INTERACTIVE EFFECTS OF NATURAL AND HUMAN DISTURBANCES ON VEGETATION DYNAMICS ACROSS LANDSCAPES

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Abstract. Accurate measures of human effects on landscape processes require consideration of both the direct impacts from human activities and the indirect consequences of the interactions between humans and the landscape. This is particularly evident in systems experiencing regular natural disturbances such as in the mountainous areas of southwestern China, where the remaining population of giant pandas (*Ailuropoda melanoleuca*) is supported. Here the spatiotemporal patterns of human impacts, forests, and bamboo episodic die-offs combine to determine the distribution of panda habitat. To study the complex interactions of humans and landscapes, we developed an integrated spatiotemporally explicit model of household activities, natural vegetation dynamics, and their impacts on panda habitat. Using this model we examined the direct consequences of local fuelwood collection and household creation on areas of critical giant panda habitat and the indirect impacts when coupled with vegetation dynamics. Through simulations, we found that over the next 30 years household impacts would result in the loss of up to 30% of the habitat relied on by pandas during past bamboo die-offs. The accumulation and spatial distribution of household impacts would also have a considerable indirect influence on the spatial distribution of understory bamboo. While human impacts influence both bamboo die-off and regeneration, over 19% of pre-existing low-elevation bamboo habitat may be lost following an episodic die-off depending on the severity of the impacts and timing of the die-offs. Our study showed not only the importance of the spatial distribution of direct household impacts on habitat, but also the far-reaching effects of the indirect interactions between humans and the landscapes they are modifying.

Key words: bamboo regeneration; Bashiana fangiana; Fargesia robusta; giant panda habitat; household impacts; human–landscape interactions; land-cover change; southwestern China; spatial modeling; vegetation dynamics.

INTRODUCTION

It is widely recognized that habitat loss is one of the leading causes of local and global species extirpation and 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 (Forman 1995). Many studies suggest that both the temporal variability of disturbances (Clark 1991) and the spatial distribution of disturbances (Moloney and Levin 1996) strongly influence community composition and landscape processes. However, few studies have examined both the direct and indirect effects of human activities on dynamic landscapes, partly because they are often complex and difficult to study (Wear et al. 1998, Hessel 2002).

One approach to studying the interactions between humans and landscapes is through the use of spatio-

temporally explicit models that simultaneously simulate human impacts and the natural dynamics inherent in the system. Spatially and temporally explicit models have become an increasingly useful and practical approach for studying landscapes over extensive time periods and provide convenient tools to examine complex systems and their interactions. Models have explored the implications of the spatial arrangement of natural (Turner et al. 1994, Franklin et al. 2001) and human (Liu 1993, Stéphenne and Lambin 2001) disturbances to landscapes. The direct consequences from human activities on habitat and landscapes are increasingly well recognized. However, the combined effects of natural and human disturbances on landscape dynamics have received less attention. These impacts may have considerable indirect influences when coupled with the dynamics of the landscape. Models that combine human activities and natural disturbances may provide better estimates of the total human impact on many species and useful insight into the potential long-term influence on landscape patterns and processes. As a case study, we developed a spatial model to examine the influence of household activities on giant panda habitat and under-

PLATE 1. (Left) A typical forest in the higher elevations (>2400 m) of the Niutoushan region of Wolong, China. *Bashania fangiana* bamboo (recently renamed *Bashania fabri*) occurs under a primarily fir (*Abies faxoniana*) overstory and a mixed fir and birch (*Betula utilis*) mid-story. This forest occurs over 3 km from the nearest house and roadway and was never harvested for fuelwood or timber. It therefore represents an unharvested, old-growth forest and is highly suitable giant panda habitat. Photo credit: S. Bearer. (Right) Over 4000 people making up over 1000 households reside within Wolong Nature Reserve. Here a typical household is shown with maize fields in the foreground. The majority of the local households are small farms around 1 ha in size utilizing fuelwood collected within the reserve for cooking and heating and are typically located in areas with suffient level ground to build structures close to sunlit slopes for agriculture and in close proximity to relatives. Photo credit: M. Linderman.

story bamboo regeneration over a time period that takes into account the natural variability of the bamboo species within a panda nature reserve in southwestern China.

Giant pandas have co-existed with bamboo, their primary food source, for thousands of years. 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). In the past, these mass die-off events were followed by a brief dormancy before the bamboo regenerated to pre-flowering biomass and distribution. Pandas have typically responded to die-off events by relying on the few remaining patches of bamboo or moving to other species of bamboo until the die-off species regenerated. However, household activities such as fuelwood collection are reducing the amount and increasing the fragmentation of remaining giant panda habitat (Liu et al. 2001) and potentially interfering with the regeneration of bamboo following episodic die-offs. As households are a basic socioeconomic consumption unit, the ecological effects of household activities need to be better understood as the number of households around the globe (including the areas with remaining panda habitat) rapidly increases (Liu et al. 2003).

The model developed for this study, HOusehold, Bamboo, Landscape Integration Model (HOBLIM), examined the spatiotemporal effects of household fuelwood collection and new household creation on forest cover and understory bamboo dynamics. The specific objectives of this study were to (1) develop a practical approach to integrating household activities and natural disturbances to understand landscape dynamics, (2) measure the quantity and spatial distribution of household impacts on giant panda habitat during times of bamboo die-offs, and (3) examine the indirect conse-

quences of household activities on bamboo regeneration. We believe this study provides a useful methodology for linking anthropological and natural disturbances and improving our understanding of the effects of human activities on ecosystems.

METHODS

Study area

Our field work was conducted in Wolong Nature Reserve (see Plate 1), which is located between 102°52′ and 103°24′ E and 30°45′ and 31°25′ N, covering ~200 000 ha (Fig. 1). It 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). Wolong also contains over 1000 households, mainly subsistence farmers, who rely on fuelwood from the reserve for heating and cooking. Over the past 30 years fuelwood collection and timber logging have resulted in a steady decline of forested area within the reserve (Liu et al. 2001).

Two bamboo species, *Bashania fangiana* and *Fargesia robusta*, make up ~80% of the total bamboo within the reserve. *B. fangiana* is the preferred food source for pandas in the reserve and *F. robusta* is utilized seasonally and during times of *B. fangiana* die-offs (Schaller et al. 1985). In 1983 a *B. fangiana* mast-seeding and corresponding mass die-off occurred throughout the reserve. Following the die-off, pandas in Wolong continued to utilize old stems and small patches of *B. fangiana* that did not flower, but were forced to migrate to lower elevations in the winter of 1986 to forage on *F. robusta* (Schaller 1987). Both *B. fangiana* and *F. robusta* are predicted to flower in Wolong in the next 30 years. *B. fangiana* has a well-established inter-mast period of 45 years. It is therefore estimated that another mast seeding of *B. fangiana* will occur between 2025 and 2030. The
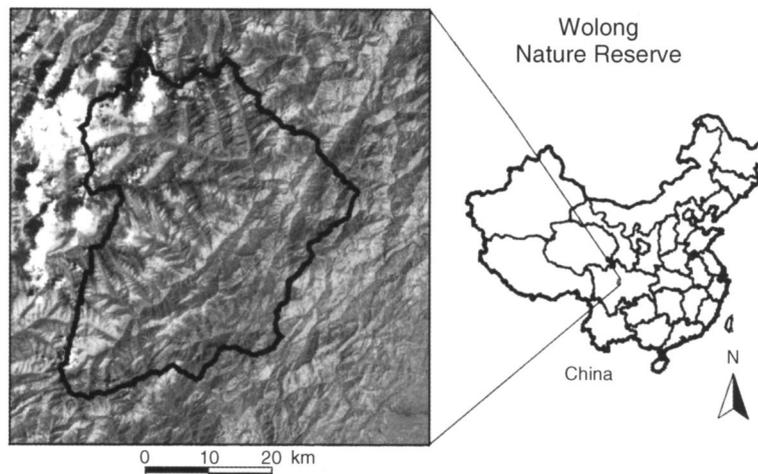
FIG. 1. Representative thermal regimes and their corresponding linear trends in warmed-water and ambient-water treatments that *Baetis bicaudatus* experienced throughout the course of the experiment. Data represent hourly measurements.

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 (Y. Tan and J. Yang, Wolong Administration, *personal communication*).

Model description

Behavioral studies have described panda habitat as a function of forest cover, slope, altitude, and bamboo (Schaller et al. 1985, Ouyang et al. 1996, Liu et al. 2001). The loss of forest cover, therefore, directly reduces potential habitat for giant pandas. The reduction of forest cover, particularly in those areas relied on by pandas during past die-offs, however, may have more significant impacts on panda populations than previously believed. The loss of forested areas may also indirectly reduce habitat as access to fragmented habitat is decreased. This is of particular importance during times of episodic bamboo die-offs. The availability of bamboo and the accessibility of alternative species of bamboo during times of mast-seeding events are essential for pandas. In addition, since environmental stress seemingly affects the tendency of understory bamboo to seed as well as regenerate associated with synchronized mass-seeding events (Taylor et al. 1991, Taylor and Qin 1993), household impacts to forests may have long-term consequences on the composition of these landscapes through changes in overstory conditions.

To study the direct and indirect human impacts, we examined the interactive effects of household activities and natural disturbances using a spatiotemporally explicit model to assess the simultaneous interactions among households, forests, and bamboo within Wolong Nature Reserve. 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

landscape processes. SELES provides the flexibility to incorporate various interacting systems as individual submodels using modeling aspects of Markov chains, cellular automata, percolation models, and others according to the process being modeled.

The model developed for this study, HOBLIM (Appendix), is based on a previous model, Household And Landscape Integration Model (HALIM). HALIM is a spatially explicit cellular model that examined the influence of abiotic factors on the spatial distribution of household activities (household creation and fuelwood collection) and household influences on the quantity and spatial distribution of forest cover and habitat over time (Linderman et al. 2005a). HALIM combined four submodels through their mutual interactions on a 90 × 90 m gridded landscape. The four submodels included: household creation (Appendix: Table A1), fuelwood collection (Appendix: Table A2), forest regrowth (Appendix: Table A3), and panda habitat suitability (Appendix: Table A4). The interactions between household activities and forest distribution and regrowth were combined to determine the impacts on habitat suitability for pandas. The initial distribution of the households, forest cover, and abiotic factors were based on household surveys conducted during 1998–2001, visually delineated forest cover information derived from satellite remote-sensing data spanning from 1965 to 1997, and topographic data.

Household characteristics (e.g., fuelwood consumption, agricultural area) and how the resulting activities related to the landscape (e.g., fuelwood collection, household creation) were derived from the household surveys. For example, the average household creation rate from 1965 to 1997 was 24 new households created per year and average fuelwood collection in 1997 was 15 m³/year (An et al. 2001). The forest characteristics such as species distribution, regrowth, and stand volume were developed from the literature (Yang and Li 1992,

Liu et al. 1999) and field measures (Liu et al. 1999). The household and forest dynamics were incorporated into the model by defining the probability of household activities such as fuelwood collection and household creation and biotic dynamics such as forest growth and regeneration for each cell in the grid (detailed information is provided in the Appendix). The grids were updated annually based on the cell probabilities with the number of event occurrences determined by the model characteristics (e.g., number of households, number of forested cells, etc.). Based on the HALIM model, we were able to predict household creation accurately 88% of the time within 270 m of measured households. In addition, household impacts on forest cover were robustly predicted relative to visual delineations of forest cover from 1974, 1987, and 1997 satellite imagery and digital classifications of forest cover as measured in 1997 (Linderman et al. 2005a).

As pandas prefer forested areas, moderate elevations and gently sloping areas, and require access to bamboo (Schaller et al. 1985), the landscape conditions such as the distribution of forest cover, slope, aspect, and elevation were combined as a multiplicative index to provide a dynamic analysis of habitat (Liu et al. 2001; see Appendix: Table A4). HALIM was therefore able to provide useful insights into many of the household and abiotic driving factors influencing the quantity and spatial distribution of giant panda habitat. However, HALIM was not able to consider the influence of the spatial distribution and periodic die-offs of understory bamboo on panda habitat.

Incorporating bamboo

In HOBLIM, we incorporated newly developed information on the spatial distribution of understory bamboo throughout the reserve and modeled the natural dynamics of bamboo die-offs and regeneration (see Appendix: Table A5). The distribution and dynamics were incorporated into the model as an additional grid and submodels. The spatial distribution of the presence or absence of bamboo in HOBLIM was derived from remote-sensing data and extensive ground surveys (Linderman et al. 2004). Species delineation was based on altitudinal range and field surveys (Schaller et al. 1985). Three classes of bamboo are included in the model: *Bashania fangiana*, *Fargesia robusta*, and all others (Fig. 2). The die-off dates for *B. fangiana* and *F. robusta* were included as scheduled occurrences. In addition, since approximate die-off dates of other species are unavailable and to provide a conservative estimate of habitat impacts from bamboo dynamics, we included the die-off dynamics for only the two main bamboo species in the model.

The growth functions and environmental influences on regrowth and die-off characteristics of the two main bamboo species were derived from the literature (Schaller et al. 1985, Taylor et al. 1991, Taylor and Qin 1993). As intervals between masting events are 45 to
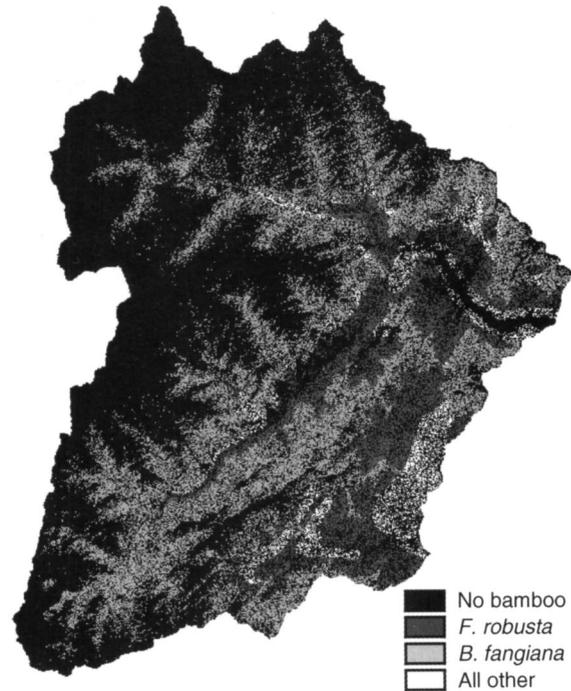
FIG. 2. The classification of presence/absence of bamboo (*F. robusta*, *B. fangiana*, other) throughout the Wolong Nature Reserve is based on extensive ground surveys and a neural network classification of Landsat TM data (Linderman et al. 2004). Species delineation is based on elevation.

70 years, the only known studies of the spatial and temporal characteristics are based on pre- and post-comparisons of the 1983 *B. fangaina* die-off and regeneration in conjunction with concurrent panda behavior studies (Schaller et al. 1985, Johnson et al. 1988, Reid et al. 1989, 1991, Taylor et al. 1991, Taylor and Qin 1993). Analyses of *B. fangiana* recovery showed that typical patches require 15–20 years to regenerate with an initial dormancy of 0–5 years (Taylor and Qin 1993). The model therefore uses a cumulative probability density function that leads to 100% regeneration after 20 years. In other words, all other factors being suitable, a cell previously containing bamboo will regenerate within 20 years. However, topography and household alterations to forest cover can reduce the probability of die-off and regeneration events from occurring.

Past studies noted that 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) less likely to flower (Taylor et al. 1991) or regenerate (Taylor and Qin 1993). While exact causes of synchronized flowering events are unknown, it was hypothesized that differences in understory microclimate conditions influenced a plant's propensity to flower during and regenerate following mass-flowering events. In this study we include these influences as changes to per pixel die-off and regeneration probabilities modified by the topogra-

phy and forest cover relative to previously observed die-off and regeneration percentages under various conditions. For example, previous studies have noted that bamboo in large clearings was one-third less likely to flower. Therefore, the probability of per-pixel die-off events in deforested pixels was one-third the probability of forested pixels, all other factors equal. Other changes to die-off and regeneration probabilities are given in the Appendix (Table A5).

In addition to bamboo, we also integrated the latest household and forest cover data into HOBLIM. First, instead of the visual classifications of forest cover used in HALIM, a supervised classification of the land cover derived from 1997 Landsat thematic mapper (TM) data was used to define the initial distribution of forest cover. This provided a more realistic distribution of forest cover and fragmentation, particularly at the household–forest interface. Second, household positions in 1998 determined from global positioning system (GPS) measurements and 1-m resolution Ikonos satellite data were used as the base distribution of households.

Model scenarios

To study the combined effects of human and natural disturbances on giant panda habitat in HOBLIM, we modeled household and bamboo spatiotemporal dynamics from 1997 through 2030. This time frame captured the predicted die-off periods of the two dominant bamboo species while maintaining confidence in the model parameterization. To examine the consequences of household and bamboo die-offs separately, we ran the model with and without bamboo. First, we measured household impacts by examining the effects of households on potential habitat not considering the distribution of bamboo throughout the reserve. Then we included bamboo in the model to compare the integrated effects of household and bamboo dynamics. We focused specific attention on low-elevation regions relied on by pandas during past bamboo die-offs. Finally, we examined household impacts on bamboo flowering and regeneration. All results shown are the average of 20 simulations per scenario.

Household impacts

To examine the influence of household activities on panda habitat, we measured changes in forest cover and potential panda habitat. These scenarios were based only on household spatiotemporal dynamics, forested area, and abiotic factors. We excluded the spatial and temporal dynamics of bamboo to highlight household effects on panda habitat. Several scenarios of household creation and fuelwood consumption were run. These scenarios included various combinations of household creation rates of 36, 24, 12, 0, and −24 households per year and fuelwood consumption levels of 30, 15, 10, and 0 m^3/yr. We used the scenario of 0 households per year and fuelwood consumption of 0 m^3/yr (i.e., no further household activity) as a baseline for comparison. The

various parameter values were chosen to reflect changes in the current averages and potential policy or socio-economic influences over the next 30 years (Linderman et al. 2005a).

Since low-elevation habitat has played an important role during previous B. fangiana die-offs and since most household impacts occur in lower elevations, we also conducted separate studies of the effects of household impacts on low-elevation habitat. These analyses examined the spatial arrangement of household activities with specific attention to known panda populations. In all the scenarios, we compared the amount of household impacts on potential habitat not including the spatial distribution of bamboo (forested habitat) and potential habitat containing bamboo. Relative comparisons were made based on differences in the quantity of giant panda habitat to baseline scenarios.

Household and bamboo impacts

To examine the combined influence of household impacts and bamboo die-offs on panda habitat, we ran the same scenarios as described above, with the addition of the spatial distribution and temporal dynamics of bamboo. For these simulations, we assumed that the next B. fangiana die-off would occur in 2027. However, since the timing of the next F. robusta die-off is less certain, we examined three die-off times for F. robusta, 2007, 2027, and a baseline scenario of no bamboo die-offs. An F. robusta die-off in 2007 is 20 years prior to the B. fangiana die-off and allows for the regeneration of F. robusta prior to the B. fangiana die-off. The 2027 die-off coincided with the B. fangiana die-off. These times allowed us to examine household impacts throughout the full range of bamboo availability. In addition, since F. robusta has played an important role during previous B. fangiana die-offs, we focused the last simulations on F. robusta. These simulations examined the spatiotemporal dynamics of F. robusta, human impacts, and the consequences for this critical panda habitat. We measured the effects in terms of the amount and quality of habitat available to pandas.

Household impacts on bamboo flowering and regeneration

Using HOBLIM we also examined the complex interactions between reductions in forest cover due to household impacts, bamboo die-offs, bamboo regeneration, and the potential impacts on the spatial distribution of forest cover during times of bamboo die-offs. Empirical studies indicated regions with less tree cover (and certain topographies) were less likely to flower (Taylor et al. 1991) or regenerate (Taylor and Qin 1993). These environmental stresses reduced the likelihood of flowering and reduced regeneration in previously flowered regions. The human impacts on bamboo flowering and regeneration are, therefore, indirect: logging and fuelwood collection change overstory cover thereby influencing flowering and regeneration of bamboo. Household influences on bamboo regeneration were
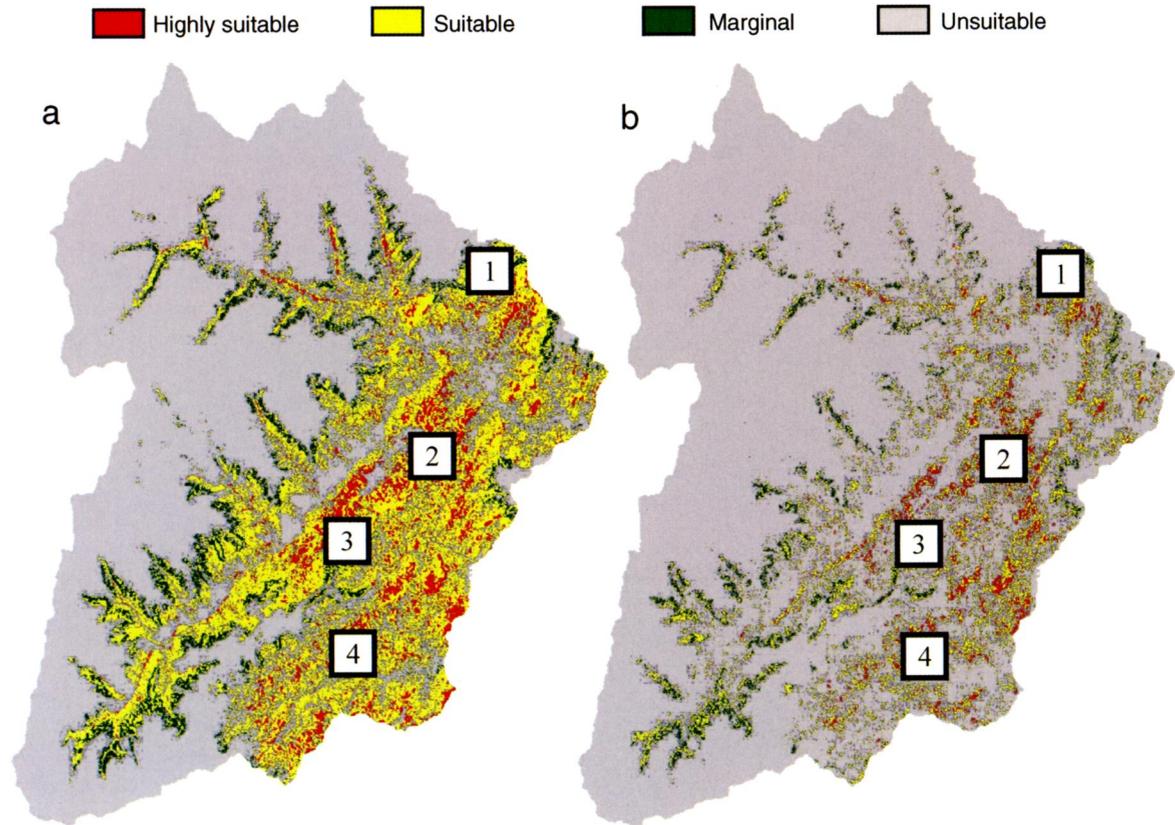
FIG. 3. Predicted spatial distribution of the remaining potential giant panda habitat, showing impacts from household activities and bamboo dynamics. The inset numbers give approximate locations of panda habitat areas: (1) Gengda, (2) Niutoushan, (3) Choushuigou, and (4) Xihe. (a) Impacts from household growth of 24 households per year and an annual fuelwood consumption of 15 m³/yr. (b) The remaining habitat after a simultaneous die-off of *F. robusta* and *B. fangiana* while other bamboo species remain.

examined relative to several bamboo die-off scenarios. Baseline scenarios were developed from model runs in which neither *B. fangiana* nor *F. robusta* experience a die-off. Household impacts on bamboo die-off and regeneration were examined based on *F. robusta* die-off times of 2007 and 2027. The range of die-off events allowed us to examine the influence of human activities on the die-off and regeneration of the *F. robusta* die-off event in more detail. Scenarios with a die-off event occurring in 2007 allowed for full regeneration of bamboo by the end of the study time, whereas only the influence on the extent of the die-off is seen in flowering events occurring in 2027 as no regeneration occurs before the end of the study period. Impacts were measured based on the difference in baseline scenarios and the area and spatial distribution of understory bamboo following various flowering episodes.

Sensitivity of flowering and regeneration rates

Limited information on the distribution of bamboo, household activities, and panda activities exists prior to the 1980s. When compared to satellite data and household surveys, HALIM was able to model household

activity fairly robustly. However, bamboo mass die-off events occur every 40–75 years. Comparable validation data of understory distribution and dynamics, therefore, are not available. Here we calculated the sensitivity of the literature-derived parameters relative to *F. robusta* die-off and regeneration rates to examine the confidence of the quantitative estimates and the importance of the qualitative relationships developed in the model.

RESULTS

Household influences on habitat not considering bamboo

The predicted spatial distribution of the remaining potential habitat not considering the spatial distribution of bamboo in 2030 is shown in Fig. 3a. Over the next 30 years, households are predicted to reduce the total amount of forested habitat in the reserve by 2.7–14% (Table 1). Even under very optimistic scenarios households are predicted to reduce the total amount of forested habitat by 2.7–3.5%. Continued fuelwood collection and household creation at past levels would reduce total potential forested habitat by up to 6.5% throughout the reserve from 1997 to 2030 compared to a complete cessation in household activities. Continued

TABLE 1. The projected influence of various levels of household fuelwood consumption and new household creation on forest-habitat quantity by the year 2030.

Fuelwood consumption (m³/yr)	Household creation (no./yr.)	Habitat (ha)			
		Marginally suitable	Suitable	Highly suitable	Total
0	0	7670	41 863	9659	59 192
15	−24	7664	40 606	9310	57 580
10	12	7662	40 228	9199	57 089
15	24	7657	38 882	8780	55 319
30	36	7635	35 749	7465	50 849

levels of household activities are also predicted to reduce high-quality forested habitat by up to 9% by 2030. Under the scenario of double fuelwood consumption and 50% increase in household creation, total forested habitat would be reduced by as much as 14% of the baseline figure and highly suitable habitat by up to 23% (Table 1).

Household and bamboo influences on habitat

The cumulative effects of household activities alone will have a tremendous impact on the total amount of habitat. However, household activities may also have more near-term consequences. The implications of household activities are more pronounced during times of bamboo die-offs. The combined losses of habitat from both household impacts and the temporary loss of bamboo during a simultaneous die-off are shown in Fig. 3b. The total area of habitat containing bamboo prior to a die-off would be ~29 000 ha (Table 2). A simultaneous die-off of both bamboo species (*B. fangiana* and *F. robusta*) would cause a loss of ~49% of habitat containing bamboo directly following the die-off and during the regeneration period. Staggering the die-off dates between *B. fangiana* and *F. robusta* by 20 years would yield ~12% less habitat loss at any one time, as some of the *F. robusta* die-off areas regenerate prior to the *B. fangiana* die-off (Table 2). These high rates of habitat loss from bamboo die-off events are not unexpected. The quantity and spatial distribution of the die-offs predicted here follow previously studied die-off occurrences. While these

extreme habitat losses do impact giant pandas, changes in habitat availability from bamboo dynamics have typically only been temporary until regeneration. However, the current level of additional habitat loss due to household activities is relatively new.

During times of bamboo die-offs, either simultaneous or staggered, households are appropriating portions of habitat in which bamboo would have still been available to pandas. In fact, even during optimistic scenarios—net emigration or marked reductions in fuelwood consumption and new households—household activities are projected to reduce the remaining habitat following a staggered or simultaneous die-off of bamboo by up to 5.2% of the remaining habitat (Table 2). However, under the scenario of doubled fuelwood consumption and 50% increase in household creation, the impacts are even more considerable. These levels of household activities would further reduce nearly 14% of habitat with bamboo and 25% of highly suitable habitat containing bamboo.

Household impacts on low-elevation forest habitat

The spatial distribution of household impacts may have additional implications for giant pandas. The spatial arrangement of the loss of forest cover is largely dictated by access and proximity to households. Therefore, the impacts occur largely in the valley bottoms and areas more easily accessed by households. As a result most losses take place in an area of less than 1/10th of the reserve, with >95% of the impacts occurring below 2600 m elevation (Fig. 4a). Even under reduced-

TABLE 2. The combined influences of bamboo die-offs and household impacts on habitat with bamboo by the year 2030.

Fuelwood consumption (m³/yr)	Household creation (no./yr)	Die-off year		Habitat (ha)			
		Fargesia robusta	*Bashania fangiana*	Marginally suitable	Suitable	Highly suitable	Total
0	0	n.a.	n.a.	3565	20 503	4982	29 049
0	0	2007	2027	3300	10 290	2976	16 565
0	0	2027	2027	3336	8865	2670	14 870
10	12	2007	2027	3323	9598	2781	15 702
10	12	2027	2027	3263	8639	2576	14 479
15	24	2007	2027	3346	9181	2652	15 179
15	24	2027	2027	3331	8191	2444	13 966
15	−24	2007	2027	3310	9865	2836	16 011
15	−24	2027	2027	3323	8722	2574	14 619

Note: n.a. = not applicable.
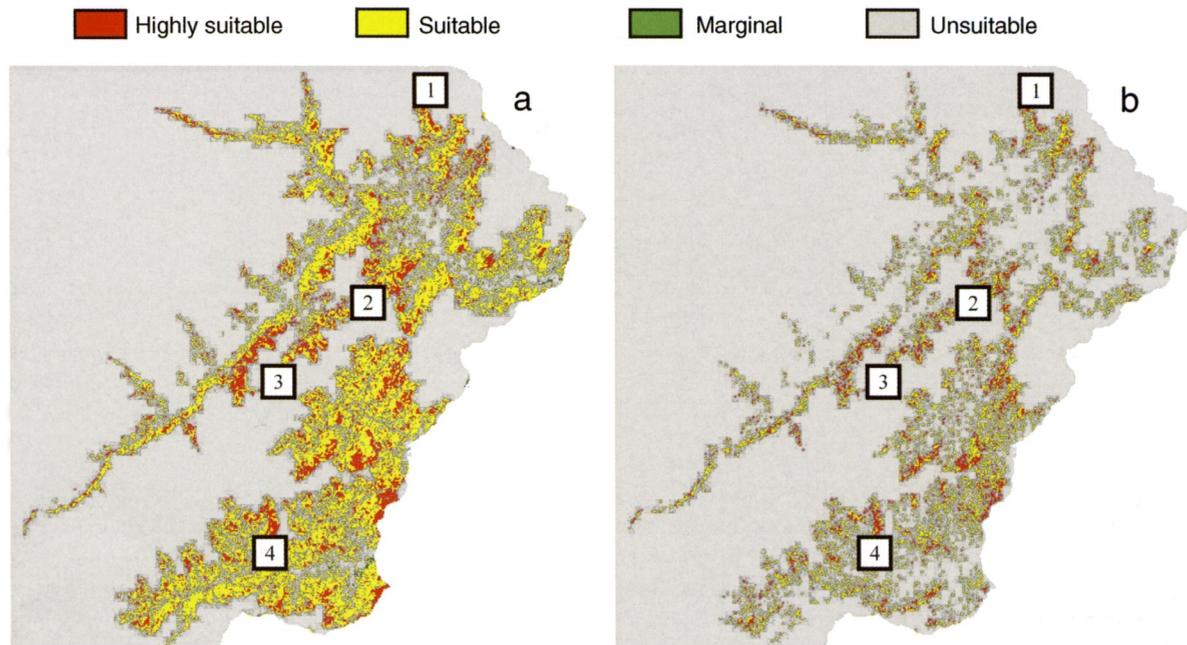
FIG. 4. Impacts of household activities and bamboo die-offs to habitat below 2600 m elevation. The inset numbers give approximate locations of panda habitat areas: (1) Gengda, (2) Niutoushan, (3) Choushuigou, and (4) Xihe. (a) Impacts from households alone; (b) impacts also include loss of habitat from bamboo die-offs.

consumption scenarios, 7–9% of habitat below 2600 m based on forest distribution and topography factors is projected to be affected (Table 3). However, if household construction and fuelwood consumption continue at 1997 levels, up to 17% of all low-elevation habitat and up to 15% of highly suitable habitat would be encroached upon by the year 2030. And under scenarios of double fuelwood consumption and a 50% increase in the number of new households, up to 30% of low-elevation habitat could be lost (Table 3).

Household and bamboo impacts on low-elevation habitat

The reduction of low-elevation forest habitat and access to these areas may have considerable impacts on giant pandas that relied on *F. robusta* during past *B. fangiana* die-offs. The combined loss of habitat based on forest cover, bamboo presence/absence, and topographic factors below 2600 m of elevation from household impacts and a simultaneous die-off of the two dominant bamboo species is shown in Fig. 4b. Bamboo

die-offs alone would generate a temporary loss of 13–29% of the total habitat below 2600 (Table 4). Household activities could have a considerable impact on the remaining area of habitat during and following bamboo die-offs. Depending on household creation and the timing of the die-offs, household activities would affect an additional 4–25% of the remaining habitat containing bamboo during times of bamboo die-offs (Table 4). Under a net-emigration scenario, household activities are predicted to contribute up to an additional 6% of habitat loss if the *F. robusta* die-off occurs 20 years prior to the *B. fangiana* die-off. If household creation and fuelwood consumption continue at current levels, up to an additional 15% of the remaining habitat containing *F. robusta* during a staggered bamboo die-off would not be available to pandas compared to the baseline scenario. Increased rates of fuelwood consumption (30 m^3/yr) and household creation (36 households/yr) would result in the loss of an additional 25% of the low-elevation habitat during a simultaneous bamboo die-off.

TABLE 3. The projected influence of various household characteristics on the quantity of forest habitat below 2600 m elevation by the year 2030.

Fuelwood consumption (m^3/yr)	Household creation (no./yr)	Habitat (ha)			
		Marginally suitable	Suitable	Highly suitable	Total
0	0	72	16 523	5391	21 987
15	−24	66	15 296	5064	20 426
10	12	65	14 929	4958	19 953
15	24	59	13 637	4580	18 276
30	36	42	11 478	3860	15 380

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TABLE 4. The combined influences of bamboo die-offs and household impacts on habitat with bamboo below 2600 m elevation by the year 2030.

Fuelwood consumption (m³/yr)	Houshold creation (no./yr)	Die-off year		Habitat (ha)			
		Fargesia robesta	*Bashania fangiana*	Marginally suitable	Suitable	Highly suitable	Total
0	0	n.a.	n.a.	2	6960	2588	9551
0	0	2007	2027	3	5962	2375	8340
0	0	2027	2027	3	4663	2088	6754
10	12	2007	2027	3	5480	2217	7701
10	12	2027	2027	3	4380	1964	6347
15	24	2007	2027	3	5049	2070	7122
15	24	2027	2027	3	4073	1847	5923
15	−24	2007	2027	3	5612	2265	7881
15	−24	2027	2027	3	4459	1997	6459

Note: n.a. = not applicable.

Household impacts on bamboo flowering and regeneration

As mentioned in the previous sections, households continue to exert considerable pressure on forest cover and, consequently, habitat throughout the reserve. Since the presence or absence of forest cover affects bamboo regeneration we also examined the effects of reductions in forest cover on bamboo regeneration. Here we focused specifically on those areas with *F. robusta* which were most significantly impacted by human activities and crucial to giant pandas. If no die-off events occur, total habitat containing *F. robusta* is 11 831 ha. The model predicts that if no additional household activities occur from 1997 through 2030 and a die-off of *F. robusta* occurs in the year 2007, only 9847 ha of the pre-existing *F. robusta* would regenerate. This suggests that *F. robusta* would regenerate to only about 83% of pre-flowering conditions, likely due to the cumulative >50 years of pre-1997 effects of broad-scale commercial and more limited household encroachment on forest cover since the last mast-seeding of *F. robusta*. Therefore, the integrated past reductions in forest cover may have a substantial effect on understory dynamics.

To measure the influences of future household activities, we examined bamboo regeneration and die-off under various household impact scenarios from 1997 through 2030. Fig. 5 shows the impact of human activities on the overall regeneration (top line) in bamboo following a 2007 die-off and only the impact on flowering (bottom line) after a 2027 die-off, for various household scenarios. The trend between impacts on total area and flowering area is reversed. An increasing quantity of *F. robusta* remains following a die-off event relative to rising intensities of household activities. So while increased human impacts decrease regeneration, it also decreases the amount of die-off. For example, there is 38% less *F. robusta* directly following a die-off in 2027 when no additional household impacts occur from 1997 through 2030. However, under intense household activity, there is only 32% less *F. robusta* directly following a die-off in 2027.

The decreased areas of bamboo undergoing a die-off from household impacts also diminish losses of bamboo under the 2007 die-off scenario. As increasing household impacts occur prior to the die-off in 2007, less bamboo may be flowering, resulting in decreased loss of area
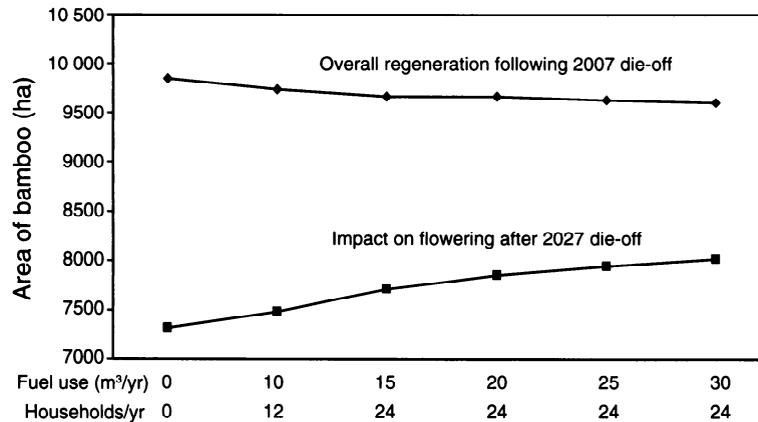
FIG. 5. The total area of *Fargesia robusta* understory bamboo by year 2030 after die-offs in years 2007 and 2027. The figure shows the effects of increasing human disturbance (based on fuelwood consumtion and household creation) on total bamboo regeneration (die-off in year 2007) and bamboo flowering (die-off in year 2027).

TABLE 5. Differences in area and the sensitivity index, SI, of the area of Fargesia robusta die-off and regeneration.

Regeneration parameter	Regeneration probability	2007 die-off		2027 die-off	
		Area (%)	SI	Area (%)	SI
Forest cover	0.5	0.2	0.00	−0.1	0.00
	1.5	−0.1	0.00	−0.1	0.00
Elevation	0.5	−11.2	0.22	3.7	0.07
	1.5	8.3	0.15	−3.7	0.07
Aspect/Slope	0.5	−1.8	0.03	6.3	0.12
	1.5	1.6	0.03	−6.0	0.12

Notes: Percentage area is given as the percentage of the difference in response when parameters are 0.5 and 1.5 times the normal value. Sensitivity is given as: $SI_x = (dY/Y)/(dX/X)$, where Y is the value of the independent variable and dY is the value of change in Y given a change, dX, in a given dependent variable, X (Jørgensen 1986).

under these conditions. However, as household impacts reduce the regeneration of any bamboo that does die-off, there is a net decrease in the overall regeneration of understory bamboo. Fig. 5 shows a consistent decline (top line) in the overall regeneration of bamboo as measured in 2030 following a 2007 die-off relative to increasing levels of household impacts. Current levels of fuelwood collection would result in 9% less *F. robusta* regeneration compared to baseline scenarios. Doubled fuelwood collection over a 30-year time period resulted in the regeneration of nearly 15% less *F. robusta* by 2030 compared to bamboo regeneration levels during circumstances involving no additional household activity after 1997. Household activities are therefore predicted to contribute to a 10–15% increase in lost bamboo area, and when added to previous forest losses, could result in the loss of >19% of low-elevation bamboo habitat following the next die-off.

Sensitivity of die-off and regeneration rates

To examine the influence of individual parameters on the results we measured the sensitivity of model response to changes in parameter values. In the given model, the *F. robusta* die-off and regeneration parameters seem relatively robust, particularly in terms of the quantitative results of the model. For example, a 50% increase in the regeneration probability relative to elevation resulted in 8.3% additional bamboo area (Table 5). Considerable differences in the *F. robusta* parameter values would, therefore, be required to match modeled decreases in habitat. However, the sensitivity of *F. robusta* die-off and regeneration rates varied depending on the parameter and timing of die-off events. Regeneration of *F. robusta* was more responsive to changes in the probability related to elevation while die-off rates after 30 years of human activity were more strongly dependent on forest-cover values. The differences in sensitivity between die-offs in 2007 and 2027 are expected. As human impacts co-opt marginal elevation areas, die-off is dependent on the combined influences of elevation and forest cover.

DISCUSSION

Quantifying the direct effects, let alone the indirect interactions, in a system such as the human-influenced panda bamboo habitat is difficult. Documentation of human activities such as logging and household fuelwood collection is limited. Satellite imagery has helped to provide more robust estimates (Liu et al. 2001, Linderman et al. 2005a). However, detailed analyses of understory bamboo and panda interactions with the landscape have only been conducted since the 1980s. In addition, the primary bamboo species are characterized by 40–75 year intervals between die-off episodes. Information on the nature of the bamboo dynamics, particularly for *F. robusta*, and validation data are, therefore, limited. Modeling is one of the few means to examine these household landscape interactions. The results of this study provide insight into the potential effects of the interactions between households and the landscape and aspects of the system that need to be examined more closely. Furthermore, these analyses may provide relevant information for preventive management of the panda reserve over the next 20 years.

Using HOBLIM we were able to examine household impacts on forests and their implications for giant panda habitat in light of episodic die-offs of bamboo. Households are predicted to reduce the total remaining low-elevation forest habitat by 8–30% over a period of 30 years. Continued household impacts of this degree are likely not sustainable. However, these numbers may even be underestimates of the overall impacts on the panda habitat when the natural variability of understory bamboo is taken into consideration. During times of simultaneous die-offs of the two main bamboo species in the reserve, nearly half of the potential habitat would be temporarily lost. Pandas have typically been able to respond to these events by relying on the remaining bamboo or moving to adjacent bamboo species. However, human impacts and the loss of forest cover increases habitat fragmentation and may restrict pandas from previously important alternative habitat, and impact the die-off and regeneration dynamics of bamboo.

The continued removal of low-elevation forests typically considered less important than core habitat areas may seriously restrict current subpopulations of giant pandas within Wolong Nature Reserve (southwestern China) from necessary *F. robusta* habitat when the next *B. fangiana* die-off occurs. The present quantity and distribution of habitat, while seemingly more than sufficient for the current population of pandas during time of high availability of bamboo, may be limiting to local populations of pandas during die-off events. Of particular concern are the sub-populations in proximity to the larger communities such as Gengda and Nuitoushan (Figs. 3 and 4). It is clear that household activities are reducing potential habitat in these areas. While it is difficult to estimate the exact influence these changes will have on panda populations, previous studies suggest

Human effects on bamboo regeneration
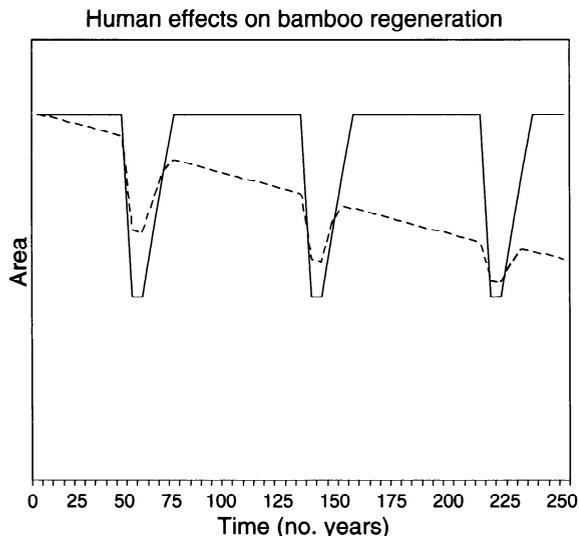
Fig. 6. A conceptual depiction of bamboo-dynamics effects on habitat (solid line) and the combined bamboo and land-use effects on habitat (dashed line), based on model predictions and projected continued effects on bamboo regeneration.

that the combination of the spatial distributions of bamboo and forest cover determine panda habitat suitability (Linderman et al. 2005b). Even the conservative projections provided here suggest that the combined habitat impacts of household activities and a simultaneous die-off of the two bamboo species may cause large reductions in habitat and reduce connectivity between viable habitat areas.

Loss of habitat during a bamboo die-off predominantly affects core bamboo areas with larger patches of habitat remaining in areas of extreme elevation ranges of the bamboo species and other more stressful areas. Without human interference, these areas would provide critical resources for pandas during simultaneous die-offs, i.e., habitat areas adjacent to core habitat that pandas could access in times of B. fangiana shortages. However, it is precisely these areas that household creation is affecting. High-elevation patches of F. robusta that may have remained intact during a die-off are being co-opted by household activities. Given the sensitivity of bamboo die-off and regeneration relative to elevation, it is clear more effort needs to be placed on analyzing the impact of elevational stress and household impacts on bamboo dynamics in these areas.

Furthermore, this study suggests that household and logging activities throughout Wolong Nature Reserve may be underestimated in regards to their effects on understory bamboo and giant panda habitat. The estimated impacts of forest removal on panda habitat and insights into the influence on bamboo cycles, however, are only apparent when considering time periods coinciding with the full range of the inherent natural variability of the landscape. While reduction in

forest cover is generally perceived as reversible, this study suggests that greater, more far-reaching impacts are occurring. Clear trends in the impacts on die-off and regeneration were found. Increased impacts will result in less area of F. robusta following a 2007 die-off. In the next 30 years, households alone may contribute to an additional 10–15% low-elevation bamboo not regenerating. Conversely, increasing levels of impacts reduce the total amount of F. robusta undergoing a mass die-off. While this decreased die-off probability does seem to temper loss of bamboo in higher impact scenarios of a 2007 die-off, forest loss also reduces habitat availability and the remaining bamboo is typically less palatable to pandas and may decrease eventual overstory regeneration.

Continued timber logging and fuelwood collection will likely cause irreparable damage to this landscape. The loss of forest cover prior to and during times of bamboo die-offs will in all probability lead to the continued attrition of bamboo in the reserve (Fig. 6). Where bamboo once maintained a natural cycle of die-off and full regeneration, households are apparently decreasing the regeneration of bamboo. This has significant implications for several other faunal species (e.g., red pandas) that rely on bamboo. In addition, changes in the distribution of bamboo in the understory may influence the current floral species' composition and distribution. Overstory has a clear influence on understory dynamics and composition. However, alterations in the understory also influence overstory regeneration. Therefore, the deforestation that has occurred and is continuing to occur, while seemingly only impacting a fraction of the reserve at any one time, may be altering the overall species composition, natural vegetation dynamics, and wildlife habitat.

Human impacts are not localized to one reserve in China or China itself. Habitat and species distributions are clearly being affected by household activities in many other parts of the world (Liu et al. 2003). Not considering the spatiotemporal distribution of the impacts is likely resulting in underestimation of the total, direct and indirect, impacts from human activities. Furthermore, given the dynamics and interdependence of human impacts, vegetation, and wildlife, even relatively small land-cover alterations may have considerable impacts on the health and maintenance of ecosystems. Models integrating households and vegetation dynamics provide a useful means to better measure and understand the interactions between the coupled human and natural systems.

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APPENDIX

A diagram of the HOBLIM model, with tables describing the HALIM submodels and a table showing the proposed probabilities of bamboo die-off and regeneration in relation to biotic and abiotic factors (*Ecological Archives* A016-021-A1).