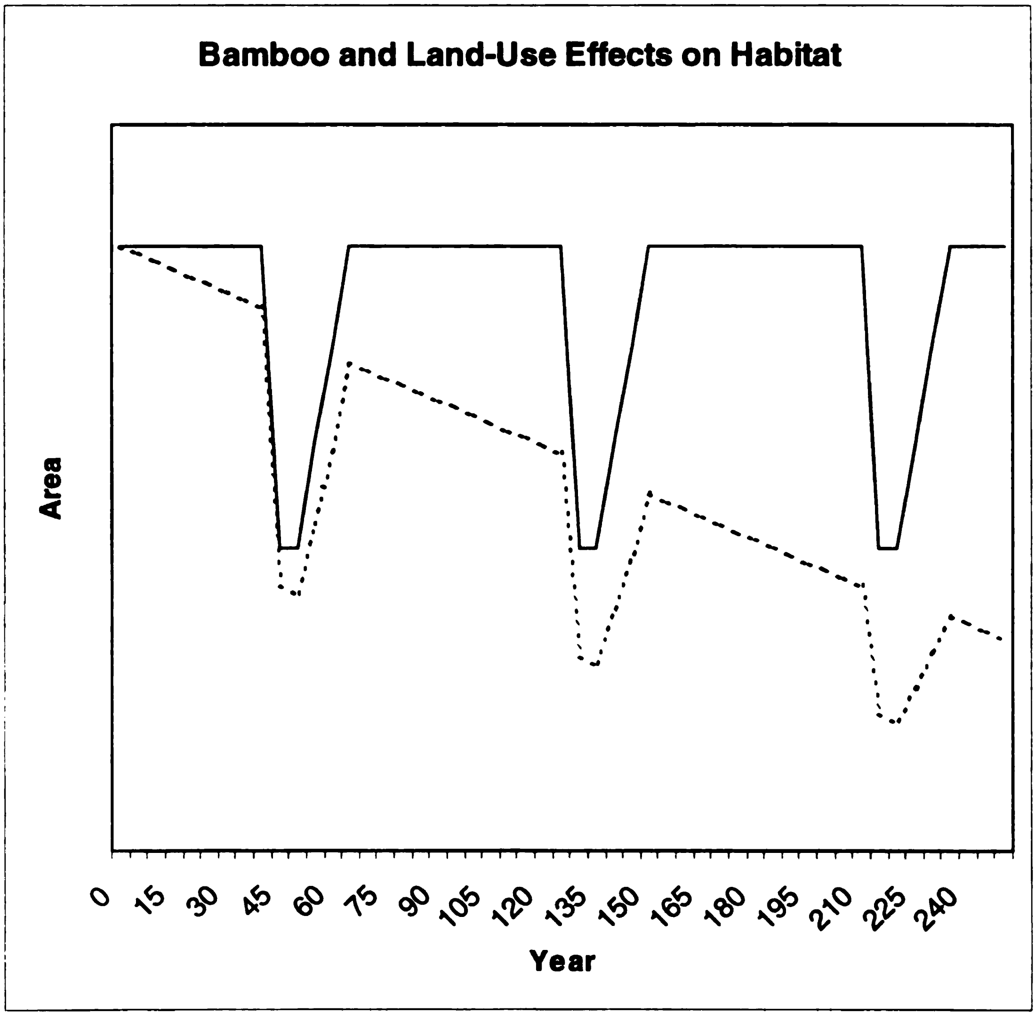

Bamboo and Land-Use Effects on Habitat
Area
0
15
30
45
60
75
90
105
120
135
150
165
180
195
210
225
240
Year

Figure 4.2

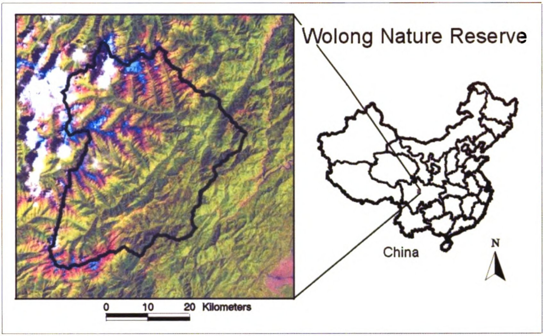


Figure 4.3

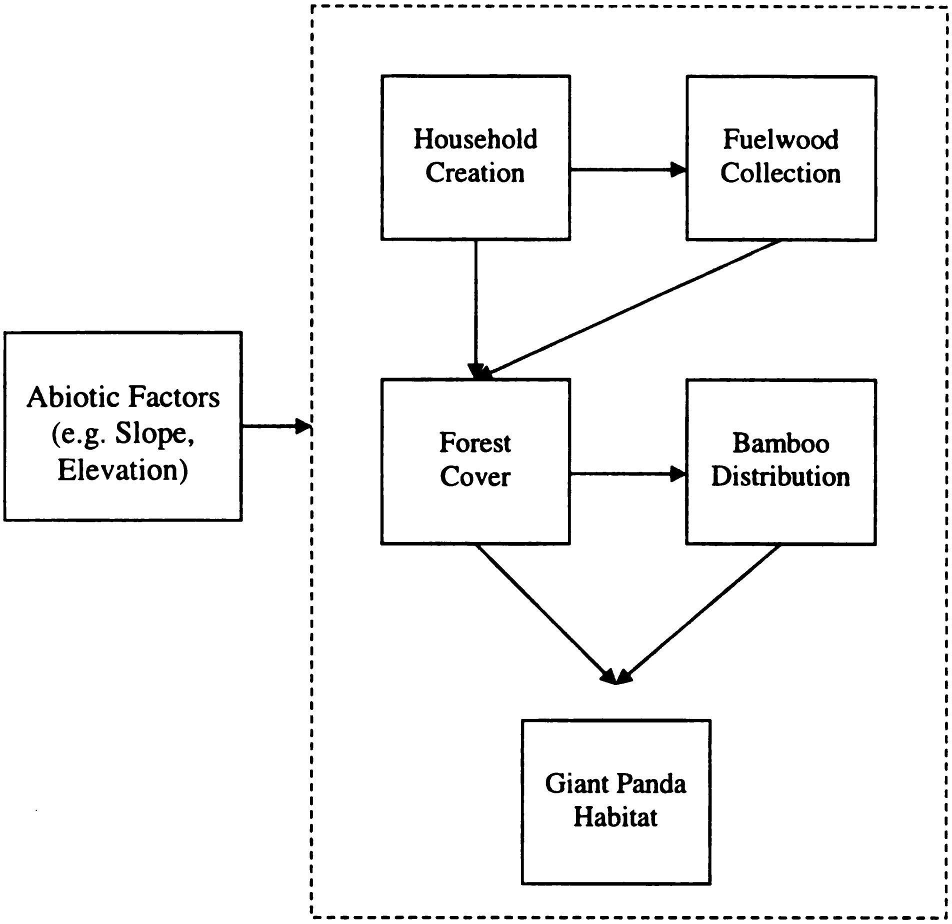

Household Creation
Fuelwood Collection
Abiotic Factors (e.g. Slope, Elevation)
Forest Cover
Bamboo Distribution
Giant Panda Habitat

Figure 4.4

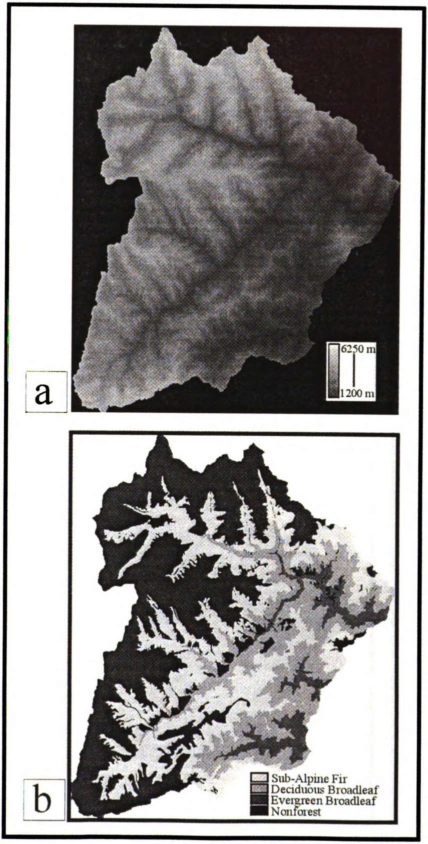

6250 m
1200 m
a
Sub-Alpine Fir
Deciduous Broadleaf
Evergreen Broadleaf
Nonforest
b

Figure 4.4

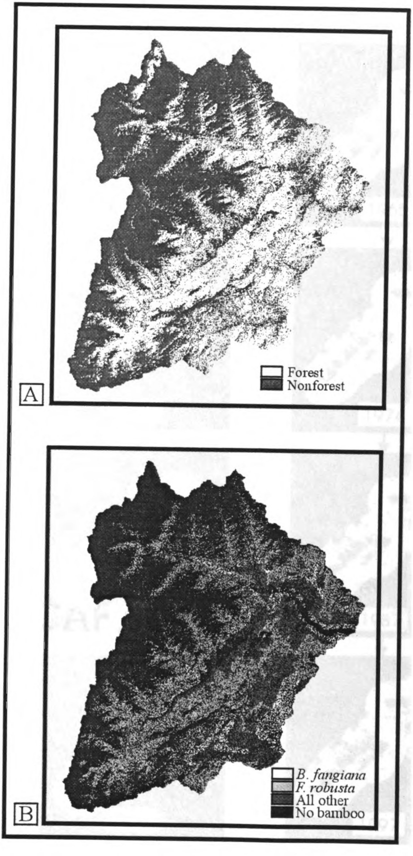
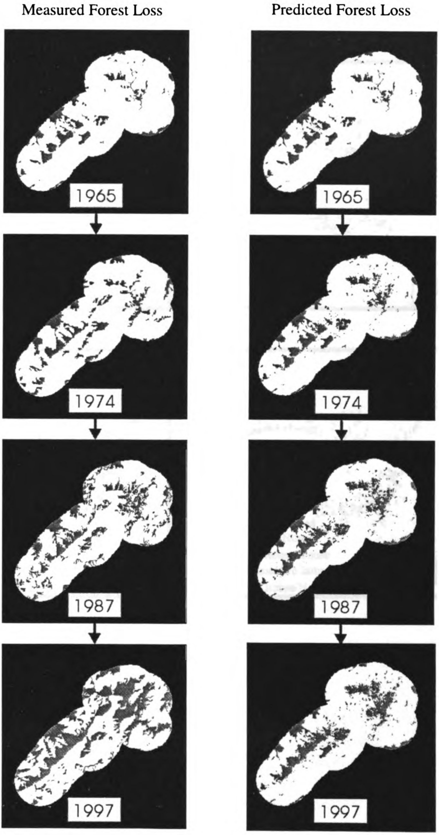

A
Forest
Nonforest
B
B. fangiana
F. robusta
All other
No bamboo

Figure 4.5



Measured Forest Loss

Predicted Forest Loss

Figure 4.6

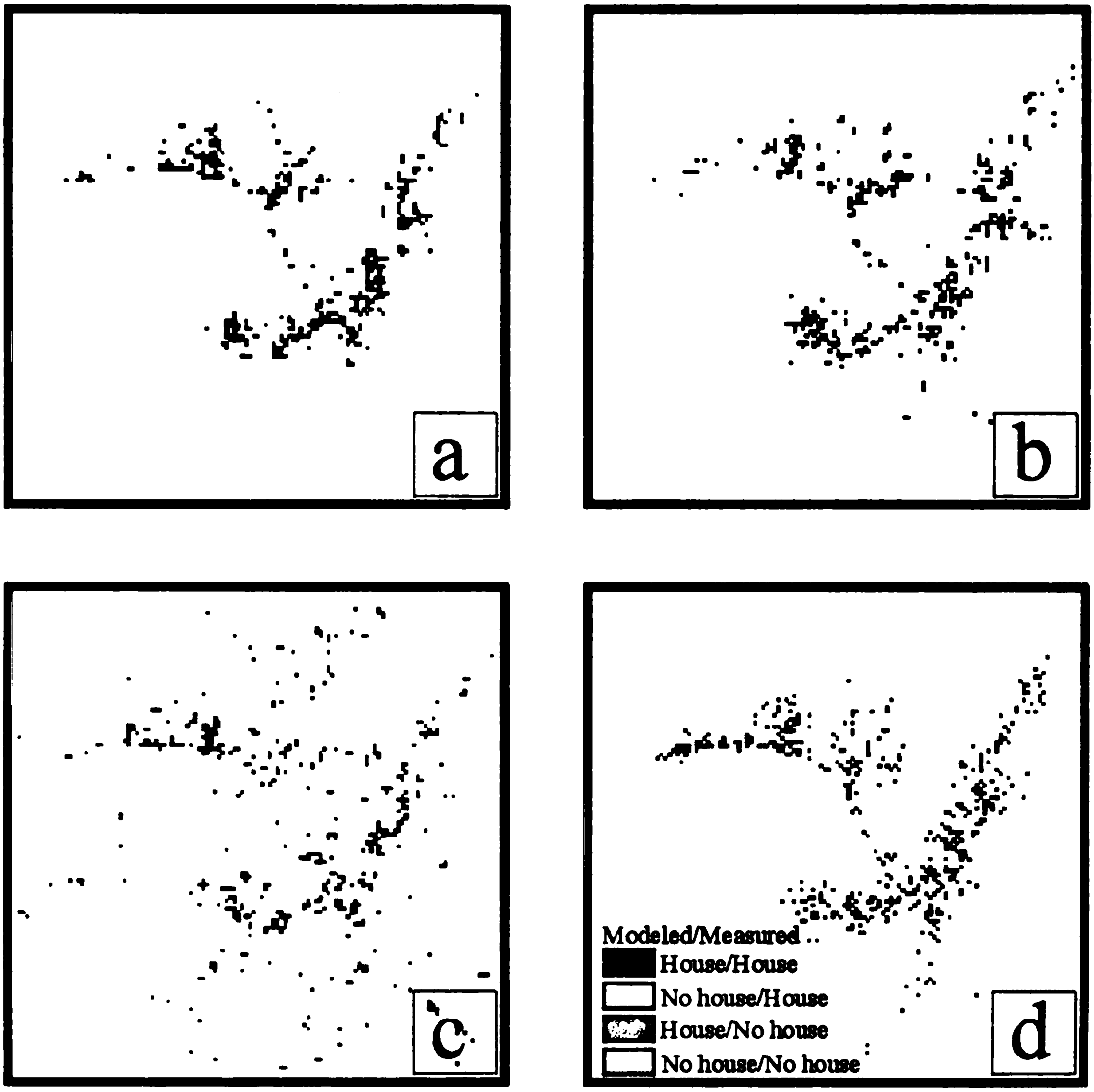

a
b
c
d
Modeled/Measured
House/House
No house/House
House/No house
No house/No house

Figure 4.8

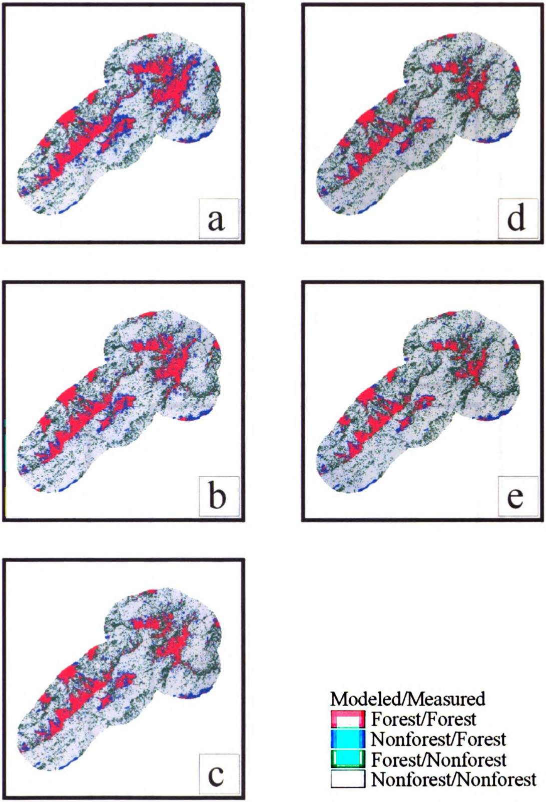

a
d
b
e
c
Modeled/Measured
Forest/Forest
Nonforest/Forest
Forest/Nonforest
Nonforest/Nonforest

Figure 4.9

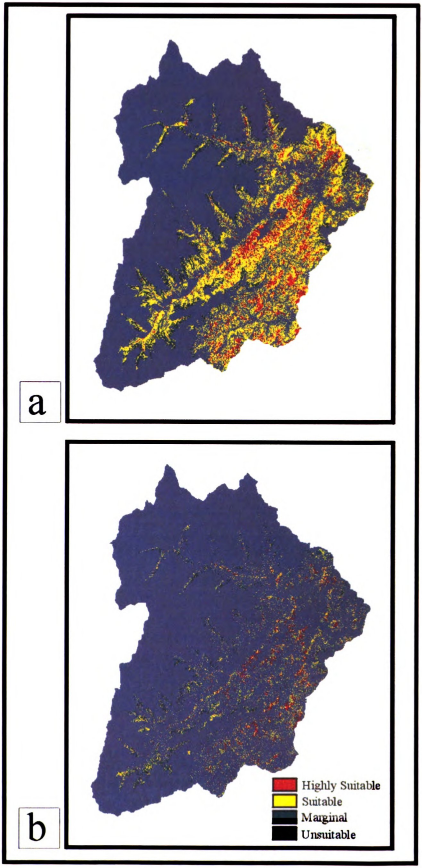
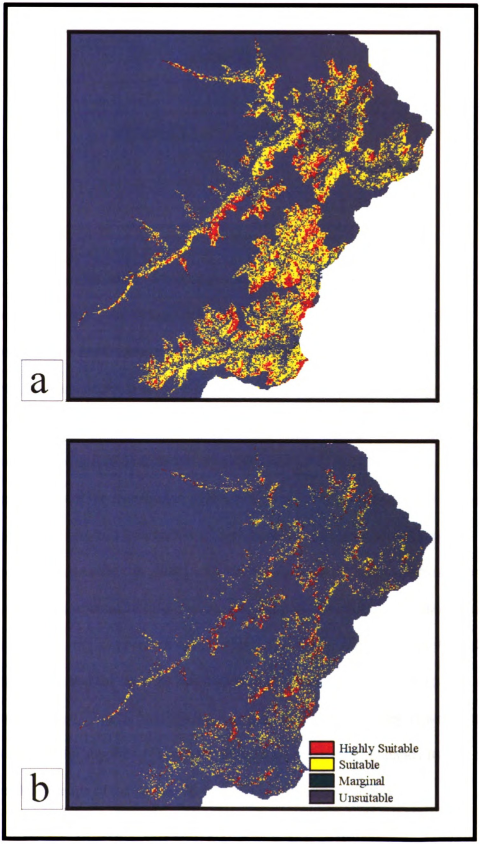


Figure 4.10



CHAPTER 5

SUMMARY AND CONCLUSIONS

5.1. Summary

Considerable research has been conducted on giant panda behavior and habitat requirements. As with all other species, however, viable conservation options will only come from detailed studies of habitat requirements, human impacts, and spatio-temporal dynamics of the environment at the time and spatial scales relevant to long-term conservation. For this dissertation, I examined three of these issues: the spatial distribution of the primary food source of pandas, bamboo, the implications of the distribution of bamboo on spatial characteristics of habitat at the landscape scale, and the combined impacts of human activities and bamboo spatiotemporal dynamics on giant panda habitat across a 200,000 ha nature reserve.

The lack of detailed information on the spatial distribution of bamboo has been a problem for panda conservation. Pandas rely on bamboo for over 99% of their diet, must feed for up to 14 hours a day, and require an average of 12.5 kg of bamboo each day. Pandas are therefore completely restricted to habitat with easy access to plentiful supplies of bamboo. Measuring and modeling panda habitat then requires knowledge of the spatial distribution of understory bamboo.

The results from the neural network classification are promising. We found the artificial neural network improved classification accuracy by 11 - 13% over maximum-likelihood classifications and resulted in a reserve-wide classification accuracy of 80%. It is difficult to assess the significance of the improvements in accuracy. The increases in accuracy may be in part to the improved classification performance of neural nets found in other classification studies. However, a 12% increase in accuracy of a binary classification is relatively large. In addition, we found evidence that the neural network classification was being influenced by understory vegetation. Co-occurring understory vegetation was strongly correlated with the misclassifications. False positives were almost always associated with the presence of other grass species. False negatives largely corresponded to significant mid-story cover. Further studies on this approach are needed. Studies on the influencing factors and the ability of the neural net to distinguish between variable vegetation conditions are needed. However, the study does point to a promising approach to understory vegetation detection from remote sensing data.

The detailed information gained from these analyses improved our ability to measure the distribution of panda habitat at a landscape scale. More accurate estimates of the quantity of habitat are now possible. In addition, more detailed assessments of the landscape characteristics of giant panda habitat in Wolong are available. Compared to previous estimates of total habitat available to pandas in Wolong, including bamboo in habitat estimates reduced the total available habitat by 29 – 56%, patch size by 16 – 48%, and carrying capacity by 41 – 60%. These results suggest that panda habitat has been overestimated. Not including bamboo into habitat analyses not only overestimates total habitat, but also underestimates fragmentation. Particularly notable is the increased isolation of larger patches. The isolation and fragmentation of habitat my lead to increased isolation of and decreased contact between groups of pandas in the reserve. However, more studies are needed on the movement patterns and dispersal abilities of pandas. Ideally, tracking devices capable of recording several positions each day to examine how pandas are interacting with the environment and long-term monitoring to examine range and dispersal tendencies of pandas are needed.

Finally, we combined predictions of the spatio-temporal dynamics of the measured distribution of bamboo with human impacts in the reserve. Commercial logging, household fuelwood collection, and agricultural activities have seriously degraded habitat throughout Wolong. Using socioeconomic characteristics of households and measured characteristics of the spatial distribution of household activities from 1965 – 1997, we were able to project future human impacts on forest cover through the year 2030. The immediate impacts from households are relatively limited compared to past commercial logging. However, when these impacts are coupled with the temporary loss of bamboo during times of die-off, the spatial distribution of household impacts may have considerable impact to panda populations.

Giant panda populations have been restricted to remnants of habitat from extensive past land-cover change and are now extremely sensitive to natural die-offs of bamboo. Continued human activities may have considerable impacts on giant panda populations in the near future. Using a spatio-temporal model of bamboo dynamics and human activities, we found that local fuelwood collection and agricultural activity will likely reduce critical habitat relied upon in past bamboo die-offs. According to the model, a simultaneous die-off of the two predominant bamboo species would result in up to 52% of the current area of habitat to be lost. Human impacts would likely only contribute up to an additional 16% loss of habitat. However, these impacts primarily occur in habitat relied upon by giant pandas during past bamboo die-offs. The spatial distribution, as well as the total quantity, of human impacts on giant panda habitat must be taken into consideration. Future policies need to take into consideration where households are being placed and fuelwood collection is taking place. A first step to protecting panda habitat would be to absolutely restrict new households in areas in these crucial areas, including secondary habitat needed by pandas in times of losses of bamboo. Second, priority should be placed on relocating current households in crucial habitat. Finally, fast growing forest plantations have been placed near households and there are areas in the reserve where pandas have been extirpated and which are unlikely to be used by pandas in the near future. Increased reliance on plantations and areas not important to pandas for fuelwood is critical to decrease pressure on panda habitat.

The coupled model of the spatiotemporal dynamics of bamboo and human activities showed that even limited impacts to critical habitat may have significant implications. Continued removal of forests considered less important as core habitat areas will seriously restrict current sub-populations of giant pandas within Wolong. The model predicts fuelwood collection alone will reduce access in many areas of prime panda habitat. Relatively large areas of low-elevation highly suitable and suitable habitat adjacent to prime habitat are predicted to be lost to household activities. Any additional impacts, as seen from 1975 to 1997, will likely considerably add to the impacts from households alone.

The model, however, also suggests other causes and driving factors leading to past habitat loss and future impacts. Past broad-scale logging likely provided conditions that exacerbated impacts from households by providing trees preferred for fuelwood collection. In addition, lower volumes resulting from logging activity led to larger areas required to meet household demands. Access also clearly plays a role in determining the spatial distribution of household activities. Households require access to roads to transport cash crops to local cities and the ease of access to preferred fuelwood also seemingly shapes fuelwood collection decisions. Finally, the model suggests that the average volume of fuelwood consumed by each household largely controls the quantity of future impacts. Providing viable energy alternatives to the local residents will likely considerably decrease impacts, particularly the fringe habitat adjacent to primary habitat.

Landscape models are useful in describing the basic driving factors of events occurring at the landscape level. Abiotic and biophysical variables can strongly control the location and distribution of human activities. However, examining the spatial distribution of human activities in conjunction with natural disturbances further highlights the relevance of these activities and potential influence on the biotic system and permit more accurate estimates of the overall habitat requirements for species persistence.

5.2 Conclusions

These studies point to the need for considerable information on environmental conditions relevant to a species for more accurate estimates of quantity, quality, and spatial arrangement of habitat. Combining these more detailed habitat assessments to dynamic models of human activities allow improved estimates of human impacts and potential consequences otherwise not available. From these studies, it is clear that more research is required on remote sensing techniques to gather relevant biophysical data and methods to incorporate these data into habitat analyses. Furthermore, studies on the coupled effects of continuing human appropriation of habitat and natural disturbance regimes would contribute to the current literature on the minimum area concept, landscape dynamics, population persistence, and the impacts socioeconomic activities on biodiversity.

Remote sensing has provided a wealth of information not available through traditional approaches. Remote sensing data have provided global land cover classifications, long-term monitoring of biophysical attributes, and even socioeconomic data. As sensors become more appropriate for measuring biophysical properties that are relevant to floral and faunal species, ecosystem processes, and human needs, more research is required on methods to extract these necessary data. For this study it was clear we need detailed information on the spatial distribution of understory bamboo, however, traditional techniques did not lend themselves to these analyses. The application of an artificial neural network provided increased classification accuracy and seemingly relied on understory vegetation. More intensive and controlled studies, however, are needed. Particularly, controlled field studies on understory contributions to the radiance measured by a distant sensor are needed. Also, field studies with well controlled overstory and understory conditions would contribute to this approach. In addition, this specific approach can be applied to the detection of other understory vegetation. The general approach, however, needs to be further developed in the application of remote sensing data to ecological studies. More accurate estimates on vegetation characteristics are needed for quantitative assessments of habitat.

More detailed biophysical data would allow more accurate assessments of habitat for particular species and biodiversity in general. Current estimates likely overestimate available habitat. Categorizing habitat based on basic land-cover information almost definitely overlooks necessary structural (cover, biomass, etc.) information, less dominant vegetation species, and sub-canopy species. These attributes have been shown repeatedly by local studies to significantly influence species presence and behavior. Certainly other variables may contribute to species distribution, persistence, or movement at broader scales (such as the landscape scale), however, ignoring these variables, as shown in this study, can result in serious misestimates of the quantity and spatial characteristics of habitat.

Viable management options will not be possible without accurate estimates of habitat. Knowledge of the spatial distribution of habitat is necessary to gauge and mitigate human impacts. For example, the spatial distribution of bamboo and location of human activities in Wolong have particular importance to pandas. More accurate assessments of habitat will have considerable implications for predicting panda population trends, particularly in light of metapopulation theory. It is now clear that there is far less habitat available to giant pandas than previously estimated. The fragmentation and isolation estimated in this study suggests pandas are likely more vulnerable than previously believed. In addition, more accurate estimates of habitat are needed to derive the full impact of human activities and viable mitigation options. We now see that the cumulative human effects to habitat in Wolong Nature Reserve may have considerable impacts on giant pandas. Management must take into consideration not only the total quantity of the impacts, but also the spatial distribution of the activities in developing viable policy alternatives. This study shows the need for more detailed landscape-scale habitat information to more accurately monitor habitat and biodiversity. In addition, these data would allow more accurate estimates of human impacts on species and more viable management alternatives.

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