

The impact of giant panda foraging on bamboo dynamics in an isolated environment

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Abstract Wildlife species are threatened by massive habitat destruction worldwide. Habitat fragmentation and isolation spatially constrain animals and in turn cause non-sustainable rates of animal foraging on plant populations. However, little empirical research has been done in large controlled settings to investigate foraging impacts. We conducted an experiment to characterize the impact of panda foraging on the sustainability of its food resource, bamboo, in an enclosed area of natural habitat (approximately 19 ha). We monitored bamboo density, age, and percent cover

throughout the enclosure across a 3-year period. We documented marked declines in bamboo density and percent cover as a result of panda foraging, particularly in younger bamboo age classes. We constructed simultaneous autoregressive models to explain bamboo loss to panda foraging and subsequent bamboo recovery as a function of habitat conditions. Areas with high initial bamboo cover not only were prone to high rates of bamboo percent cover loss but also experienced high rates of subsequent bamboo recovery, as bamboo cover loss opened up the understory for new growth. Variograms of ordinary least squares model residuals revealed that the range of spatial autocorrelation in bamboo loss increased over time as available bamboo forage declined. The results have implications for understanding the impact of animal foraging on vegetation and also highlight the importance of preventing further habitat fragmentation and isolation.

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Introduction

Over the course of the last century, threats to biodiversity have been increasing worldwide due to human impacts on ecosystems (Liu et al. 2003b; Pimm et al. 1995). In the animal kingdom alone, nearly 18% of mammals, 11% of birds, and 5% of fish

are threatened with extinction (Pimm et al. 1995). One of the main threats to the survival of animal species is habitat destruction (e.g., loss, fragmentation, and isolation), which causes animals to experience food shortages and congregate in remnant islands of high-quality resources (Morrison et al. 2006). Spatially constrained resource use by large herbivores in areas too small to support them may threaten sustainability of plant populations (Augustine and McNaughton 1998) and in turn, the animal populations that rely on them (Côté et al. 2004).

Large herbivores impact plant communities in various ways (Rooney and Waller 2003). Animal foraging can alter the abundance and diversity of plant species (Martin et al. 2010), change canopy structure (Ammer 1996), impact plant succession (Côté et al. 2004), and affect plant regeneration (Rooney and Waller 2003). However, questions remain about the magnitude and spatial pattern of responses of plant populations to such effects, as there are rarely opportunities to conduct experiments to isolate concentrated foraging impacts, particularly with endangered species.

The endangered giant panda (*Ailuropoda melanoleuca*) is an herbivore that has experienced severe habitat isolation and fragmentation. The 1,600 wild pandas that remain (State Forestry Administration 2006) inhabit an area of just over 21,000 km² in southwestern China (Hu and Wei 2004), fragmented into over 20 isolated areas (Loucks et al. 2001). Expansion of human population, households, and associated human activities, such as farming, road construction, and timber harvesting are among the primary causes (Liu et al. 2003a, 1999).

A critical factor for giant panda survival in the face of these threats is their bamboo food resource. Pandas are known for having enormous food requirements. Because of their carnivore-adapted digestive systems, pandas digest less than 20% of what they consume and eat up to 38 kg of bamboo daily (Schaller et al. 1985). As a result, pandas are particular about the species, age, and part of the bamboo plants they consume based on seasonal variation in nutritive qualities (Schaller et al. 1985).

Wild pandas inhabiting large, contiguous patches of habitat only use 10% of their 4–6 km² home range in any given month, which may relieve foraging pressure on the bamboo population in any one area (Schaller et al. 1985). However, foraging

impacts in low elevation, increasingly fragmented areas of habitat, where there may be higher foraging pressure, have not been studied. In addition, since wild pandas are elusive and difficult to track, researchers have been unable to follow individual pandas for extended periods in order to isolate foraging impacts.

A novel opportunity arose to study panda–bamboo interactions in a controlled setting after an enclosure was constructed in an area of panda habitat in Wolong Nature Reserve, China. The 19-ha enclosure housed a once-captive panda prior to its reintroduction to the wild. Because the panda is an endangered species undergoing experimental ex situ management in this study, we were not afforded the luxury of animal replicates. Nevertheless, we were compelled to conduct this study because it has important implications for management planning, considering that it could demonstrate how bamboo might respond if pandas are forced to concentrate in fragmented patches of habitat.

When exploring bamboo dynamics, it is important to identify factors that make an area susceptible to bamboo loss via panda foraging. Areas with high bamboo densities (Liu et al. 2005; Reid and Hu 1991) and high bamboo biomass (Yu et al. 2003) are preferred foraging areas. The relationship between trees, bamboo, and panda use is complex and context-dependent (Reid and Hu 1991; Taylor et al. 2004). Trees not only compete with bamboo for resources (Taylor et al. 2004), but also encourage bamboo growth (Taylor and Qin 1997). Nonetheless, pandas prefer foraging in areas with adequate tree cover (Schaller et al. 1985), in addition to areas with gentler slopes that are closer to water (Reid and Hu 1991; Zhang et al. 2006).

However, there has been little appreciation in the literature for spatial patterns of panda foraging and what they mean for bamboo loss and recovery. One useful characteristic for understanding patterns of panda–bamboo interactions is spatial autocorrelation. Habitat use patterns are often positively spatially autocorrelated, since animals concentrate in localized areas more similar to one another than areas farther apart (Lichstein et al. 2002). This pattern can arise from animals responding to an underlying clustered habitat structure (Meisel and Turner 1998), as a result of social organization patterns (Stamps 1998; Valcu and Kempenaers 2010), or in this case, due to a

constraint on the animal's movement (Abrahams 1986). Within the context of multivariate analysis, spatial autocorrelation is defined as a lack of independence of errors in model data due to a relationship between errors and the distance between sites (Legendre et al. 2002).

The goal of our study was to characterize the impact of giant panda foraging on bamboo in a controlled setting over a multi-year period. We examined bamboo loss due to panda foraging during the 18 months of panda occupancy in the enclosure and bamboo recovery during the subsequent two bamboo growing seasons. We characterized the following attributes of both bamboo loss and recovery: (a) magnitude, (b) underlying habitat characteristics, and (c) spatial pattern. We characterized the last two attributes using spatial simultaneous autoregressive (SAR) models that examined bamboo loss and recovery as a function of habitat variables believed to be predictors of panda use. These models accounted for spatial autocorrelation, which was characterized using variograms depicting the variability of bamboo loss and recovery across space. The results will contribute to understanding the relationship between pandas and bamboo with potential implications for conservation of increasingly isolated habitat in the face of the panda's large food demands.

Methods

Data collection

The enclosure (19.019 ha) was located in Wolong Nature Reserve, Wenchuan County, Sichuan, China ($31^{\circ}04'30''\text{N}$, $103^{\circ}13'41''\text{E}$), where there is a mean annual precipitation of 888.0 mm and a mean annual temperature of 8.9°C (Fu et al. 2004). There were three constructed water pools in the enclosure (2-m wide) and three perennial streams (40–90-m long). The enclosure was situated at 2,150–2,300-m elevation on a west-facing slope (20° – 30°) in a mixed coniferous and deciduous broad-leaved forest (Fig. 1). Dominant deciduous species included the Chinese walnut (*Juglans cathayensis*), huaxi wingnut (*Pterocarya insignis*), and mono maple (*Acer mono*), while the coniferous tree community was comprised mainly of hemlock (*Tsuga* sp.) and spruce (*Picea* sp., Zhou et al. 2004).

The forest understory consisted mainly of umbrella bamboo (*Fargesia robusta*), which covers 40% of the understory at altitudes of 2,000–2,600 m throughout the reserve (Taylor and Qin 1993b). This species produces shoots via pachymorph rhizomes each May, which grow to a full height of 2.5–3 m by mid-June (Taylor and Qin 1993b). Shoots produce leaved first-order branches in the first growing season and leaved second-order branches in subsequent growing seasons (Taylor and Qin 1993b). The only other bamboo species present was *Yushania brevipaniculata*, which we excluded from the analysis because it covered less than 1% of the enclosure.

The enclosure was mapped using a Pathfinder® Pro XRS GPS unit (Trimble Navigation Ltd., Sunnyvale, CA, USA) equipped with OmniSTAR differential GPS (OmniSTAR USA Inc., Houston, TX, USA). All sampling took place during a roughly 2-week period each July in 2005, 2006, and 2007. We established transects ($n = 19$) running south to north every 30 m throughout the enclosure. We set up contiguous 10×10 m sampling plots along each transect ($n = 537$). We placed a marker at each center point, where we measured slope and aspect. Diameter at breast height (DBH) was measured for all trees with DBH > 5 cm. Woody vegetation was classified into the shrub (<5 m), midstory (5–14 m), or overstory (≥ 15 m) height class. We counted the plants in each layer in each plot. Percent canopy cover was visually estimated for bamboo, shrubs, and midstory and overstory trees. Distance (m) to the nearest water source was computed for each plot using the Nearest Features extension (Jenness 2004) for ArcView GIS (Environmental Systems Research Institute 2001).

The 2-year-old male panda, Xiang Xiang (studbook #531), weighed 62.2 kg at the start and 68.2 kg at the end of the study. The panda was previously housed in captivity at the CCRCGP, and subsisted on a diet of bamboo, bamboo cakes, milk, and fruits and vegetables. The panda was moved to a small reintroduction enclosure (2.7 ha) in the summer of 2003 and stayed for a little over a year. During the course of this study, the panda only received supplemental feeding during procedures such as weighing (about once per month).

The panda was placed in the current study's enclosure in late September 2004 and stayed until late April 2006. The 2005 July sampling period thus measured panda foraging in the first 9 months (late September 2004–late June 2005) and the 2006 July

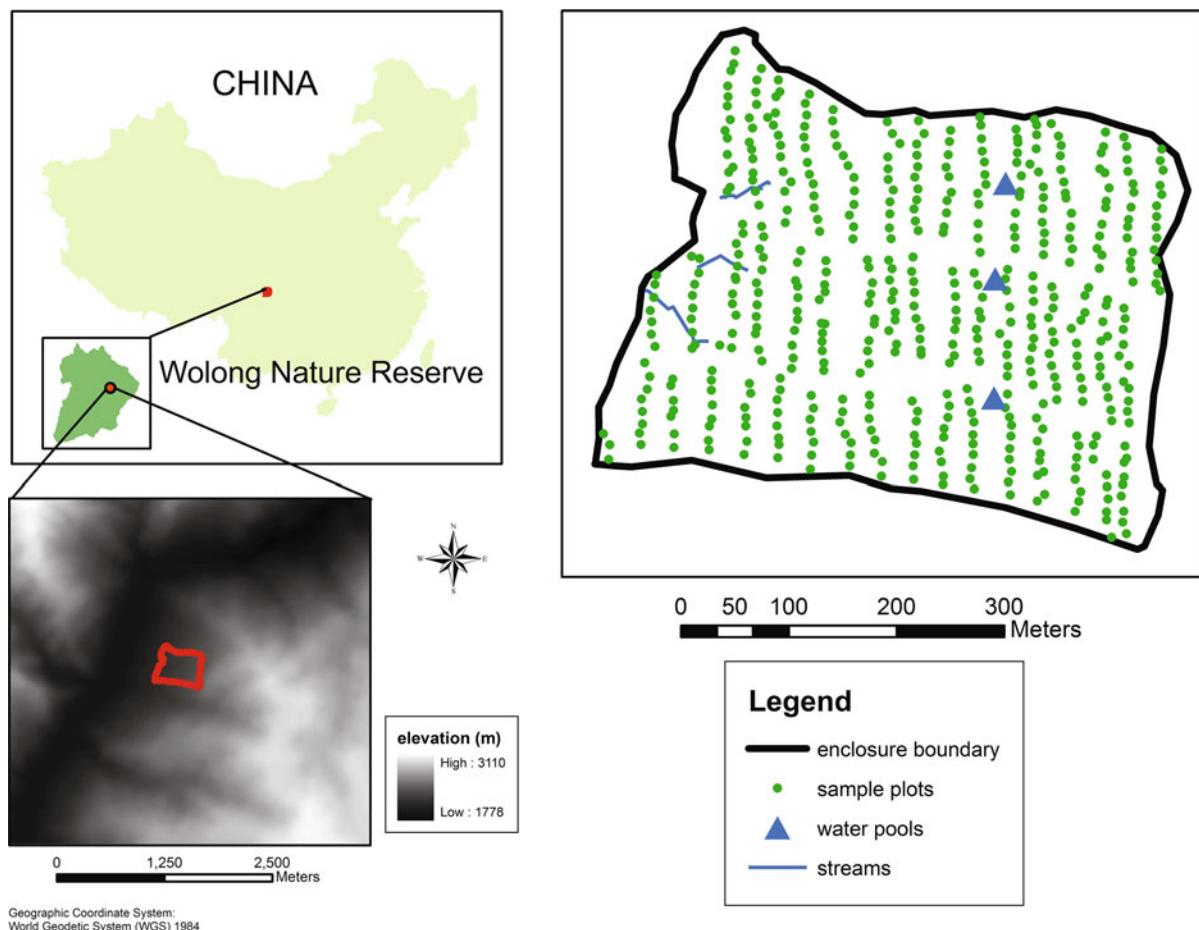


Fig. 1 The panda reintroduction enclosure in Wolong Nature Reserve, Sichuan, China

sampling period measured panda foraging in the second 9 months (late July 2005–late April 2006) of panda occupancy. Although the two periods were roughly equivalent in duration, the first period encompassed a bamboo growing season while the second did not.

We visually estimated the percent bamboo cover lost to panda foraging once in each of these two sampling periods in the 10×10 m plots. Percent bamboo cover lost was a visual estimation of percentage of the total bamboo cover in the plot (at waist height) that was taken up by bamboo culms foraged by pandas. Foraged culms were distinguishable from un-foraged culms due to their stunted nature in having been bitten off at sub-meter height by pandas. Wild pandas were observed to have used a

small portion of the enclosure, but left the area when enclosure construction began in early 2004.

Since bamboo shoots grew each spring (May–June) and the panda left the enclosure in April 2006, the July 2006 and 2007 sampling periods documented bamboo recovery with no panda present. We visually estimated bamboo recovery, or the percent of total bamboo cover taken up by new shoots that sprouted during the latest growing season at waist height in the 10×10 m plots once during each of these two sampling periods. We interpreted “recovery” to be a proxy for bamboo recruitment. We also counted all bamboo culms in 1×1 m sub-plots centered within each plot. We classified bamboo culms into three visually differentiable age groups: first year, second year, and third year or older (Taylor and Qin 1993a).

We also recorded which ones were broken culms consistent with panda foraging.

The only other animals that feed extensively on umbrella bamboo are insects, which consume primarily first-year culms (Taylor and Qin 1987). Insects foraged a percentage of first-year bamboo that was comparable to other areas of wild habitat (2005, 9.54%; 2006, 15.71%; Taylor and Qin 1987). Foraging by pandas was distinguishable from insects because insect foraging caused rotting inside the culm. Only one plot had evidence of browsing by another herbivore (likely prior to enclosure construction). Ungulates such as sambar, serow, and tufted deer occasionally forage on umbrella bamboo, but are not main sources of herbivory (Schaller et al. 1985).

Data analysis

Multiple regression models were constructed to analyze the relationship between (a) percent bamboo cover loss due to panda foraging (in 2005 and 2006) and (b) percent bamboo cover gained via recovery (in 2006 and 2007) and all other habitat variables measured in the 10×10 m plots. Since percent bamboo cover loss and recovery were dependent on the presence of bamboo, all plots with no bamboo cover ($n = 71$) were removed prior to analysis. Because characteristics related to the same forest class were correlated (e.g., midstory deciduous tree cover, density, and DBH), we only included the characteristic of the three that had the strongest correlation to the response variable in the model. Interaction terms were also included. Stepwise regression was used to remove non-significant terms from each model. Diagnostic plots including Cook's D , residual histogram, and a plot of fitted versus actual values were consulted to ensure that the assumptions of unbiased, normal, and homoscedastic errors were met. The response variables were \log_{10} -transformed to meet assumptions.

The presence of spatial autocorrelation in the residuals required the development of SAR models. They incorporated an additive spatial component in the form of a non-zero covariance structure (Lichstein et al. 2002) and should produce superior coefficient estimates when observations are not independent. Two SAR models, one for panda foraging and the other for bamboo regeneration, were defined according to the equation:

$$\begin{aligned} y &= A + \rho W(Y - A) + \varepsilon, \text{ where } A \\ &= (\text{slope})\beta_1 + (\text{aspect})\beta_2 + (\text{overstory})\beta_3 \\ &\quad + (\text{midstory})\beta_4 + (\text{shrubs})\beta_5 + (\text{bamboo})\beta_6 \\ &\quad + (\text{distance to water})\beta_7 + (\text{interaction term})\beta_8. \end{aligned}$$

where

$$\begin{aligned} A &= (\text{slope})\beta_1 + (\text{aspect})\beta_2 \\ &\quad + (\text{overstory})\beta_3 + (\text{midstory})\beta_4 + (\text{shrubs})\beta_5 \\ &\quad + (\text{bamboo})\beta_6 + (\text{distance to water})\beta_7 \\ &\quad + (\text{interaction term})\beta_8. \end{aligned}$$

The response variable y represented either the percent bamboo cover lost or the percent bamboo cover recovered, W was a spatial neighbor matrix and ρ was an interaction parameter specifying the degree of autocorrelation between neighboring points (Bailey and Gatrell 1995). ρ corresponded to the inter-point distance over which neighborhood values were spatially autocorrelated (Lichstein et al. 2002). We determined this distance by visual interpretation of semi-variograms (subsequently called variograms in this paper). Variograms plot semi-variances—average squared differences of values for all point pairs separated by a particular distance—against distance. Autocorrelation was evident when the semi-variance increased as the distance between points increased. The distance at which the semi-variance leveled off marked the maximum spatial extent of spatial autocorrelation (Lichstein et al. 2002).

In order to better understand the spatial pattern of bamboo loss and recovery from panda foraging, we constructed variograms for each linear model on the residuals of an ordinary least squares (OLS) model that had the same predictor variables as the SAR model. Since the OLS models did not account for spatial autocorrelation, the residuals isolated this component (Lichstein et al. 2002). Cressie and Hawkin's robust estimator (Cressie and Hawkins 1980) was used to transform the variograms to remove the influence of outliers. Directional residual variograms of varying azimuths ($0^\circ, 45^\circ, 90^\circ, 135^\circ$) showed no evidence of anisotropy. We used a weighting scheme of $1/\text{lag distance}$, whereby the impact of neighbors on the target location decreased linearly with distance. We employed likelihood ratio tests to assess the significance of model covariates and plots of actual versus SAR model-predicted response variables to evaluate model fit. All analyses

were performed using the R software package (R Development Core Team 2005).

Results

Magnitude of bamboo loss and recovery

Panda foraging had a considerable impact on bamboo in the enclosure, particularly with respect to the younger bamboo age classes. Approximately half of the available first-year culms in the 1×1 m sub-plots were foraged by the panda by the first sampling period in July of 2005, compared to 20% of the second-year culms and less than 10% of the third-year and older culms (Table 1). Because the panda left the enclosure prior to the majority of the growing season in 2006, few first-year culms were lost to panda foraging during the second period, although over 60% of the remaining, un-foraged second-year culms were consumed. Bamboo recruitment also varied across the sampling periods. We recorded a total of 262 first-year culms recruited in 2005 (including those foraged). In the two growing seasons after the panda left the enclosure, recruitment increased to 331 (2006) and then decreased to 152 (2007).

The 10×10 m plot data also revealed an impact of panda foraging on bamboo. In 2005, the majority of plots (68%) experienced bamboo cover loss at or below 5% (Fig. 2a). However, there were an additional 127 plots (29%) that had up to 20% bamboo cover loss, and 10 plots between 20 and 70% bamboo cover loss. Although the average percent bamboo foraged was similar from the first and second periods of the panda's occupancy (2005: mean = 6.38, SD = 7.54; 2006: mean = 4.47, SD = 4.53), foraging intensity was more evenly distributed in 2006 than 2005. A higher percentage of plots had less than 5% bamboo cover loss (73%), and all but one of the remaining plots had under 20% bamboo cover loss.

Table 1 Number of bamboo culms and percent of total culms in a given age class consumed by the panda within the 1×1 m sub-plots in the enclosure

Age class	2005	2006
First year	133 (50.76%)	7 (2.11%)
Second year	54 (20.85%)	75 (66.96%)
Third year and older	69 (8.66%)	33 (3.46%)
Total	256 (24.83%)	115 (9.35%)

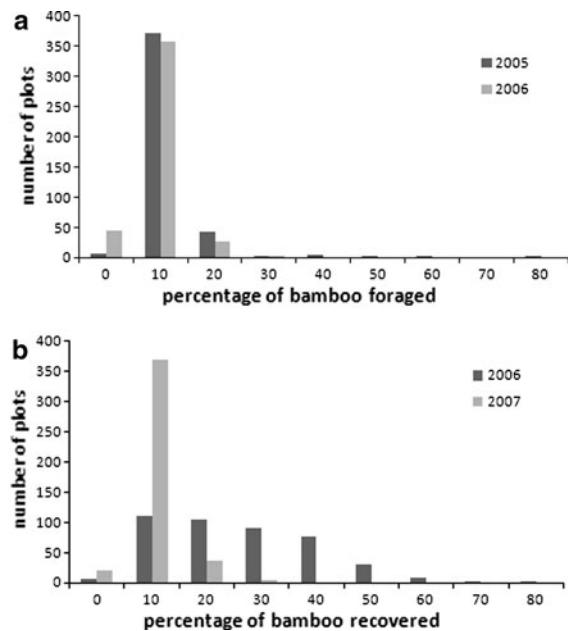


Fig. 2 Frequency distributions of visually estimated **a** percent bamboo foraged by a giant panda and **b** percent bamboo recovered through bamboo recruitment in 10×10 m plots in the reintroduction enclosure in Wolong Nature Reserve. The giant panda was present in the enclosure for approximately 9 months of each of the 2005 and 2006 sampling periods and left prior to the bamboo growing season in 2007

Bamboo recovery was high in 2006 (mean = 23.45%, SD = 14.82), while 28% of plots containing bamboo gained over 30% of new bamboo cover and another 45% of plots gained between 10 and 30% of new bamboo cover (Fig. 2b). In comparison, bamboo recovery in 2007 was lower (mean = 4.82, SD = 4.44), while 95% of plots had between 10 and 30% new bamboo cover and the remainder were all below 10%.

Habitat characteristics explaining bamboo loss and recovery

Across both sampling periods, percent bamboo cover loss to panda foraging was significantly positively related to percent bamboo cover (cubic relationship, Table 2). Bamboo cover contributed more to explaining percent bamboo cover loss than any other variable. Percent bamboo cover loss was also significantly negatively related to distance to water in both periods and significantly positively related to the number of understory trees in 2005 only. There was a

Table 2 Predictors of percent bamboo lost to panda foraging in (a) 2005 and (b) 2006 and percent bamboo recovered in (c) 2006 and (d) 2007 within 10 × 10 m plots in the reintroduction enclosure according to a simultaneous autoregressive (SAR) model

Variable	β	SE	p	Likelihood ratio
(a)				
Bamboo cover ² (%)	-0.15	0.03	<0.001	17.57
Bamboo cover ³ (%)	0.11	0.02	<0.001	41.34
Distance to water (m)	-0.23	0.06	<0.001	14.58
Bamboo cover (%) × distance to water (m) ^a	0.1	0.03	<0.001	11.71
Number of understory deciduous trees	0.05	0.03	0.04	4.10
(b)				
Bamboo cover ³ (%)	0.14	0.02	<0.001	15.64
Distance to water (m)	-0.22	0.07	0.002	3.95
(c)				
Bamboo cover (%)	0.39	0.03	<0.001	122.41
Bamboo cover ² (%)	-0.17	0.03	<0.001	24.85
Bamboo cover lost to foraging in 2006 (%)	0.22	0.03	<0.001	53.77
Understory coniferous cover (%)	-0.1	0.03	<0.001	12.27
Number of overstory deciduous trees	-0.09	0.03	<0.001	11.9
Shrub density × understory coniferous cover ^b	0.08	0.03	0.003	8.61
Shrub density	-0.07	0.03	0.011	6.35
(d)				
Bamboo cover (%)	0.27	0.03	<0.001	63.45
Bamboo cover ² (%)	-0.16	0.03	<0.001	25.55
Bamboo cover lost to foraging in 2005 (%)	0.1	0.03	<0.001	11.14
Number of understory deciduous trees	0.06	0.03	0.04	4.04
Distance to water (m)	0.07	0.04	0.09	2.91

^a Both bamboo cover and distance to water contributed positively

^b Shrub density contributed positively and understory coniferous cover contributed negatively

significant interaction in 2005 between bamboo cover and distance to water in explaining bamboo loss, which was highest when bamboo cover was high and distance to water was great.

In both recovery periods, bamboo recovery was most strongly predicted by the percent bamboo cover present prior to the growing season and the relationship was negative quadratic. There was also a significant positive relationship between percent bamboo lost to foraging and bamboo recovery (loss in 2006 was associated with recovery in 2006, loss in 2005 was associated with recovery in 2007). Bamboo recovery was significantly negatively related to forest characteristics in 2006, including shrub density, understory coniferous cover, and number of overstory deciduous trees. The effects of shrubs and understory trees interacted, where bamboo recovery was highest when shrub density was high and understory

coniferous cover was low. However, the effects of forest characteristics were reversed in the following year (2007), as areas with more understory deciduous trees experienced more recovery. In this year, bamboo recovery was also significantly positively related to distance to water. For both bamboo loss and recovery, SAR model fit was low (Fig. 3). Models tended to overestimate low values and underestimate high values of bamboo loss and recovery.

Spatial pattern of bamboo loss and recovery

Spatial autocorrelation had a significant effect on all models, as the spatial parameter ρ was significant ($p < 0.005$). There was significant spatial autocorrelation in bamboo loss in 2005 up to a lag distance of 40 m (Fig. 4). The radius over which spatial autocorrelation occurred for bamboo loss increased in

Fig. 3 Actual versus SAR model-fitted values for percent bamboo lost to panda foraging in **a** 2005 and **b** 2006 and percent bamboo recovered in **c** 2006 and **d** 2007 in the 10 × 10 m plots in the reintroduction enclosure

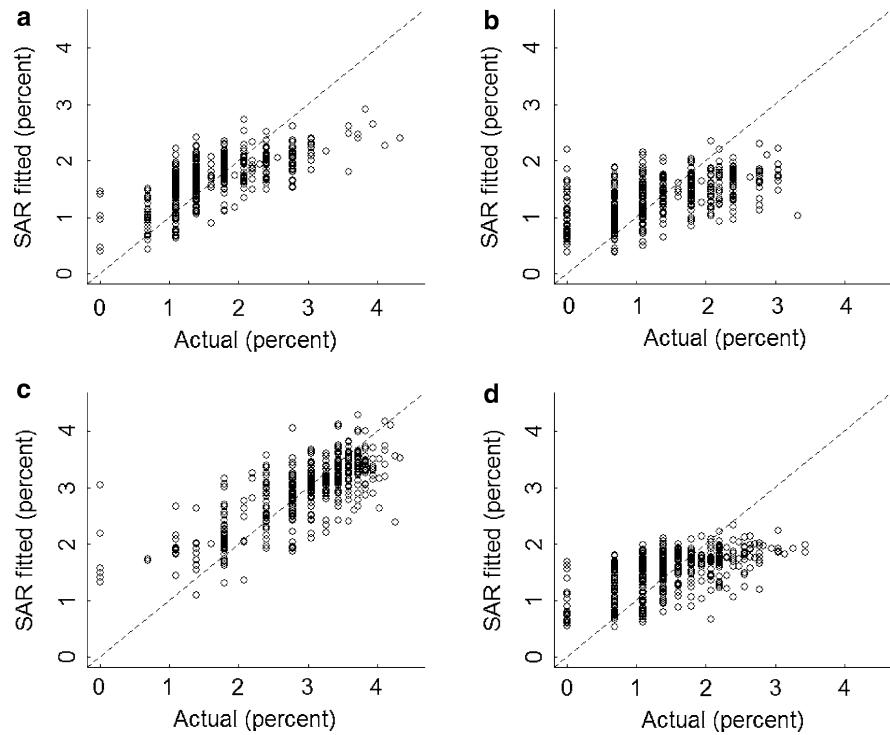
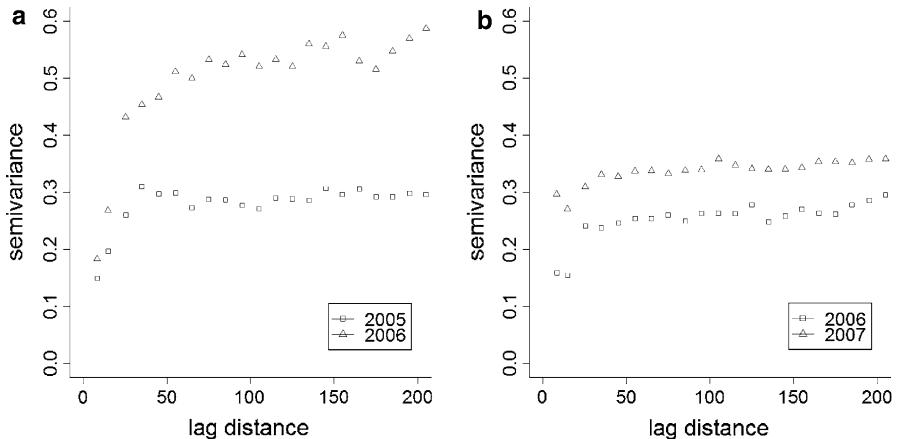


Fig. 4 Semi-variograms of residuals of OLS models for **a** percent bamboo lost to panda foraging in 2005 and 2006 and **b** percent bamboo recovered in 2006 and 2007 as a function of their corresponding significant predictor variables (shown in Table 2). The semi-variograms extended to 1/2 the shortest length of the enclosure (200 m), after which semi-variance estimates became unreliable



2006 to a lag distance of 70 m. In addition, there was a greater magnitude of change in semi-variance with lag distance in 2005 compared to 2006, which can be interpreted as a higher degree of spatial autocorrelation. For bamboo recovery in both 2006 and 2007, the change in spatial autocorrelation across lag distances was less prominent and the effect leveled off at about 30 m. However, analysis of variograms of all SAR model residuals showed some remaining autocorrelation unaccounted for at short lag distances.

Discussion

The impact of panda foraging on bamboo

This study provides new insights into the impact of panda foraging on bamboo. Past studies have estimated average daily bamboo consumption by individual pandas from droppings (Schaller et al. 1985), but logistical constraints of following elusive pandas across rough terrain have prohibited characterization

of foraging impacts on bamboo across space, with the exception of a few samples in select locations (see Schaller et al. 1985; Taylor and Qin 1987). The isolation of an animal for an extended time in this study provided a novel opportunity to gain knowledge on the impact of panda foraging on bamboo in a controlled setting.

The bamboo population in the enclosure sustained rates of panda foraging that were orders of magnitude higher than wild settings, particularly for first-year culms, which normally experience only 16–25% loss to panda foraging (Schaller et al. 1985; Taylor and Qin 1987). These studies present a good baseline for normal panda foraging because the data were collected over a 5-year period in variable-sized plots selected via stratified sampling to capture variability in bamboo density ($n = 37\text{--}724$; plot = 2.25–80 m²) (Schaller et al. 1985; Taylor and Qin 1987). The high rate of foraging on younger bamboos we observed in this study, coupled with the fluctuation in bamboo recovery across time, suggests that age structure was affected by this disturbance.

Habitat predictors of bamboo loss and recovery

Our results suggest that areas with high bamboo cover are at the highest risk for bamboo cover loss under spatially constrained panda foraging. This relationship was expected, as pandas are known to positively associate with bamboo (Reid and Hu 1991; Schaller et al. 1985). However, it is important to note the cubic relationship between foraging and bamboo cover, where foraging peaked at around 65–70% cover. This trend may be related to findings that pandas avoid areas where extremely high bamboo coverage provides no gaps, instead preferring openings created by bamboo patch edges for easier travel (Yu et al. 2003). It would be useful in the future to combine bamboo cover with measures of fragmentation to better understand this effect. Areas close to water also experienced heavier foraging, as was seen in previous studies. However, this study did not corroborate previously recorded correlations between panda habitat use and low slope (Reid and Hu 1991; Schaller et al. 1985), likely because of the relatively uniform slope within the enclosure.

Our study corroborates studies on other bamboo species demonstrating the capacity for bamboo to vegetatively recover from disturbance (Tripathi and

Singh 1996). It is not surprising that bamboo recovery was most significantly predicted by existing bamboo cover, since bamboo reproduction is asexual and derives from the rhizome (Taylor and Qin 1993b). The fact that recovery leveled off at high bamboo cover suggests that resource competition dictates an upper limit to growth.

One new finding in this study was that panda foraging was positively related to future bamboo recovery. Research on other clonal plants has shown mixed results, as some studies find positive (Dyer et al. 1991; Paige and Whitham 1987) and other studies find negative (Bullock et al. 1994; Rooney 1997) effects of herbivory on clonal reproduction. The mixed results are likely due to differences in degree of herbivory and species-specific sensitivities to understory light and nutrient levels.

One reason for the lack of appreciation for this phenomenon in pandas in the past is that most studies have not tracked changes in bamboo across multiple years, as we have done here. The exception is a recent 3-year study by Wang et al. (2007), which found no relationship between panda herbivory and subsequent bamboo growth under heavy foraging by an unknown number of wild pandas (about 19% of culms foraged in 3 m² plots spaced 50 m apart). The reason could be that their study involved a different bamboo species (*Fargesia qinlingensis*), but it may also be related to a difference in spatial context (foraging occurred in a spatially constrained space in our case) and spatial scale of analysis (our study detected an effect at a larger plot size).

Umbrella bamboo may be especially prone to high intra-specific competition because it grows from a pachymorph root system that has short root extensions, thus creating a tightly packed bamboo patch (Taylor and Qin 1993b). Interspecific competition was also manifested in the significant negative relationships we found between bamboo recovery and understory coniferous cover and shrub density in the first recovery period, since understory trees and shrubs discourage bamboo growth by utilizing available light, nutrients, and water (Taylor et al. 2004). This finding corroborates other studies on the genus *Fargesia* that note a high sensitivity to light and tendency for the bamboo to take on a dense, clumped distribution in forest canopy gaps where more light is available (Tao et al. 2008; Wang et al. 2006). Nonetheless, differences in bamboo recovery between

the first and second periods in our study suggest its dynamic nature and highlight the need for long-term studies.

One reason our models did not explain a larger percentage of variability could be due to the inherent uncertainty in estimating bamboo cover. The models could be improved by incorporating data on bamboo age classes within the 10×10 m plots, since pandas prefer young shoots (Schaller et al. 1985; Taylor and Qin 1987). In addition, we may have measured data at inappropriate scales, since little is known about the spatial scale at which each of the predicted habitat characteristics is important for pandas. Further studies should be conducted on varied spatial scales.

Spatial patterns of bamboo loss and recovery

The spatial analysis in this study was informative because it provided a means to quantify the clumped distribution of bamboo loss and recovery. While the significant positive spatial autocorrelation in bamboo loss to foraging was typical of an animal foraging effect (Meisel and Turner 1998), the variation we observed across the 2 years of foraging was especially meaningful. The increase in range of spatial autocorrelation of panda foraging from the first to the second year (Fig. 1) suggests that the panda foraged across a larger spatial scale as resources became limited. This pattern could reflect the decline in bamboo availability, particularly at previously heavily foraged sites. Thus, the panda may have been forced to use what could have been lower quality sites over a broader surrounding area.

This hypothesis is supported by the marked decrease in the panda's consumption in the second period (Table 1). Certainly, the two periods are not equivalent because only the first included a bamboo growing season. However, one would expect more culms to be consumed in the second period, given that older culms contain only about one-fifth of the protein of the first-year culms during their growing season (Schaller et al. 1985). Not only did the panda forage on fewer bamboo culms in the second period, but it was forced to feed on the less suitable older bamboos, since it depleted the preferred first-year culms during the growing season.

The range of spatial autocorrelation of bamboo recovery across the two recovery periods was probably similar because recovery was spatially constrained by

the bamboo rhizome structure, making spatial clustering consistent and limited to short lag distances. It was nonetheless interesting to measure this component relative to bamboo loss, a phenomenon dictated by an animal roaming across a greater spatial range with temporal variability in behavior.

Implications for conservation

The panda's impact on the enclosed bamboo population offers a glimpse into the damage a single panda could do to a bamboo population in a constrained setting. At the same time, the marked recovery of the bamboo population after one growing season without a panda present highlights the value of forest connectivity in this system. Forest connectivity allows a panda to freely move from one place to another as it consumes large amounts of bamboo each day, thereby diluting its foraging impact across a broader area and allowing periods for bamboo recovery.

Nonetheless, it is important to recognize the limitations in this study which stem from the actions of a single, non-wild panda living in an enclosure. The results thus cannot be directly extrapolated to wild conditions. However, the study presented an interesting opportunity for an experiment about the response of a bamboo population subjected to constrained panda foraging for a sustained period, which is certainly a theoretical future scenario for bamboo–wild panda interaction without further management intervention, given past rates of habitat destruction (Liu et al. 1999, 2001).

This study has implications for foraging impacts of other animal species on vegetation, particularly those with increasingly isolated habitats. The insights we gathered across multiple years suggest that there are temporal dynamics in vegetation responses to constrained foraging that make persistent monitoring necessary. As human impacts threaten natural resources worldwide, studies like this, including replications in fragmented habitats, are needed to empirically examine responses of animals to isolated resources.

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