Landscape change in southwest China's Himalayan Mountains:

Implications for old-growth forests, alpine meadows, and avian diversity

By

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Abstract

Land use and land cover change (LULCC) is the main cause of biodiversity declines worldwide. Many of the remaining high-diversity ecosystems are located in developing countries, which are undergoing rapid development and population growth. High biodiversity often occurs in the same areas where people dwell, and our understanding of how to balance livelihoods and conservation is limited. Population growth, economic development, conservation policies and climate change interact at multiple spatial and temporal scales to form complex LULCC dynamics, with unexpected consequences for biodiversity.

My overarching goal was to identify effective conservation strategies in developing countries. To this end, I focused on a case study in northwest (NW) Yunnan, a biodiversity hotspot in the remote Chinese Himalayas. NW Yunnan is subject to many forces of change acting at multiple scales, including environmental protection policies, rapid economic development, indigenous land use practices, and climate change. I used satellite imagery to investigate the patterns and drivers of land cover change from 1974 to 2009, and I integrated ecological field data to understand how the observed changes influenced biodiversity.

My results showed that the two highest-diversity ecosystems in NW Yunnan – old-growth forest and alpine meadows – underwent rapid land cover changes that have negative implications for biodiversity. First, I studied change in forest ecosystems, which cover approximately 65% of NW Yunnan. I found that after the landmark logging ban in 1998, overall forest cover increased from 62% in 1990 to 64% in 2009. However, clearing of high-diversity old-growth forest accelerated, from approximately 1100 hectares/year before the logging ban (1990 to 1999), to 1550 hectares/year after the logging ban (1999 to 2009). Paradoxically, old-growth forest

clearing accelerated most rapidly where ecotourism was most prominent. Increasing forest cover represented mainly non-pine scrub forests, which were not on a trajectory towards becoming high-diversity forest stands.

Second, I analyzed change in alpine meadows, which have exceptionally high species richness, beta diversity, and endemism. I found that, between 1990 and 2009, at least 39% of alpine meadows converted to woody shrubs. The patterns of change suggest that a catastrophic regime shift is occurring, driven by feedback mechanisms involving climate change, environmental policy that prohibited intentional burning and economic development that increased grazing pressure. Shrub expansion threatens alpine meadow biodiversity and local Tibetan yak herder livelihoods, and more generally, these trends serve as a warning sign for the greater Himalayan region where similar vegetation changes could greatly affect biodiversity, livelihoods, hydrology, and climate.

Finally, I studied the role of Tibetan sacred forests for avian biodiversity. I collected breeding bird and habitat data in six Tibetan sacred forest sites and their surrounding matrix. I found that sacred forests protected old-growth forest ecosystems, supported a significantly different bird community than the surrounding matrix, and had higher bird species richness at multiple scales. While bird community composition was primarily driven by the vertical structure of the vegetation, plots with the largest trees (height or diameter) and bamboo groves had the highest bird diversity and abundance, indicating the importance of protecting old-growth forest ecosystems for Himalayan forest birds.

In general, my dissertation shows that complex interactions between environmental policy, economic development strategy, and climate change in tightly coupled human-nature systems

can lead to unexpected trajectories of land cover change. Satellite imagery, when paired with ecological field data, can measure these broad-scale changes and their implications for biodiversity, thereby informing policy and management in a timely manner.

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Introduction

Biodiversity loss is a global crisis because it profoundly alters ecological processes and disrupts ecosystem services. As humans take up an ever-increasing proportion of the Earth's resources, biodiversity continues to decline (Chapin et al. 2000; Myers & Kent 2003; Dobson et al. 2006). Land use and land cover change (LULCC) is one of the most important factors threatening species diversity, because it changes species habitat. However, many aspects of the relationship between biodiversity and LULCC are not well understood.

For example, the species-area relationship derived from island biogeography (MacArthur & Wilson 1967) asserts that the larger an area, the higher species diversity it will support. But this is not universally true. At broad spatial scales, there are "biodiversity hotspots", or regions that contain disproportionately high levels of biodiversity (Myers et al. 2000). At finer scales, there are "keystone structures", discrete spatial features that maintain biodiversity despite being small in proportion to the entire ecosystem (Tews et al. 2004). In an increasingly human-dominated world, protecting biodiversity hotspots and identifying keystone structures is critical for conservation.

Many biodiversity hotspots are located in developing countries (Myers et al. 2000; Zimmerer et al. 2004). Developing countries are undergoing rapid development and population growth, government institutions are often weak, and enforcement levels are low. Furthermore, biodiversity is frequently located in the same areas where people dwell, creating conflicts between livelihoods and conservation (Naughton-Treves et al. 2005; Wittemyer et al. 2008; Ferraro et al. 2011). For effective environmental management, it is thus essential to align conservation and development goals, but our understanding of how to balance conservation and livelihoods is still limited (Ferraro et al., 2011).

The challenge is that development typically involves land use change but the dynamics of land cover change are increasingly complex, and difficult to predict. More and more of Earth's resources have been appropriated for human use, with negative consequences for biodiversity (Foley et al. 2005). Although intensification of human land use does often result in direct losses of habitat, simplistic explanations of the drivers of LULCC, such as population growth and poverty, are inadequate (Lambin et al. 2001). LULCC is a result of people's responses to economic opportunities, which in turn result from complex interactions of political, social and economic drivers acting at multiple scales (Lambin & Meyfroidt 2010).

As economies have changed, novel LULCC trajectories have become increasingly common (Hostert et al. 2011). For example, more and more countries have undergone a forest transition, i.e., a change in forest trajectory from decreasing to increasing forest cover (Meyfroidt et al. 2010; Meyfroidt & Lambin 2011). Forest transition theory assumes that as a country develops, its forest trajectory follows an environmental Kuznets curve, i.e., the environment first worsens but then improves as incomes rise (Mather et al. 1999). The opportunities of returning forests for carbon sequestration, climate and hydrologic cycles, and biodiversity conservation are substantial (Rudel et al. 2005; Kauppi et al. 2006), yet we have very little understanding of the patterns, drivers, and consequences of forest transition in developing countries (Chazdon 2008; Chazdon et al. 2009; Meyfroidt & Lambin 2009; Perfecto & Vandermeer 2010).

Another LULCC dynamic that is not well-understood are regime shifts (Scheffer 2009). Regime shifts occur when multiple interacting factors reach a critical threshold, triggering unexpected, and potentially irreversible, transitions to an alternate state. Predicting critical thresholds and identifying contributing factors is necessary to avoid ecosystem shifts, but

untangling these factors is challenging in coupled natural and human systems (Liu et al. 2007; Brock & Carpenter 2010).

One key to understanding forest transitions, regime shifts, and conservation in biodiversity hotspots is to monitor land cover change over broad spatial and temporal scales in response to climate changes, protection strategies and economic development. Remote sensing is a crucial tool for land cover change mapping and monitoring. It provides a tool to study landscape pattern and understand its influence on ecosystem processes and biodiversity at spatial and temporal scales that are otherwise impossible to study (Nagendra 2001; Turner et al. 2003).

Remote sensing is an especially important monitoring and conservation tool in developing countries. Official records of land use and land cover are limited, and thus satellite imagery is often the only source of historical data. In addition, remote and rugged landscapes inhibit field data collection, making satellite imagery the best source of consistent data across broad spatial scales. Despite its importance, there are real challenges associated with remote sensing analyses in developing countries, including the limited availability of satellite, ground-truth and biological field data to train and validate remote sensing algorithms. Therefore, applied research that tests the potential, and the limits, of remote sensing to achieve accurate and meaningful land cover change monitoring and biodiversity assessment in developing countries is crucial.

The overarching goal of my research was to identify effective strategies for biodiversity protection in developing countries. To reach this goal, I addressed broad questions of LULCC, biodiversity, and conservation in a highly diverse, rapidly changing, and little-studied region of Southwest China. My study area was NW Yunnan (Figure 1), a global biodiversity hotspot (Myers et al. 2000) and a UNESCO World Heritage site. NW Yunnan is still relatively

undeveloped but experiencing rapid change. Local peoples continue to practice subsistence-based agriculture and pastoralism, but since the 1970s, NW Yunnan has undergone major changes due to national policies aimed at fostering both economic development and environmental protection. These policies stimulated rapid infrastructure development, immigration of culturally-dominant Han Chinese, tourism, new protected areas, and changes in land use. In addition, NW Yunnan is experiencing accelerated climate change (Baker & Moseley 2007a). However, the implications of these diverse factors for land cover change and biodiversity are largely unknown.

My research characterized LULCC patterns, and the consequences of LULCC for NW Yunnan's unique floral and faunal diversity. I used remote sensing coupled with field-based measurements, and statistical modeling to address my research questions. My dissertation consists of an introduction, which provides a summary of the entire dissertation, and three chapters, which examine specific research questions in detail.

Chapter 1 Summary

Research Question: How did forest ecosystems change from 1974 to 2009 in response to economic and environmental protection policies?

Hypothesis: Logging decreased following the 1998 logging ban.

NW Yunnan's temperate forest ecosystems are the most biologically diverse temperate forests globally and the primary target of conservation efforts in this biodiversity hotspot. In 1998 the Chinese government instituted the National Forest Protection Plan (NFPP), whose primary objective was to ban logging of all forests in southwest China, except for small quotas

allowed to local people for non-commercial uses. Furthermore, since the 1990s China has invested heavily in reforestation programs and ecotourism.

In order to understand how forest ecosystems changed in response to these various protection and development policies, I used Landsat TM/ETM+ images and multi-temporal change classification to analyze forest change in three time periods: Historic (1974 – 1990), Pre-ban (1990 – 1999) and Post-ban (1999 – 2009). I summarized forest loss and regeneration for the three time periods, and at three different scales (entire study area, county-level, and township-level).

My results showed that total forest cover increased from 1974 to 2009. However, the logging of high-diversity old-growth forest accelerated, especially in forests around Shangrila. Old-growth forest logging accelerated because of high demand for old-growth timber due to rapid ecotourism-based economic development of Shangrila. Much of the new construction for tourists (guesthouses, tourist attractions, restaurants, and vacation homes) uses old-growth forest timber, and increasing wealth of local people resulted in more – and larger – house construction.

Increasing forest cover represented mainly non-pine scrub forests, which were not on a trajectory towards becoming high-diversity forest stands. The accelerated loss of high-diversity old-growth forest and the proliferation of scrub forests indicated that despite increasing forest cover, forest biodiversity in NW Yunnan likely continued to decline. My results highlighted that forest monitoring must incorporate multiple forest classes to assess forest change in the context of the conservation of biodiversity and ecosystem services. Simple forest versus non-forest cover assessments in areas with remaining unprotected old-growth forests are inadequate to understand the implications of protection and development strategies for high-diversity forest types, and can obscure important environmental degradation processes.

Ecotourism, or nature-based tourism, is expanding around the world because of increasing demand, and because it may offer a strategy to wed sustainable economic development with environmental protection (Balmford et al. 2009; Karanth & DeFries 2011). However, my research suggests that rapid development may pose inherent risks to biodiversity given that our study area, with strong forest protection policies and ecotourism-based development, arguably represents a "best-case scenario" for balancing development with maintenance of biodiversity.

Resulting paper: Brandt, J. S., T. Kuemmerle, H. Li, G. Ren, J. Zhu, and V. C. Radeloff. 2012. Using Landsat imagery to map forest change in southwest China in response to the national logging ban and ecotourism development. Remote Sensing of Environment 121: 358-369

Chapter 2 Summary

Research question: What are the rates and drivers of shrub expansion into alpine meadows in Northwest Yunnan?

Hypothesis: Shrub encroachment was driven by cessation of controlled, intentional burning in alpine shrublands since the 1998 burning ban.

Historically, Himalayan alpine meadows have been used by indigenous agro-pastoralists whose rangeland management practices sustained both local livelihoods and biodiversity (Klein et al. 2011). Since the 1950s, numerous environmental changes have affected Himalayan ecosystems. Climate warming rates are higher than the global average, changing ecosystem productivity (Peng et al. 2010), phenology (Yu et al. 2010b), and permafrost (Xu et al. 2009). Changing political and social structures have led to economic development, and abandonment of traditional land use practices (Yeh & Gaerrang 2010; Klein et al. 2011). However, despite

grassland degradation throughout the Himalayas (Harris 2010), rates of shrub encroachment have not been quantified, and its drivers are not well understood.

The alpine meadows of NW Yunnan have higher species richness, beta diversity, and endemism than elsewhere in the Himalayas (Salick et al. 2009; Xu et al. 2009). Their disappearance represents a threat to both biodiversity and local livelihoods. I used Landsat TM/ETM+ satellite image analysis and dendrochronology to map shrub encroachment in the alpine zone (3,800 - 4,500 m) from 1974 to 2009. In addition, I reconstructed changes since the 1950s using interviews, livestock records, and climate data.

Results showed that alpine meadows remained largely unchanged from 1974 to 1990 despite changes in climate and land use, but an abrupt shift occurred from 1990 to 2009 when at least 39% of all meadows were encroached by shrubs. This represents a very rapid encroachment rate (2.1% per year) higher than rates reported elsewhere (Briggs et al. 2005; Coop & Givnish 2007; Thompson 2007; Sankey & Germino 2008). Given the exceptionally rich flora with many endemics, this shrub encroachment is likely to seriously deplete plant diversity in the region (MacArthur & Wilson 1967) and represents a major conservation threat.

The patterns of shrub encroachment suggested that the alpine meadows of NW Yunnan are undergoing a regime shift from an herbaceous to a shrub-dominated ecosystem. Despite multiple perturbations to the climate and land use systems starting in the 1950s, alpine meadows remained resilient to shrub expansion until the late 1980s. Thereafter, rhododendron establishment across several alpine territories appears to correspond to two potential triggers. First, May temperatures at 4000 m shifted from sub-zero to above-freezing levels in the mid 1980s, likely reducing snowpack and snowfall. Second, the 1988 burning ban immediately reduced burning by about 20%, providing another potential trigger. Once established, shrublands

rapidly expanded due to feedback mechanisms involving climate, woody cover, and grazing. Shrubs spread most rapidly in areas with some prior woody vegetation (shrub autocatalysis) and areas without spring snow cover. Burning historically controlled shrubs, and as intentional burning decreased, shrubs expanded. As shrubs expanded, remaining meadows were subject to overgrazing, promoting further shrub expansion.

The results call for immediate, adaptive management in alpine ecosystems of NW Yunnan. The regime shift poses a serious threat to both endemic meadow biodiversity and local livelihoods. Traditional herding systems sustained both local livelihoods and endemic biodiversity. However, the socio-economic and climatic conditions in NW Yunnan have changed greatly. Grazing and burning were compatible with sustaining alpine ecosystems in the past, but may be less sustainable now given climate change and heavy shrub encroachment. Furthermore, our study area may represent a sentinel for the rest of the greater Himalayan region, where similar vegetation changes could greatly affect livelihoods, hydrology, and climate.

Related paper (In review): Brandt, J.S., M.A. Haynes, T. Kuemmerle, Fang Zhendong, D. Waller, and V. C. Radeloff. Regime shift on the roof of the world: Alpine meadows convert to shrublands in the southern Himalayas. *Biological Conservation.*

Chapter 3 Summary

Research question: What is the ecological and conservation role of sacred forests for forest birds?

Hypothesis: Sacred forests are keystone structures for avian diversity in NW Yunnan.

In Chapter 1, I found that logging of old-growth forests accelerated in recent times, and non-pine scrub forests have become more widespread. This raises the question how these changes affected forest bird communities.

Although our study area is within a center of avian endemism in China (Lei et al. 2003), no research had been done on forest songbird distribution, diversity, population trends, or habitat selection. Sacred forests retain old-growth forests, and these forests and their surrounding matrix together encompass a wide range of forested habitats, providing a convenient study design to understand 1) what birds are breeding in different forest types of NW Yunnan, 2) what habitat characteristics the birds are selecting, and 3) the ecological and conservation role of sacred forests for avian diversity in our study area.

To answer these questions, I surveyed birds and their habitat in and around six Tibetan sacred forest patches over two years. I found that sacred forests supported a significantly different bird community than the surrounding matrix, had higher bird abundance, and higher bird species richness at the plot, patch and landscape scales. Furthermore, while I encountered a single matrix bird community, the sacred forest patches provided high within and between-patch heterogeneity, and supported multiple distinct sacred-forest bird communities. I also identified habitat characteristics important for forest birds. While bird community composition was primarily driven by the vertical structure of the vegetation, plots with the largest trees (height or diameter) and bamboo groves had the highest bird diversity and abundance, indicating the importance of protecting old-growth forest ecosystems for Himalayan forest birds.

Old-growth forest clearing and degradation have accelerated throughout the Himalayas, and our results offer hope for forest birds, because they indicate that existing sacred areas protect a variety of habitat niches and increase avian diversity at multiple spatial scales. As population

growth and rapid economic development continues throughout the Himalayas, sacred sites are an important opportunity for biological conservation at the local, landscape and regional scales.

Related paper (In prep.) Brandt, J. S., Han Lianxian, Fang Zhendong, E. M. Wood, A. M. Pidgeon, V. C. Radeloff. Sacred forests are keystone structures for forest bird conservation in southwest China's Himalayan mountains. *Conservation Biology.*

Significance of my dissertation

My research addressed broad themes of LULCC, biodiversity, and conservation, with NW Yunnan as my case study. NW Yunnan represents a unique opportunity to study linkages between LULCC and biodiversity in developing countries, yet very little is known about the region because access for foreign scientists was limited. What makes the region particularly interesting though is that China has implemented over the last 30 years several strong social, economic and environmental policies in NW Yunnan that led to dramatic changes in human land use practices. During the same time period, the region has experienced climatic change greater than the global average. Measuring land cover changes at broad temporal and spatial scales allowed me to understand the implications of and interactions among policies, climate change and development strategies. What I learned in NW Yunnan provides an opportunity to gain insights to future LULCC dynamics in other developing regions world-wide, and my dissertation makes scientific contributions in three dimensions: to ecology, to remote sensing and to conservation.

My dissertation advances **ecological** knowledge. My research focused on two unique and relatively unknown ecosystems, temperate forests and alpine ecosystems in the Himalaya. Gathering baseline information on relatively unknown ecosystems is important in and of itself,

and a necessary first step on which to base future ecological research. My research on forest birds described avian communities and their habitat selection in NW Yunnan forests, which had not yet been done. Furthermore, the bird research highlighted the ecological differences between remnant old-growth forest patches, forest edges, and disturbed forest ecosystems for bird communities in NW Yunnan. In alpine meadows, I identified an unexpected and previously undocumented regime shift from herbaceous- to shrub-dominated ecosystem, attributable to interactions between changes in land use and climate. Little is known about woody encroachment of grasslands in Asia, and my research highlights that rapid shifts can occur in sensitive high-elevation ecosystems previously adapted to traditional land management.

I made advances in **technical approaches** that are relevant to a wider remote sensing audience. I used multi-temporal image analysis to overcome the challenges inherent for remote sensing analysis of mountainous ecosystems with a monsoonal climate. I used Support Vector Machines (SVM), a machine-learning algorithm only recently adapted for multi-class image analysis, and I tested the ability of SVM to tackle multi-class problems with non-random training data. Furthermore, in such a remote and data-poor study area, remotely-sensed data alone was not sufficient to map LULCC and understand factors contributing to that change. Pairing remote sensing with field and interview data, I accurately characterized relatively subtle, but biologically significant, changes among land cover types. I integrated economic, social and ecological data into the remote sensing analysis to analyze LULCC patterns and explore hypothesized drivers of the observed changes.

Finally, my research is highly relevant for **conservation**. I investigated the consequences of forest transitions, ecotourism expansion, and climate change, all of which are global biodiversity conservation issues. In the case of forest ecosystem change, I identified unexpected

acceleration of old-growth forest logging due to ecotourism-based development in NW Yunnan. Ecotourism is expanding around the world, but my research suggests ecotourism-based development is not in all cases a panacea for economic development and environmental protection. In the alpine ecosystems of NW Yunnan, I identified rapid rates of shrub expansion, which threatens alpine meadow biodiversity and local Tibetan yak herder livelihoods. More generally, my study area could be a sentinel for alpine ecosystems of the Greater Himalayas and world-wide, where similar vegetation changes could greatly affect biodiversity, livelihoods, hydrology, and climate. Finally, my research highlighted that sacred forests are promising keystone structures for avian diversity in this region, and perhaps in the greater Himalayas. In an increasingly human-dominated world, the identification of keystone structures and understanding how they function is critical for conservation.

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Chapter 1: Using Landsat imagery to map forest change in southwest China in response to the national logging ban and ecotourism development

Abstract

Forest cover change is one of the most important land cover change processes globally, and old-growth forests continue to disappear despite many efforts to protect them. At the same time, many countries are on a trajectory of increasing forest cover, and secondary, plantation, and scrub forests are a growing proportion of global forest cover. Remote sensing is a crucial tool for understanding how forests change in response to forest protection strategies and economic development, but most forest monitoring with satellite imagery does not distinguish old-growth forest from other forest types. Our goal was to measure changes in forest types, and especially old-growth forests, in the biodiversity hotspot of northwest Yunnan in southwest China. Northwest Yunnan is one of the poorest regions in China, and since the 1990s, the Chinese government has legislated strong forest protection and fostered the growth of ecotourism-based economic development of the region. We used Landsat TM/ETM+ and MSS images, Support Vector Machines, and a multi-temporal composite classification technique to analyze change in forest types and the loss of old-growth forest in three distinct periods of forestry policy and ecotourism development from 1974 to 2009. Our analysis showed that logging rates decreased substantially from 1974 to 2009, and the proportion of forest cover increased from 62% in 1990 to 64% in 2009. However, clearing of high-diversity old-growth forest accelerated, from approximately 1100 hectares/year before the logging ban (1990 to 1999), to 1550 hectares/year after the logging ban (1999 to 2009). Paradoxically, old-growth forest clearing accelerated most rapidly where ecotourism was most prominent. Despite increasing overall forest cover, the proportion of old-growth forests declined from 26% in 1990, to 20% in

2009. The majority of forests cleared from 1974 to 1990 returned to either a non-forested land cover type (14%) or non-pine scrub forest (66%) in 2009, and our results suggest that most non-pine scrub forest was not on a successional trajectory towards high-diversity forest stands. That means that despite increasing forest cover, biodiversity likely continues to decline, a trend obscured by simple forest-versus-non-forest accounting. It also means that rapid development may pose inherent risks to biodiversity, since our study area arguably represents a "best-case scenario" for balancing development with maintenance of biodiversity, given strong forest protection policies and an emphasis on ecotourism development.

Introduction

Land cover and land use change are the main causes of biodiversity declines (Vitousek et al. 1997; Chapin et al. 2000; Foley et al. 2005), and old-growth forests are among the most threatened habitats globally. Old-growth forests are economically valuable for timber (Chazdon et al. 2009) and as agricultural land (Gibbs et al. 2010; Perfecto & Vandermeer 2010), and they continue to disappear despite many efforts to protect them. Most of the remaining high-diversity old growth forests are located in developing countries (Myers et al. 2000; Zimmerer et al. 2004), which are undergoing rapid development and population growth. High biodiversity often occurs in the same areas where people dwell (Naughton-Treves et al. 2005), and our understanding of how to balance livelihoods and conservation is still limited (Ferraro et al. 2011).

However, while old-growth deforestation continues, more and more countries have undergone a forest transition, i.e., a change in forest trajectory from decreasing to increasing forest cover (Meyfroidt et al. 2010; Meyfroidt & Lambin 2011). Forest transition theory assumes that as a country develops, its forest trajectory follows an environmental Kuznets curve, i.e., the environment first worsens but then improves as incomes rise (Mather et al. 1999). While the opportunities of returning forests are substantial (Rudel et al. 2005; Kauppi et al. 2006; Rudel 2009), increasing forest cover alone does not necessarily mean that biodiversity and natural ecosystems are on a pathway towards recovery. Secondary forests are not equal to old-growth forest in terms of biodiversity, carbon storage, and ecosystem service provision (Chazdon 2008; Rudel 2009; Perfecto & Vandermeer 2010) and do not always return to high-diversity ecosystems (Chazdon et al. 2009).

As old-growth forests dwindle and new forests proliferate, two key challenges are to 1) identify effective protection strategies for remaining old-growth forests, and 2) understand the fate and implications of the increasing area of new forests. The key to both is to monitor forest

change dynamics over broad spatial and temporal scales in response to different protection strategies, government policies, and economic development.

Remote sensing is a crucial tool for forest cover change mapping and monitoring. Mapping old-growth forest distribution (Congalton et al. 1993) and post-disturbance forest succession (Fiorella & Ripple 1993; Cohen et al. 1995; Jakubauskas 1996) have long been recognized as essential components of forest biodiversity assessment, and in recent years, multiple forest classes have been mapped even in extremely complex and little-studied environments (Helmer et al. 2000; Liu et al. 2002; Schmook et al. 2011).

However, detailed forest type classifications are usually performed for only a single time period, because there are formidable challenges associated with mapping change for multiple classes over several timesteps. First, using single-date classifications to detect change (i.e. post-classification change detection analysis) over multiple timesteps is problematic because errors multiply over each timestep (Kennedy et al. 2009). Composite change detection minimizes multiplicative error by stacking multi-date imagery together and classifying change directly. However, change classes typically have non-normal distributions. For example, even though deforested areas transition to grassland, agriculture, bare land, or shrub, all are included into a single "deforestation" class, and most classification techniques are ill suited to handle such complex class distributions.

Recently, non-parametric classification techniques, such as decision trees (Hansen et al. 2008; Potapov et al. 2011) have been tested for composite change detection because they can accommodate the non-normal and multi-modal distributions of multi-date imagery. The major disadvantage of non-parametric techniques for composite change detection is that they typically perform better with training datasets that provide a complete and representative sample of the

classes (Pal & Mather 2003). In composite change detection, overall change class numbers increase exponentially with each added land cover class, and adequate training data for rare land cover classes over multiple time-steps are difficult to acquire (Kennedy et al. 2009).

Support Vector Machines (SVM) are an alternative non-parametric classifier that offer particular promise for change detection of multiple forest classes because they can handle complex distributions of multi-temporal imagery (Huang et al. 2002), but they do not require training datasets that completely describe each class. SVM place hyperplanes to separate different classes, and only training points at the class boundaries are necessary for optimal hyperplane placement (Foody & Mathur 2004). Therefore, SVM can perform effectively with a small sample of "mixed pixels" collected from purposefully selected locations (Foody et al. 2006).

Our overarching goal was to use remote sensing to map different forest types and forest loss in complex environments in order to understand processes affecting high-diversity forest types. Our study area was Diqing Prefecture of northwest (NW) Yunnan Province in the Himalayan mountains of southwest China, a global biodiversity hotspot (Myers et al. 2000) and rapidly developing region. Home to the most biologically-diverse temperate forests in the world (Morell 2008), and historically relatively undisturbed (Goodman 2006), large expanses of NW Yunnan's old-growth forests were clear-cut by state logging companies from the 1960s through the 1990s to fuel China's national development (Harkness 1998; Morell 2008) and the logging industry dominated the local economy (Melick et al. 2007).

However, in response to catastrophic flooding along the Yangtze River, in 1998 the Chinese government instituted the National Forest Protection Plan (NFPP). One of the primary objectives of the NFPP was to ban logging of all forests in southwest China, except for small

quotas allowed to local people for non-commercial uses (e.g. construction materials and fuelwood). Furthermore, since the 1990s China has invested heavily in reforestation programs (Liu et al. 2008) and ecotourism (Kolas 2008; Jenkins 2009). As a result, forest cover in SW China is increasing (Weyerhauser et al. 2005), but fine-scale studies indicate that old-growth forests continue to be logged (Melick et al. 2007; Xu & Melick 2007; Zackey 2007) and the ecological integrity of the new forests is unclear (Liu et al. 2008; Xu 2011).

Using remote sensing to map forest change is a logical first step towards understanding the consequences of forest protection and economic development policies since the 1980s in SW China. However, remote sensing in the region is challenging. Because of the monsoonal climate, clouds cover the region during the growing season, but winter image analysis is challenged by snow cover, illumination effects from topography, and senescent vegetation. Furthermore, the collection of ground-truth data is difficult because topography is extremely rugged and roads are few, aerial photos are not freely available, and different forest types are difficult to separate visually in either Landsat or high-resolution imagery.

To overcome these challenges, and to understand complex processes of forest change in our study area, we used SVM, multi-temporal Landsat TM/ETM+ satellite imagery, purposefully-selected ground truth data, and a combined post-classification and composite change detection technique to map multiple classes of forest cover and change in NW Yunnan from 1974 to 2009. Our specific objectives were to:

1. Map multiple forest classes and forest loss for the historical period (1974-1990), the decade before the logging ban (1990-1999) and the decade after the logging ban (1999-2009).

2. Assess the spatial and temporal patterns of logging in relation to geographic, demographic, and economic factors.

3. Determine overall forest cover change, and types of forest that have regenerated.

Study Region

Our study area (22,834 km²) was the Diqing Tibetan Autonomous Prefecture in the Hengduan Mountains of northwest (NW) Yunnan Province, bordering Tibet and Sichuan Province (Fig. 1a). Elevations in the study area range from 1500 to 6000 m above sea level (Fig. 1b), creating a large array of ecological niches in a relatively small area. Forest cover in our study area has been estimated at 60% (Weyerhauser et al. 2005), but the high-diversity old-growth forests, which are the primary conservation target in this biodiversity hotspot, are just a fraction of the total forest cover. The old-growth montane conifer and mixed forests are the most biologically diverse temperate forests globally (Morell 2008). Over 7,000 plant, 410 bird, and 170 mammal species have been documented in NW Yunnan, many of which are endemic to native old-growth forests (Xu & Wilkes 2004; Chang-Le et al. 2007; Ma et al. 2007). Among the different land cover types, the old-growth forest community is richer in endemic, endangered and culturally useful species than any other land cover types (Wen et al. 2003; Anderson et al. 2005; Ma et al. 2007; Salick et al. 2007; Li et al. 2008; Wang et al. 2008), and is essential habitat to the endangered Yunnan snub-nosed monkey (Wen et al. 2003; Li et al. 2008), and to several rare species of pheasants (Wang et al. 2008).

NW Yunnan is also an UNESCO world heritage site because of its centuries-long history of indigenous subsistence cultures, including Tibetan, Lisu, Bai, Naxi, and Yi peoples. Historically, the region was sparsely populated (approximately 15 people/km^2), with a decreasing population gradient from the lower-elevation South to the higher, harsher-climate

North (Fig. 1c). Most people live at a subsistence level, relying heavily on forests for their livelihoods. Forests are still the primary source of fuel for cooking, heating, and construction, and are intensively used for livestock grazing, hunting, food gathering, and traditional medicines. Old-growth trees are especially valuable to Tibetans, as large logs are required to construct traditional Tibetan houses.

NW Yunnan is one of China's poorest regions, making it a primary target of economic development programs since the 1980s, including the Great Western Development program in 1998, which emphasizes infrastructure development, ecological rehabilitation, foreign economic investment, and education throughout western China (Xu et al. 2006). Furthermore, tourism development in NW Yunnan's natural areas has been promoted as a strategy for both environmental protection and economic development (Li & Han 2000; Wang & Buckley 2010).

Methods

General Approach

We used Landsat MSS/TM/ETM+ images and a multi-temporal change classification technique to map forest cover and change in NW Yunnan from 1974 to 2009. We focused on the classification of forest cover loss and of three biologically distinct forest types. A field-derived training dataset and multitemporal Landsat imagery (Fig. 2) enabled accurate classification of the three different forest classes. We performed a combination of composite and post-classification change detection, using multi-temporal imagery from four different time periods (1974, 1990, 1999 and 2009) to quantify land cover/land use change during three intervals (1974-1990, 1990-1999, and 1999-2009) (Fig. 3). One composite change classification mapped forest types and forest loss in the 'Historic' time period (1974-1990), and another mapped forest types and forest loss in both the 'Pre-ban', i.e., the decade before the logging ban (1990-1999), and 'Post-ban',

i.e., the decade following the logging ban (1999-2009) periods. We then performed post-classification change detection from the two composite change classification to identify which types of forests were logged in the Pre-ban and Post-ban periods, and to measure what was the share of total forest cover in 2009 that had been logged in the Historic period. The three forest types were:

(a) Old-growth forests represent the main target of biodiversity conservation in this region (Xu & Wilkes 2004; Chang-Le et al. 2007; Ma et al. 2007). We define old-growth forests as the native, original forest vegetation community of this region. The old-growth forest community is composed of mixed evergreen and deciduous species, including fir (*Abies* spp.), spruce (*Picea* spp.), pine (*Pinus* spp.), larch (*Larix* spp.), evergreen oak (*Quercus* spp.), birch (*Betula* spp.) and rhododendron (*Rhododendron* spp.) with specific species composition highly related to topographic variability (Li & Walker 1986b). The vast majority of this category consists of old-growth forest vegetation community in its climax state, but also includes this community in its secondary state, because the primary and secondary states are spectrally indistinguishable with our Landsat imagery because of the similarity in species composition.

(b) Pine/oak woodlands can occur naturally in NW Yunnan, and often colonize and persist in cleared areas after a disturbance (Li & Walker 1986b), but many pine forests have been planted after logging. In our study area, old-growth pine/oak woodlands are rare, and existing pine forests are typically homogeneous stands of young pines (*Pinus densata*) with oak shrub understory.

(c) Non-pine scrub represents a mix of deciduous and evergreen shrublands that regenerate and persist following logging. This forest type is especially common near villages and along

roads, where forests are heavily used by livestock and people. Based on interviews with local people, many scrub forests have persisted for many decades after logging.

Satellite images

The study area is covered by two Landsat TM image footprints (path/row 132/040 and 132/041). We used a total of 14 images (Table 1), all from late October through early April, because cloud free images are not available during the growing season in this region due to the monsoonal climate. Images were obtained from the USGS Landsat archives and from the China and Thai International Ground Stations. We georeferenced all images to the Landsat 2000 GeoCover Dataset using ERDAS IMAGINE AutoSync, which was already orthorectified, and used a gap-filled Digital Elevation Model (DEM) from the Shuttle Radar Topography Mission (SRTM) to account for relief displacement. Root mean square error for the georeferencing was less than 0.4 pixels (<12 m). Clouds and cloud shadows were masked manually from the images prior to all image analyses. We did not apply any other pre-processing of the images.

Field data

Field data for training and validation were collected during six months of field work, from September to November of 2008, and August to October of 2009. We sampled at least 40 locations for each land cover class to aid the interpretation of spectral subclasses during image analysis. The ground truth dataset consisted of 1,573 polygons containing 93,300 pixels (Table 2). For a full description of the field data and classification scheme, see Appendix 1. Due to the ruggedness of the study area, a random sampling design was not feasible. Ground truth data for uncommon classes, such as old-growth forests, required extensive trekking in remote locations. We hired local villagers to guide us to old-growth forests, alpine pastures, and areas of logging,

and while trekking we conducted interviews with our guides about land use history and practices. We recorded land use and land cover observations and took photographs for an approximate 100 x 100 m area surrounding each GPS point (Justice & Townshend 1981). We collected points for both "pure pixels" (i.e., homogeneous areas of a single land cover type), as well as "mixed pixels", (i.e. areas were a mixture between land cover types prevails) to aid the SVM in hyperplane placement.

We supplemented field data with ground-truth data from high resolution imagery available in Google Earth[TM], which covered approximately one-third of the study area, and the Landsat imagery. For the forest type classes, we relied entirely on field data, since these classes cannot be distinguished reliably based on visual inspection of single-date satellite imagery alone. For forest loss classes, approximately 60% of training data were derived from field data, and approximately 40% were selected by visual interpretation of the Landsat imagery. We identified forest loss classes in the field by visiting areas of past logging, and asking our local guide when the logging had occurred. Similarly, approximately 20% of the training areas for agriculture, grassland, sparse shrub, and bare/urban classes were collected from the high-resolution imagery, and 80% in the field.

Change detection

We used Support Vector Machines (SVM), implemented in the software imageSVM (Janz et al. 2007), for our change detection. To train and validate our SVM, we used a random selection of approximately 1000 points from each class in our ground truth dataset. We performed a classification for the Historic period (1974-1990) by combining 1974 Landsat MSS images, ca. 1990 Landsat TM images, and elevation and hillshade from the DEM. The hillshade for the

'Historic' classification was calculated with a sun elevation angle of 34.04°, and a sun azimuth angle of 146.62° (corresponding to the November 19th 1990 Landsat TM image (Path/Row 132/40). For the 'Historic' classification, all images were resampled to the resolution of the MSS image (57 m pixels). We classified six classes, including the three forest types, a forest cover loss 1974-1990 class, agriculture and grassland, and other (bare/urban/snow/water).

Using the Landsat TM/ETM+ imagery from 1990, 1999, and 2009, we performed a second composite classification for the decade leading up to the logging ban (Pre-ban, 1990-1999), and the decade following the logging ban (Post-ban, 1999-2009). We stacked the five TM/ETM+ images along with elevation and hillshade data. The hillshade image for the Pre-ban and Post-ban classifications was derived using the image acquisition time of the October 28, 1999 image, Path/Row 132/40 (sun elevation = 41.87°, azimuth = 147.17°). One hillshade image was sufficient to represent shading caused by topography. For this classification, all images were resampled to a spatial resolution of 28.5 m. We classified the image stack into 11 classes, including three permanent forest types and forest loss classes in different periods (1990-1999 and 1999-2009), agriculture, grassland, alpine shrub expansion, sparse shrub, bare/urban, and other (snow/water) . To eliminate isolated misclassified pixels, we identified contiguous groups of pixels (using the 4-neighbor rule) and merged small patches (<2 pixels for the Historic classification and <6 pixels for the Pre-ban and Post-ban classification) into the largest neighboring patch (minimum mapping unit of 0.65 ha for the historic classification and 0.49 ha for the Pre-ban and Post-ban classification).

We randomly withheld 10% of the dataset for the accuracy assessment and 90% of the pixels were used for training. We classified the image stack a total of ten times, with a different random training dataset each time, and the final accuracy measures are derived from the mean error

estimates of all ten classifications. The final classification was produced from 100% of the data points.

For accuracy assessment, from the confusion matrix we calculated an area-adjusted error matrix, including area-adjusted user, producer, and overall accuracies, that take into account the areal proportions of each class (Card 1982). This is necessary to correct for potential bias due to the differences in the proportions of classes in the validation data and the true areal proportions of these classes in the map. We also adjusted the total area estimates from the classified map according to the bias correction, to produce an adjusted area coverage for each class, and then calculated 95% confidence intervals for these area estimates (Cochran 1977; Card 1982) to provide a more accurate and intuitive representation of error.

Analyzing logging rates and patterns

We compared forest change among the three different time periods, and at three different scales: the entire study area, county-level, and township-level. We used two different measures of forest disturbance. First, we calculated the number of hectares of forest loss. Second, we calculated an area and time-adjusted disturbance rate (Eq. 1)

ADR = ((D$_j$/FCB$_j$)/t)*100 Eq. 1

where *ADR* is the annual disturbance rate, *Dj* is the number of pixels in the forest cover loss class for time period *j*, *FCBj* is the total number of forest pixels at the beginning of time period *j*, and *t* is the number of years in time period *j*.

To understand the influence of humans on forest change patterns, we used spatial data on road networks, villages, and provincial and township boundaries, all digitized from 1:250,000

topographic maps from the late 1990s. We calculated township-scale village density (as a proxy for population density, which was not available), and road density (including national, provincial, county and village-level roads). Pearson correlation and multiple linear regression analyses were performed to determine the relationship between logging rates, village density, and road density during the three time periods. To understand the economic and demographic implications of NW Yunnan's rapid development, we gathered economic statistics from official Chinese sources, compiled at the scale of Diqing Prefecture. Data sources included the Yunnan Statistical Yearbooks, the Diqing Prefecture Statistics Bureau, the Diqing Tourism Bureau, and the Bank Loan Registration Information System of Diqing Prefecture. Economic data were corrected for inflation using the World Bank's GDP deflator values for China (World Bank 2011).

Results

Multiple forest class change detection

Area-adjusted overall accuracy (i.e., accuracy measures that are corrected for potential bias due to the differences in the proportions of classes in the validation data and the true areal proportions of these classes in the map (Card 1982)) was 92% for the Historic classification and 93% for the Pre-ban and Post-ban classification (Table 3). Old-growth forests were mapped with an accuracy of at least 91% in both classifications. For the change (i.e. deforestation) classes, producer accuracies were lower than the user accuracies, representing a high error of omission, which means that our estimates of forest loss were conservative.

The lowest accuracies were the producer accuracies for the forest cover loss classes during the Historical (78%), Pre-ban (79%) and Post-ban (73%) periods. Accuracies from the raw

confusion matrix for these change classes were much higher (ranging from 91 - 94%). However, when adjusting for potential areal biases, accuracies for classes with small areal proportions (e.g. a change class) can diminish dramatically even when just a few points of a smaller class are mis-classified, because these pixels are frequently mis-classified as a class with larger areal proportion (e.g. a no-change class), creating a high error of omission and a low producer accuracy. By generating area estimates for each class, and confidence intervals around those area estimates, a more accurate representation of error was provided (Table 3).

Logging rates and patterns

During the Historic period, 94,763 ± 6,304 ha of forest were logged (95% confidence interval). Logging dropped dramatically during the Pre-ban (58,467 ± 4,645 ha) and Post-ban (57,880 ± 5,202 ha) periods. In the entire study area, the annual disturbance rate decreased from 0.37% in the Historic period, to 0.29% and 0.27% in the Pre- and Post-ban periods, respectively.

The spatial pattern of logging changed over time. Multiple linear regressions to predict logging rates as a function of population and road density were significant during the Historic (p = 0.04, Adj. R^2 = 0.15) and Pre-ban (p = 0.01, Adj. R^2 = 0.25) periods, but not significant (p = 0.59) during the Post-ban period. In univariate correlations of logging rates with either road or population density, logging rates were positively correlated with road density (p = 0.05, r = 0.36) during the Pre-ban period, and negatively correlated with village density during both the Historic (p = 0.01, r = -0.46) and Pre-ban periods (p = 0.002, r = -0.53). However, during the Post-ban period, there was no significant correlation between logging rates and road density (p = 0.46) or logging rates and village density (p = 0.74).

Logging rates decreased dramatically throughout the study area after the Historic period, except for the area around Shangrila City, where logging rates were consistently high in all three time periods (Fig. 1e). Furthermore, in Shangrila County, the area of old-growth forest cleared after the ban doubled compared to old-growth forest loss during the Pre-ban period (Fig. 4). Meanwhile, logging of other forest types (pine/oak woodlands and non-pine scrub), and in other counties, remained relatively consistent during the Pre- and Post-ban periods.

Forest cover and regeneration

Total forest cover (old-growth forest, pine/oak woodlands and non-pine scrub combined) increased in the study area from 62% in 1990 to 64% in 2009 (+ 50,000 ha) (Fig. 5a and 5b). This forest area increase represented mainly an increase in the non-pine scrub class (from 11% to 24%), while old-growth forests and pine/oak woodlands declined (from 26% to 20% and from 25% to 20%, respectively). Other land cover types remained fairly constant.

We summarized land cover in 1990-2009 for those pixels that were deforestation or non-pine scrub forest classes in the Historic period to understand trends in the regeneration (Fig. 6). Fourteen percent of the areas logged during the Historic period remained non-forested in 2009 (Fig. 5c). Of the areas where forest cover regenerated, only 14% had a species composition similar to the old-growth forest community, and 8% regenerated as pine/oak woodlands. The remaining 64% of the logged area regenerated as non-pine scrub. Similarly, only a small proportion of the non-pine scrub during the Historic period transitioned to either the old-growth forest community (8%) or pine forest (9%) as of 2009, and a substantial proportion (17%) lacked forest cover (Fig. 5d). The majority of the non-pine scrub in the Historic period remained as such

in 2009 (66%). Furthermore, regeneration rates varied spatially. Areas with abundant old-growth forest (Fig. 7a) often had low rates of regeneration of the old-growth forest community (Fig. 7b).

Socioeconomic changes

Economic data indicated that there was rapid development since the logging ban in 1998, due to a rapidly developing tourism industry (Fig. 8a). In 1995, only 40,000 tourists visited Diqing Prefecture, but as of 2009, it received 5.3 million visitors annually. Income from tourism rose from 19 million RMB in 1995 to 5,400 million RMB in 2009. Local government revenue increased 40-fold, from 11 million RMB in 1987 to 440 million RMB in 2009, and annual rural net incomes more than tripled from 661 RMB in 1989 to 2100 RMB in 2009 (Fig. 8b).

Discussion

Multiple forest class change detection

Remote sensing in our study area faces many obstacles, and our study represents the most detailed forest change detection analysis to date for SW China (Willson 2006; Vina et al. 2007; Vina et al. 2008; Tuanmu et al. 2010). Image analysis is challenged by snow cover, strong illumination effects from topography, and senescent vegetation. The collection of ground-truth data is difficult, and forest distribution and composition is extremely heterogeneous. We employed a range of techniques to overcome these obstacles. First, we used SVM to handle complex distributions of our land cover classes. Samples from a wide range of intra-image variability, including dramatic illumination effects and variable snow cover, were included in the training dataset to accommodate the multi-modal and non-normal distributions inherent in such a complex environment. Furthermore, in the field, we specifically identified training data in areas at the spectral boundaries of a class (e.g., 45% pine/oak woodlands and 55% old-growth forest)

as input for the SVM. These "mixed pixels" were crucial to aid the SVM to identify precise hyperplanes between the classes.

Second, multi-temporal imagery (Wolter et al. 1995) from late fall and early spring aided the separation of old-growth forest from the pine/oak woodlands and the non-pine scrub classes (Fig. 2. Average mean and SD for all training points in these classes can be found in Appendix 2). In southwest China, November through April is a period of extended drought, and the fact that different tree species respond differently to drought, was a crucial factor to discriminate forest types. The composite of the multitemporal TM imagery from 1990 with the single winter MSS imagery from 1974 was essential to accurately classify different forest types during the historic period.

Finally, we combined two common approaches to multitemporal change detection -- composite and post-classification change detection techniques – to reduce multiplicative error. The "historical" classification gave us the baseline maps necessary to compare logging rates for different forest types during the Pre- and Post-ban time periods, but we reduced much of the cumulative error that would have resulted from a pure post-classification change detection methodology.

Despite the high level of accuracy achieved by our classifications, there are uncertainties in our estimates. First, it is possible that classification accuracies were overestimated because our ground-truth dataset was not random, possibly resulting in spatial autocorrelation among the pixels within polygons. On the other hand, accuracy was underestimated to some degree because we purposefully included "mixed pixels" in our training and validation dataset to aid SVM in

hyperplane placement. These points were often classified inaccurately, even though in the field the appropriate classification is ambiguous.

Second, forests in this region are extremely heterogeneous and we had to limit our classification scheme to just three forest types to achieve a balance between classification accuracy and thematic detail. Third, our classification could not discriminate logging from other forest disturbances (insects and fire), which are not frequent events in our study area, but do occur in isolated patches. In addition, selective logging is not well captured in our land cover classifications. Finally, during post-classification processing we eliminated small, isolated patches to remove noise, and small patches of logging may have been falsely removed. Selective and small-scale logging do occur in our study area, and further research is necessary to quantify the extent and consequences of these logging practices.

Logging Patterns

The logging patterns that emerged from our satellite image analysis reflect NW Yunnan's turbulent history since the mid 1900s, and highlight its consequences for old-growth forest and biodiversity conservation. Our analysis confirmed that logging was indeed intense throughout the study area during the Historic period (1974-1990) (Fig. 1b). Logging rates decreased dramatically during the Pre-ban period (1990-1999), and during the Post-ban period (1999-2009), logging was reduced even further. Thus, our analysis indicates that the bold forest protection policies that China implemented were successful and increased forest cover in our study area.

However, substantial logging still occurred despite the logging ban. Approximately 60,000 ha was logged in each of the Pre-ban and Post-ban periods, and the spatial distribution of logging

changed dramatically. We expected that areas with high road density would have high rates of logging (Chomitz & Gray 1996; Cropper et al. 2001). Surprisingly, this was the case during the Historic and Pre-ban periods, but not in the Post-ban period. Village and road density had some predictive value for logging rates during the Historic and Pre-ban periods, but not during the Post-ban period, indicating that the processes influencing regional-scale patterns of logging changed.

For example, most logging during the Historic and Pre-ban periods was performed by state logging companies. Easily accessible areas (i.e. along major roads) were already logged in high-population density areas, but abundant old-growth forests remained along major roads in low population-density areas, which explains the positive correlation of logging with road density and the negative correlation of logging with village density during these early periods. After the logging ban, state-sponsored logging companies disbanded, and logging was only allowed by local people for non-commercial use. Logging and population/road density became divorced (i.e. relationships became insignificant) during the Post-ban period because logging became concentrated in a "hotspot" around Shangrila.

Old-growth forest logging accelerated in the Post-ban period around the city of Shangrila most likely because of high demand for old-growth timber due to rapid ecotourism-based economic development. Local and national government officials responded to the logging ban by initiating the development of NW Yunnan into one of the premiere ecotourism destinations in China (Morell 2002; Kolas 2008; Jenkins 2009). Shangrila City is the tourism "gateway" into NW Yunnan, and transformed since the 1980s from a backwater town into a one of the premiere tourist destinations in China (Morell 2002; Kolas 2008; Jenkins 2009). The region's only airport

(built in 1999) is located 5 km outside of Shangrila City. In 2007, China's flagship National Park Pudacuo (Jieng 2008), was established just 30 km from Shangrila City.

The development of Shangrila resulted in a growing demand for tourism accommodations (Fig. 8a) and a growing population (Fig. 8b). From 2002 to 2007, new tourism-based businesses received 2.3 billion RMB in government loans. Shangrila's tourism industry capitalizes on both the natural beauty of the region, and on Tibetan culture (Jenkins 2009). Therefore, much of the new construction for tourists (guesthouses, tourist attractions, restaurants, and vacation homes) uses a Tibetan architecture style (Kolas 2008). In addition, increasing wealth resulted in more - and larger - traditional Tibetan-style houses for local families. Villagers reported to us that each new Tibetan house requires between 50-100 trees, and that the primary sources of timber were the old-growth spruce and fir forests around Shangrila City. Among 23 houses that we visited, those built after 2001 had, on average, central pillars with an average diameter of 79 cm, while pillars in those built before 2001 were only 51 cm in size. These data are too limited to be representative, but indicate potential effects of increasing wealth. In addition to construction materials, each household needs 10-30 m^3 of fuelwood/ year (Xu & Wilkes 2004). Higher demand for firewood due to the increasing number of households, and the restaurants and guesthouses of the tourism industry, thus likely accelerated forest cover loss around Shangrila.

Increased logging rates were likely not a result of increasing demand for wood products in other parts of China, as we did not encounter logging camps or logging trucks, and export of timber to the rest of Yunnan is strictly prohibited and enforced by logging checkpoints. Instead, the increasing demand for old-growth timber in Shangrila is due to the rapidly growing tourism industry and the increasing income levels of the local people. Research in the Wolong Giant Panda Reserve in neighboring Sichuan Province similarly revealed accelerated forest cover loss

following reserve implementation, due to tourism, a growing population, and greater wealth (Liu et al. 2001).

Ecotourism, or nature-based tourism, is expanding around the world because it offers a strategy to wed sustainable economic development with environmental protection (Balmford et al. 2009; Karanth & DeFries 2011). However, what constitutes true ecotourism, and the consequences of ecotourism for biodiversity conservation, is still a matter of great debate (Yu et al. 1997; Nash 2009; Kirkby et al. 2010; Sims 2010; Wang & Buckley 2010). In Shangrila, the tourism industry encompasses a wide range, including nature, adventure, ethnic, and protected area tourism. We used the term "ecotourism" to represent this wide range because, first, appreciation of nature is undeniably the primary attraction of Shangrila. Second, and perhaps more importantly, Shangrila's tourism industry is branded as ecotourism, i.e., both the producers (advertisers, local businesses, tour guides) and consumers (i.e. tourists) believe that they engage in ecotourism. As such, it is particularly noteworthy that our result showed continued deforestation.

Forest cover trends

While old-growth forests declined, forest area overall increased from 62% in 1990 to 64% 20 years later. However, only a fraction (20%) of deforested or non-pine scrub areas during the Historic period returned to either pine/oak woodlands or the old-growth forest vegetation community (Fig. 5c and d). This is not to say that with time and appropriate forestry management, the non-pine scrub forests in our study area could not potentially return to the original vegetation community, but we did not observe this. No information is available about successional trajectories of Shangrila forests, but in general, regeneration to climax forest in

temperate regions takes centuries to thousands of years, much slower than the observed rate of

old-growth forest clearing around Shangrila. Furthermore, our field observations indicated that

land use intensity was high in regenerating areas, inhibiting the regeneration of the original

vegetation community. Likewise, our remote sensing results suggest that non-pine scrub may not

be in a process of natural succession, since we observed small proportions of regeneration to pine

or vegetation communities typical of old-growth forests in those areas that were non-pine scrub

forest from 1974-1990.

The assumption of forest transition theory is that increasing forest cover indicates that

environmental conditions are improving (Mather et al. 1999), but here we show that increasing

forest cover alone does not necessarily mean that biodiversity and natural ecosystems are on a

pathway towards recovery (Meyfroidt & Lambin 2011). We observed that secondary and scrub

forests are a growing proportion of forests in our study area, which is similar to many countries

around the world (Chazdon 2008; Grau et al. 2008). Yet, most studies showing shifts in forest

trajectory have not distinguished between primary and secondary forest types, even though the

value of regrowing forests, in terms of species habitat and ecosystem services, is far lower than

that of old-growth forests (Chazdon 2008; Meyfroidt & Lambin 2008; Perfecto & Vandermeer

2010). Land use largely determines whether the forests regrowing after harvest will eventually

recover to a high-diversity ecosystem (Chazdon et al. 2009), but unfortunately, land use intensity

in secondary forests is not included in forest transition theory (Meyfroidt et al. 2010; Perfecto &

Vandermeer 2010). Likewise, forest transitions and increasing forest cover may be only due to

monoculture plantations with little biodiversity value (Rudel 2009) or result in more intense land

use of surrounding forests, with potentially negative effects on overall biodiversity (Perfecto &

Vandermeer 2010). Furthermore, countries experiencing a forest transition may simply export

their ecological footprint elsewhere (Mayer et al. 2005; Meyfroidt & Lambin 2009; Meyfroidt et al. 2010).

Conclusions

Our results highlight that forest monitoring must incorporate multiple forest classes to assess forest change in the context of the conservation of biodiversity and ecosystem services. Simple forest versus non-forest cover assessments in areas with remaining unprotected old-growth forests are inadequate to understand the implications of protection and development strategies for high-diversity forest types, and can obscure important environmental degradation processes. This represents a major challenge for the remote sensing community, because error and complexity increases when multiple dates or multiple classes are examined via change detection. We used multi-temporal imagery, carefully selected training data with SVM and a combination post-classification and composite classification technique to reduce error and accurately detect change in multiple forest classes in a complex environment.

One of the primary objectives of the NFPP is to ban commercial logging of all forests in southwest China, and allow only small quotas for local consumption. Our results show that, overall, China's forest protection policies effectively reduced forest loss in NW Yunnan. Logging decreased over most of the landscape, and forest cover increased. However, the logging ban was trumped in areas of rapid economic development, as old-growth forest loss accelerated due to a growing ecotourism industry. Ecotourism has expanded rapidly in developing countries around the world (Balmford et al. 2009; Karanth & DeFries 2011), because it offers a strategy to wed sustainable economic development with environmental protection. However, our results show that even in Shangrila – an arguably best-case-scenario with strong institutions, well-funded environmental protection efforts, and strong government policies aimed at forest

protection -- the negative impacts of ecotourism-based economic development on the environment outweighed conservation efforts. As tourism development continues to expand into previously remote and little-visited regions, the negative impacts observed near Shangrila City in the last decade may soon follow unless steps are taken to mitigate the threats that development poses.

Acknowledgements

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Table 1. Images used for the analysis.

	Time Period						
	ca. 1974	ca. 1990		ca. 1999		ca. 2009	Reference
Landsat Sensor	MSS	TM	TM	TM	ETM	TM	ETM
Acquisition Date	1/5/1974	11/20/1990	4/13/1991	10/28/1999	4/13/2000	11/24/2009	12/25/2000

Table 2. The number of ground truth polygons and pixels in each class.

Land Cover Class	Polygons	Pixels
Old-growth forest	396	18664
Pine/oak woodland	184	9713
Non-pine scrub	329	24149
Deforestation - historic	51	5442
Deforestation pre-ban	85	3435
Deforestation post-ban	81	3970
Agriculture	141	5710
Grassland	98	2244
Alpine shrub expansion	41	1826
Sparse shrub	78	12198
Bare/urban	45	2063
Other	44	3886
Total	1573	93300

Table 3. Producer (PA) and user (UA) accuracies, adjusted areal extent and confidence intervals

(CI) for each land cover class.

Class	PA	UA	Adj. Area (ha)	±CI (ha)	±CI (%)
HISTORIC CLASSIFICATION					
Old-growth forest	93%	95%	566233	11976	2%
Pine/oak woodland	93%	89%	513940	13562	3%
Non-pine scrub	86%	86%	236890	10001	4%
Deforestation Historical	78%	95%	94763	6304	7%
Agriculture and Grassland	89%	94%	226072	7527	3%
Other	95%	93%	500732	10247	2%
Overall accuracy =	92%				
Khat =	0.92				

Class	PA	UA	Adj. Area (ha)	±CI (ha)	±CI (%)
PRE-BAN AND POST-BAN CLASSIFICATION					
Old-growth forest	91%	91%	501165	12435	2%
Pine/oak woodland	93%	92%	517316	11836	2%
Non-pine scrub	97%	90%	533596	11696	2%
Deforestation Pre-ban	79%	96%	58467	4645	8%
Deforestation Post-ban	73%	95%	57880	5202	9%
Agriculture	97%	98%	138090	2600	2%
Grassland	92%	99%	68710	3201	5%
Alpine Shrub Expansion	93%	99%	79476	3153	4%
Sparse Shrub	95%	97%	96842	2850	3%
Bare/Urban	86%	95%	106076	5215	5%
Other	97%	96%	392733	6097	2%
Overall accuracy =	93%				
Khat =	0.93				

Figure 1. a) Location of Diqing Prefecture, in Northwest Yunnan, China, b) elevation, c) population density, d) road density, and e) annual disturbance rates by township for the Historic (1974-1990), Pre-ban (1990-1999) and Post-ban (1999-2009) periods.
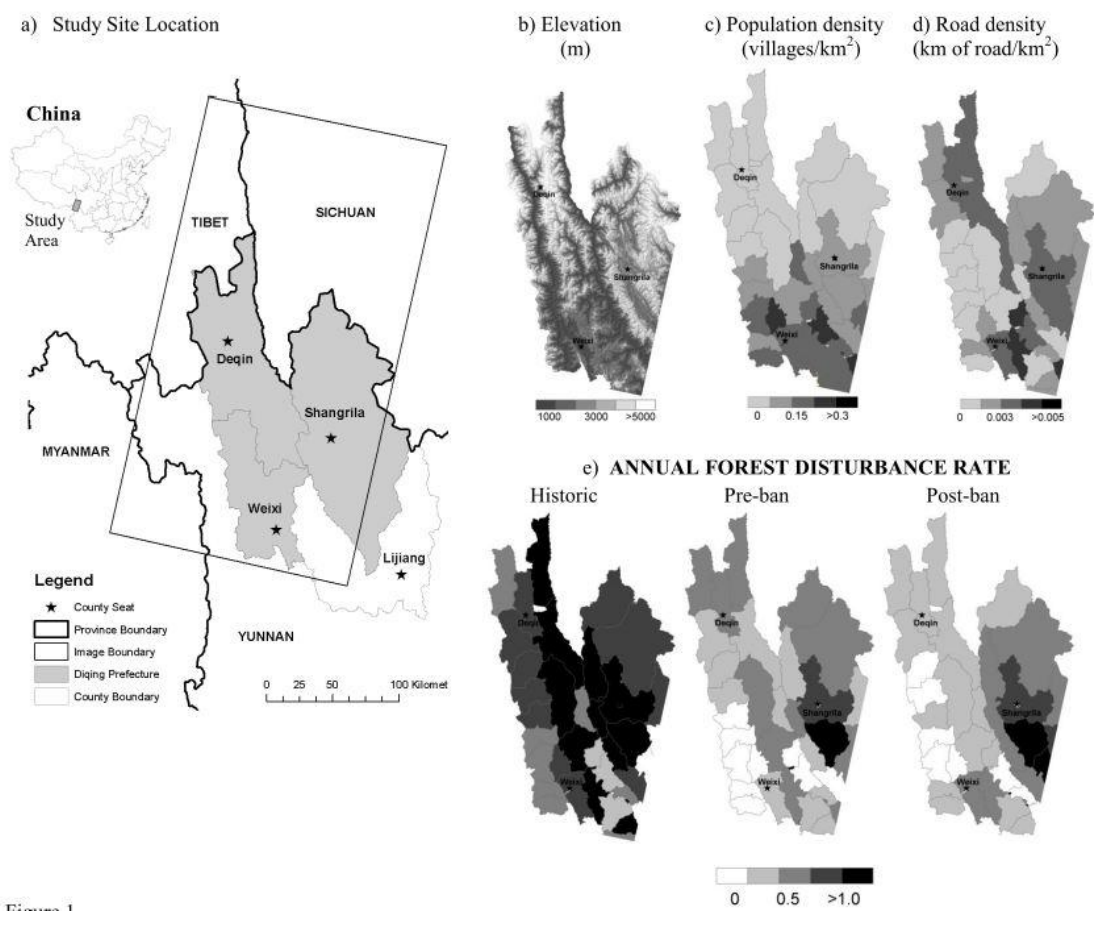
Figure 2. Examples of how phenology was used to discriminate the different forest classes. Representative pixels from the three forest classes look similar under visual inspection on Landsat images from A) November 20, 1990 and B) April 13, 1991, but C) spectral plots (Landsat bands 1 through 6) show that different forest types vary in their response to winter drought, enabling discrimination between forest types with multi-temporal imagery.
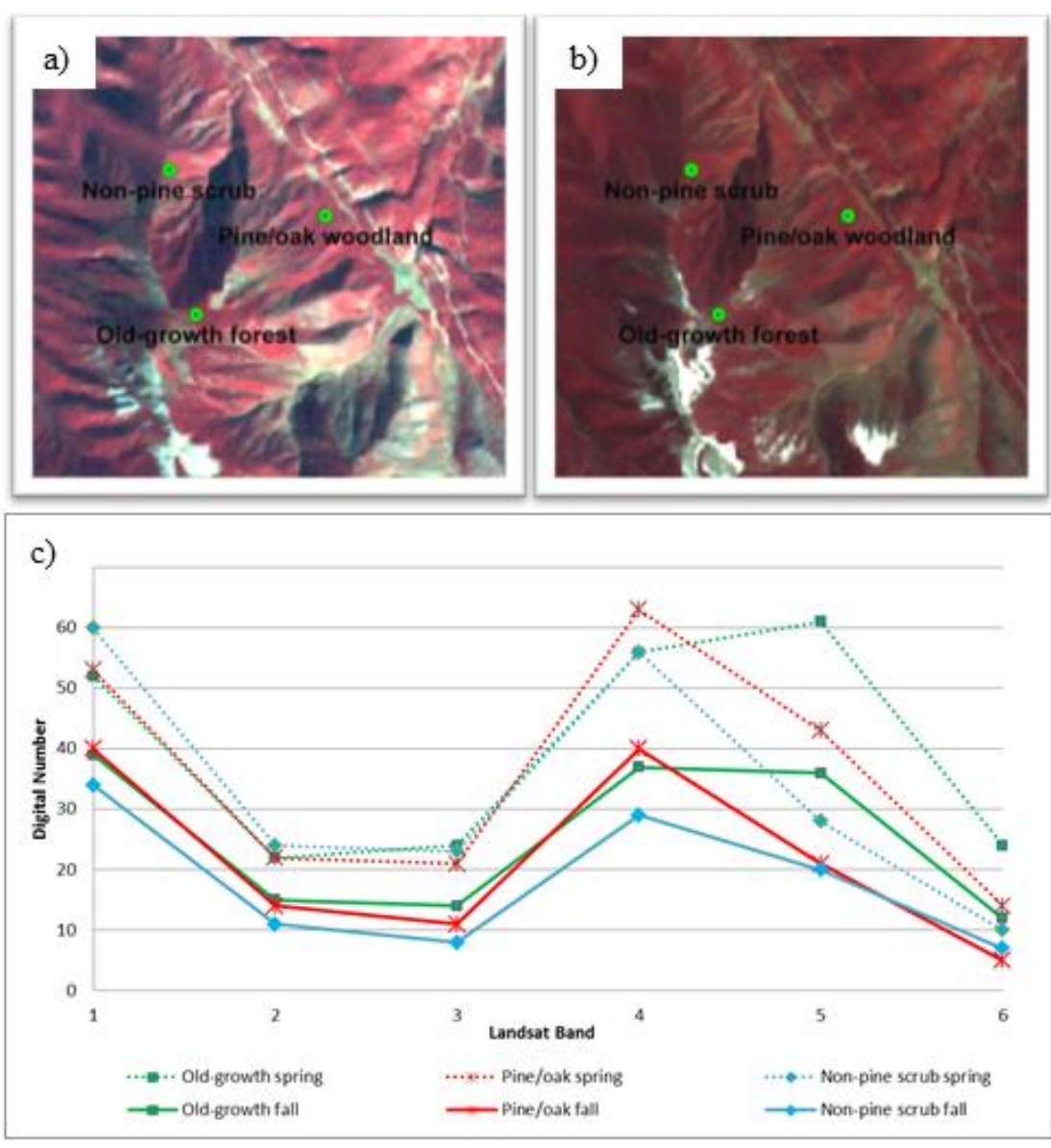
Figure 3. Description of how multitemporal imagery was used in a combined composite and
post-classification change detection approach.
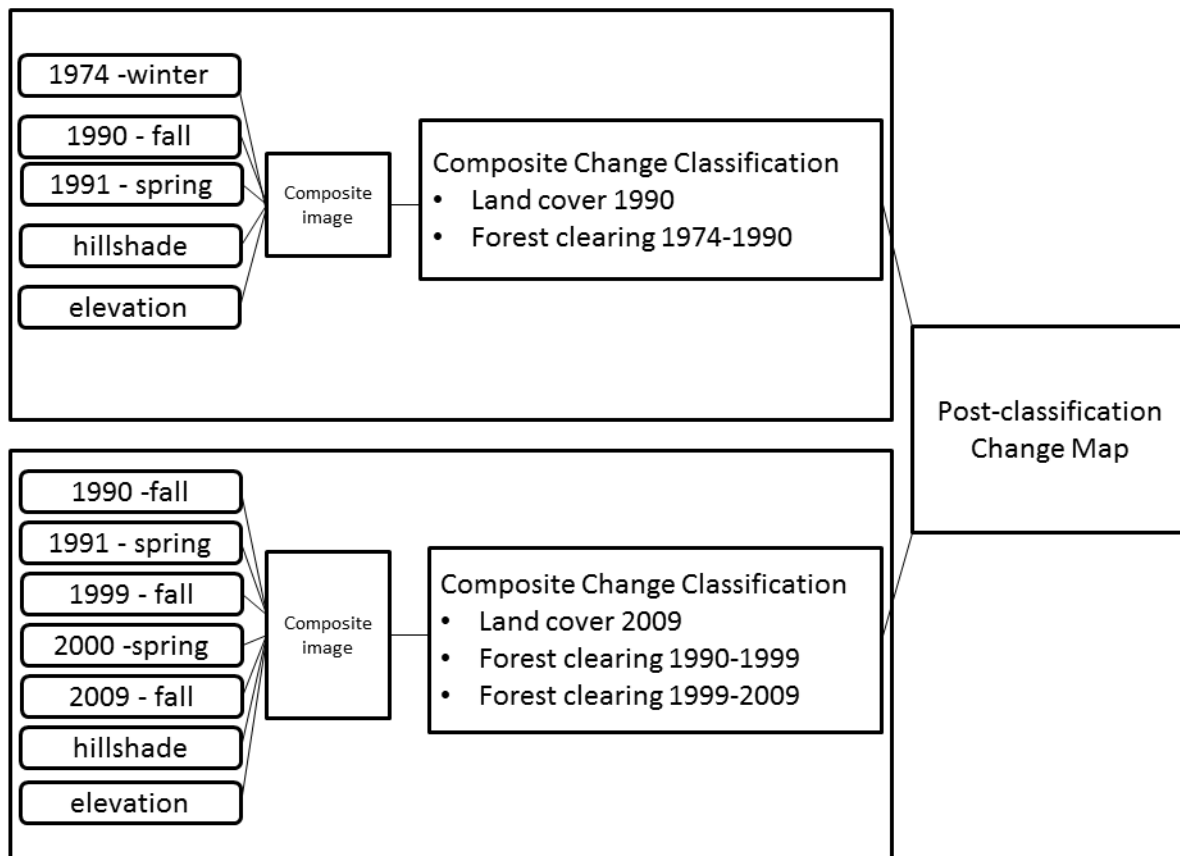
Figure 4. Hectares of forest loss by forest type during the Pre-ban (1990-1999) and Post-ban (1999-2009) periods.
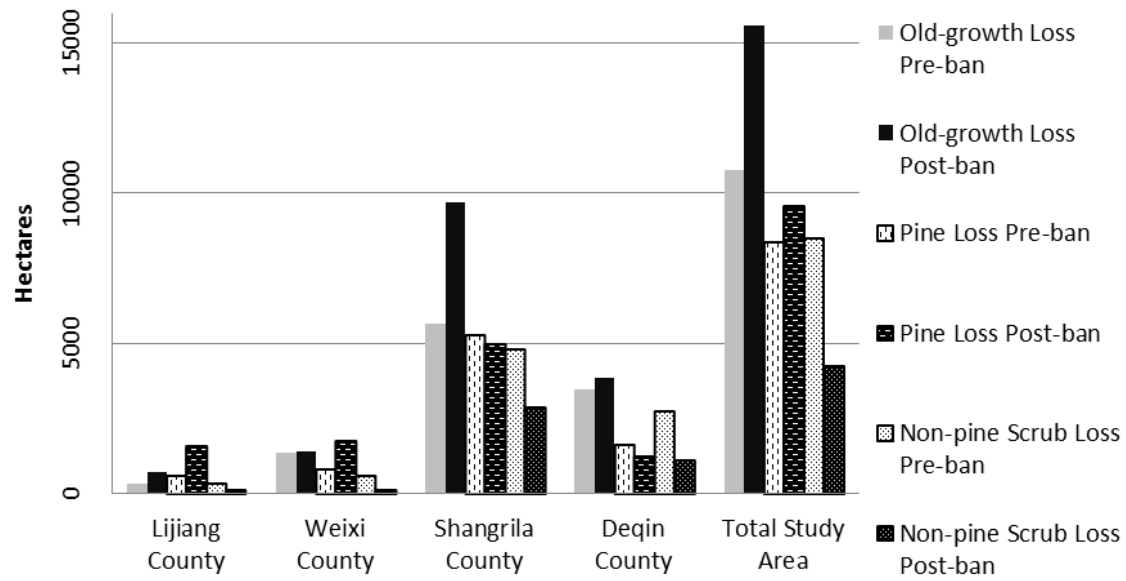
Figure 5. Land cover distributions in a) 2009 and b) 1990 for the entire study area. The 2009 land

cover of areas c) logged during the Historic period (1974-1990) and d) classified as secondary

forest/shrub during the Historic period.
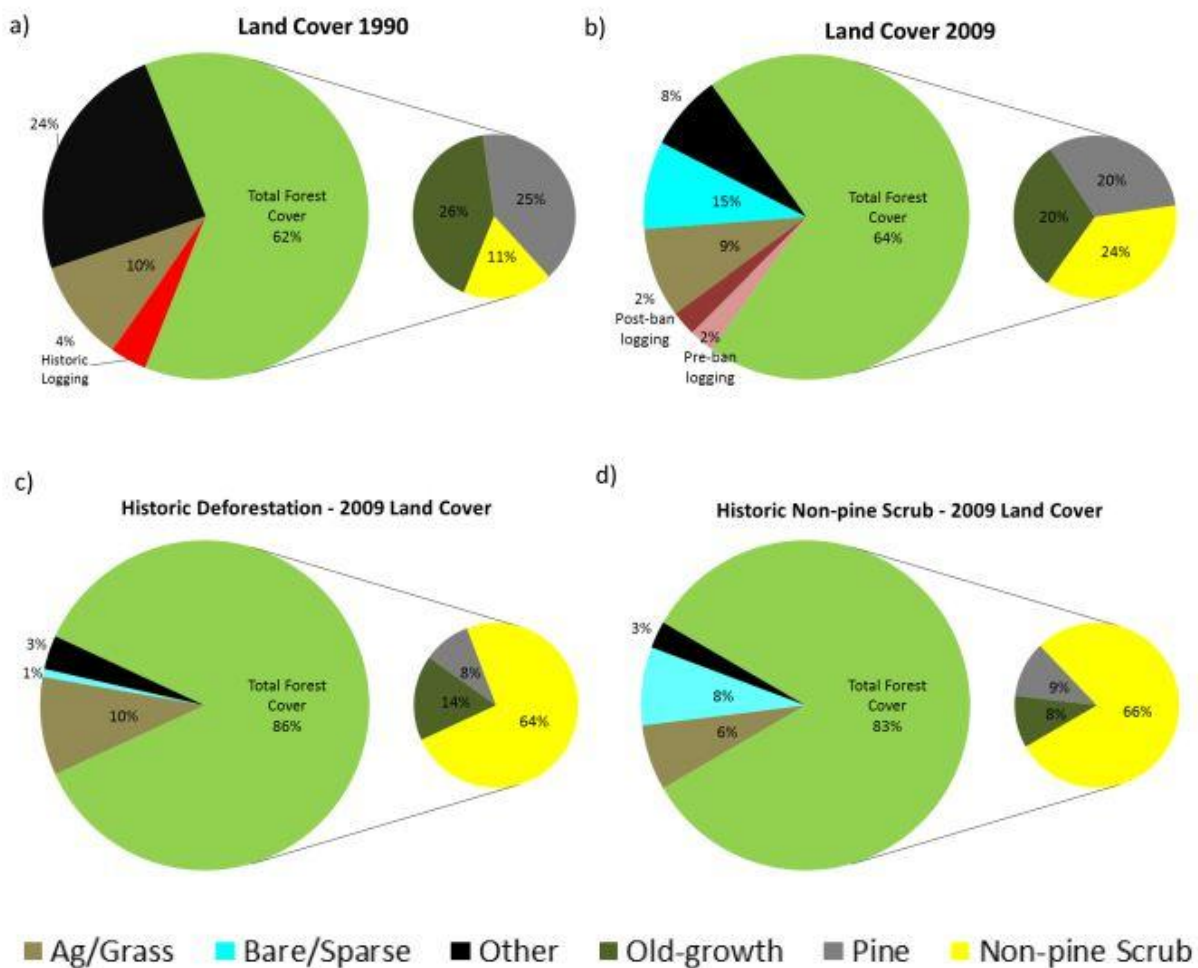
Figure 6. A subset of the classifications for an area 8 km north of Shangrila that experienced intense logging during the Historic, Pre-ban and Post-ban periods. a) Logging activity and non-pine scrub surrounded a large patch of old-growth and pine forests during the Historic period. b) The composite classification from 1990-2009 for only those areas that were logged or non-pine scrub during the Historic period show that the majority of these areas regenerated as non-pine scrub. Exceptions include regenerating pine plantations and sites that continued to be logged. c) During the Pre-ban and Post-ban periods, the large patch of pine and old-growth forest from (a) experienced intense logging.
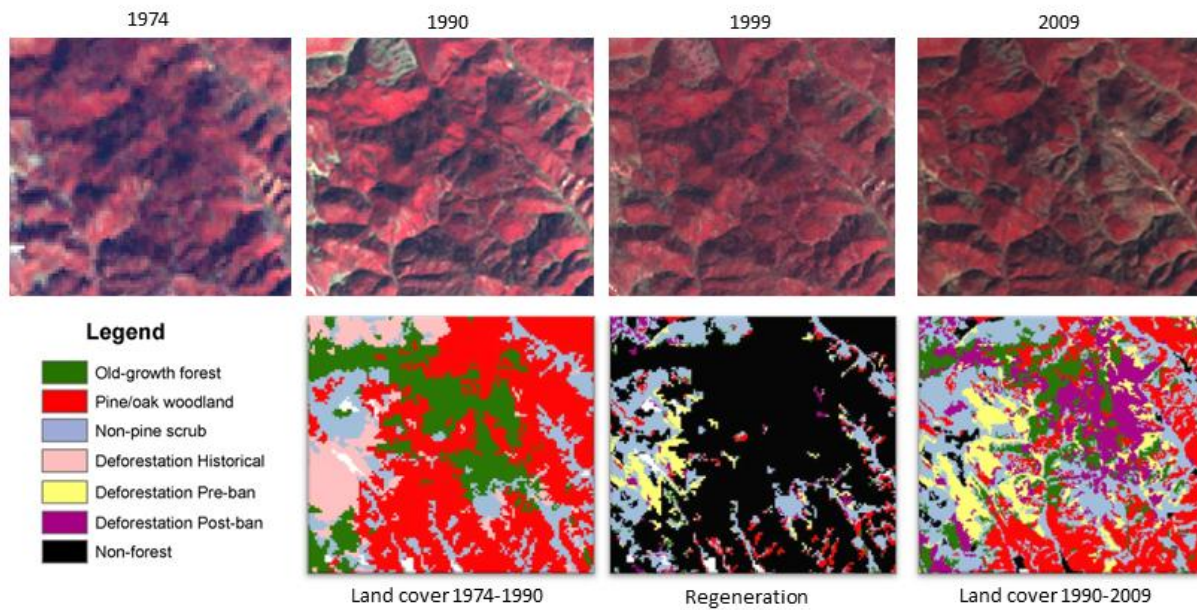
Figure 7. Patterns of (a) current proportion of old-growth forest on the landscape and (b) relative rates of regeneration as old-growth forest.

**a) 2009 Proportion of   b) Regeneration as
Old-growth Forest   Old-growth Forest**
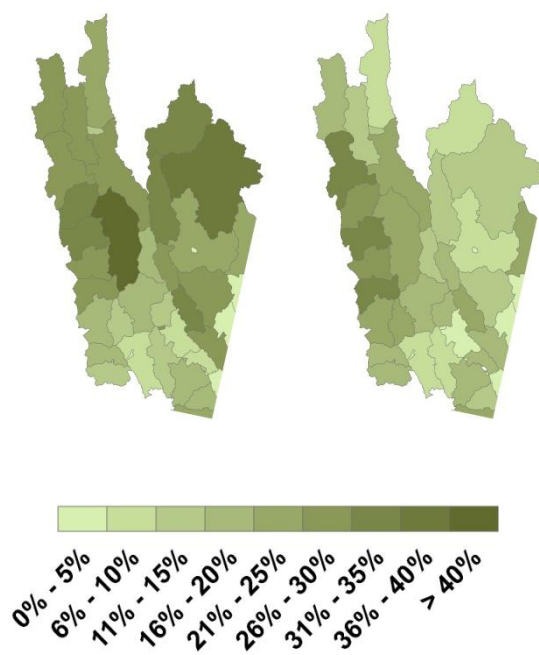
Figure 8. a) Economic development and population growth, and b) growth of the tourism industry in Diqing Prefecture.

a)

Growth of Tourism Industry

b)

Economic and Population Growth
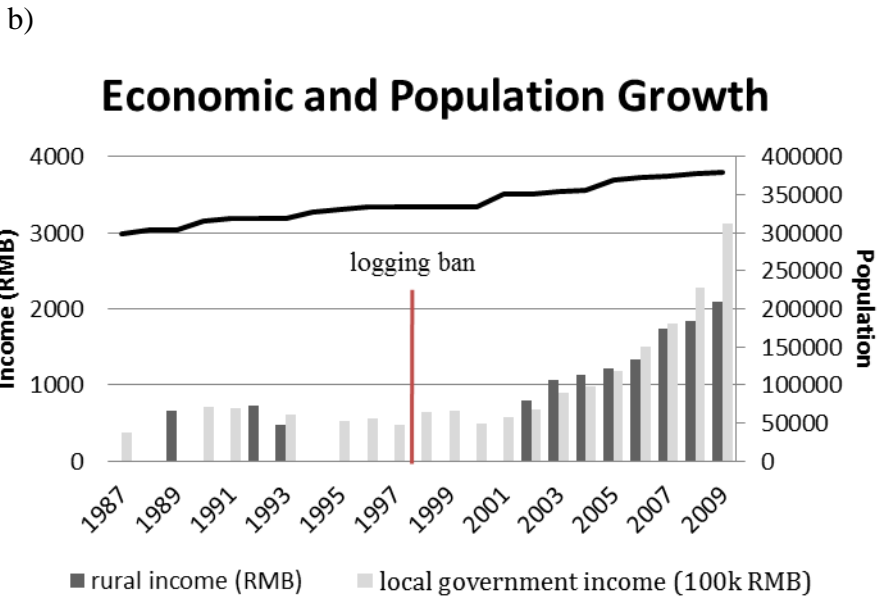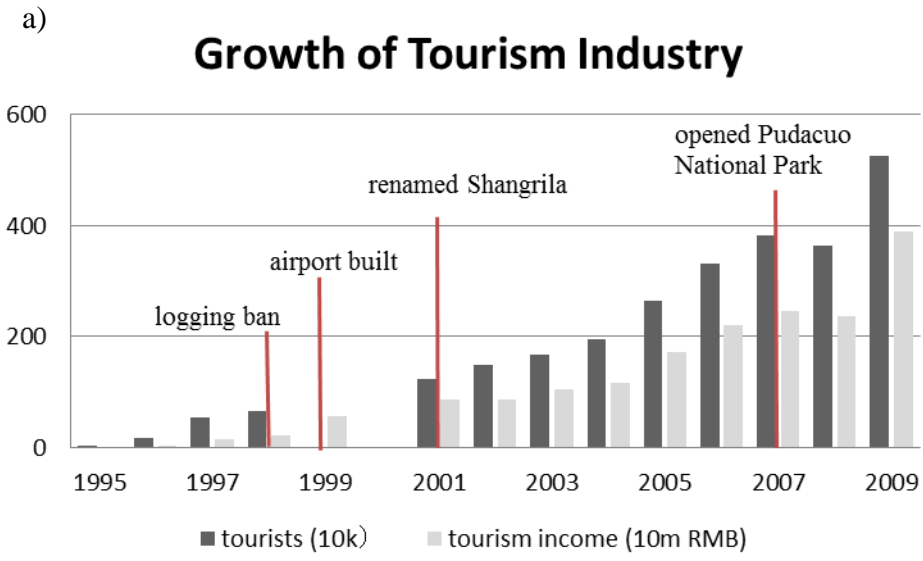
Appendix 1. Description of classification scheme, training data, and species composition of forest classes.

Final image class	Training data class	Shapefile	Description	Imprtant species
Old-growth Forest	Primary Fir/Spruce Forest	fir_prim	Mature forest dominated by fir	*Abies Georgii, Picea Brachytyla*
	Primary Mixed forest	mix_prim	Mature forest with mixed species composition	*Pinus densata, Abies Georgii, Picea Brachytyla, Larix potaninii var. macrocarpa, Betula albo-sinensis, Quercus aquifolioides, Quercus pannosa, Rhododendron sp.*
	Primary Oak Forest	oak_prim	Mature forest dominated by evergreen oak	*Quercus acuifolioides, Q. pannosa*
Pine forest	Pine/oak Woodlands	pine	Forest dominated by pine overstory (typically secondary) and evergreen oak understory.	*Pinus densata, Pinus yunnanensis, what quercus?*
Non-pine scrub	Mixed shrub	shrub_mixed	Shrub and scrub species with a mix of deciduous and evergreen species.	*Rhododendron spp., Quercus spp., Rosa sp., Cotoneaster spp., Sabina spp., Spiraea spp., Lonicera spp., Ribes spp. and Dasiphora spp.*
	Oak shrub	shrub_oak	Shrub dominated by evergreen oak shrub	*Quercus monimotricha*
	Alpine shrub	shrub_rhod	Alpine shrub communities.	*Sabina squamata, Rhododendron spp. Quercus pannosa, Berberis wilsonae, Rhodendron adenogynum and polifolium*
Grassland	Grassland	grassland	Herbaceous, < 10% woody.	
Agriculture	Agriculture	ag		
Dry valley scrub	Dry valley scrub	mtn_shrub_bare	This is typical of the steep, dry soils of the Mekong and Lancang river valleys. A mix of shrub and scrub woody species on bare soil and rock	
Bare	Bare Rock	barerock09	High-elevation bare rock outcrops	
	Bare Soil	baresoil	Barren soil	
	Urban development	urban	Developed areas	
Other	Snow	snow		
	Water	water		
	Other	other		
Encroachment	Encroachment	cd_grass-shrub_90-09	Areas that were grassland in 75 and 90, but had converted to shrubland in 2009	
Deforestion - Pre-ban	Deforestion - Pre-ban	cd_mf-loss_90-99	Forest clearing between 90 and 99	
Deforestation - Post-ban	Deforestation - Post-ban	cd_mf-loss_99-09	Forest clearing between 99 and 2009	
Deforestation - Historic	Deforestation - Historic	mf_loss_75	Forest clearing between 74 and 90	

Appendix 2. Average reflectance values in each Landsat bands for all three forest classes in the October 1999 and the April 2000 images.
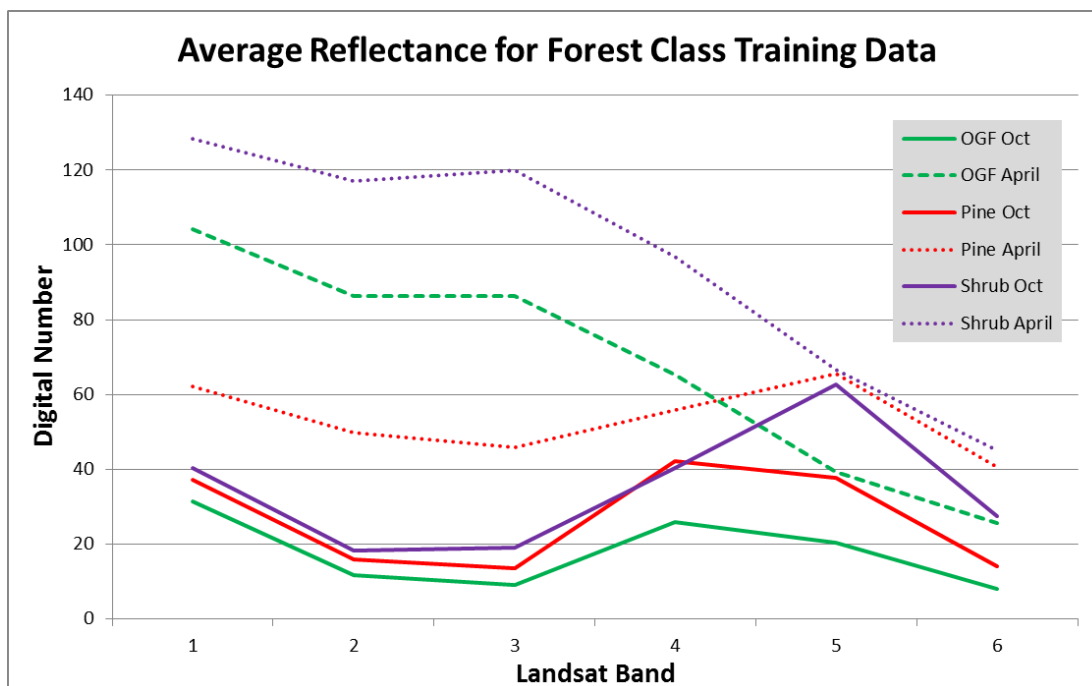
Class/Image Date		Band 1	Band 2	Band 3	Band 4	Band 5	Band 6
OGF Oct	Mean	31	12	9	26	20	8
	SD	2.7	1.4	1.4	7.8	6.5	2.6
OGF April	Mean	104	86	86	65	39	26
	SD	46.2	44.7	49.9	21.0	14.3	8.5
Pine Oct	Mean	37	16	14	42	38	14
	SD	3.6	2.6	3.1	13.7	13.7	5.6
Pine April	Mean	62	50	46	56	66	41
	SD	7.5	7.5	8.9	10.2	14.8	9.7
Shrub Oct	Mean	40	18	19	40	63	28
	SD	6.0	4.0	6.2	13.5	25.4	12.8
Shrub April	Mean	128	117	120	97	67	45
	SD	78.7	82.5	84.4	60.5	27.1	17.7

Chapter 2: Regime shift on the roof of the world: Alpine meadows converting to shrublands in the southern Himalayas

Abstract

Worldwide, changing climates and land use practices are escalating woody-plants encroachment into grasslands, reducing biodiversity and altering ecosystem functions. The loss of alpine grasslands is a major conservation concern as they harbor many rare and endemic species. Alpine meadows in Northwest Yunnan, China, represent a global biodiversity hotspot with high species richness, beta diversity, and endemism. Shrubs have expanded greatly in the region and threaten alpine meadow biodiversity. To measure rates of meadow loss due to shrub encroachment and identify its mechanisms, we reconstructed alpine land cover, climate, and land use change from 1950 to 2009 across Northwest Yunnan using satellite data, ground surveys, and interviews. Between 1990 and 2009, at least 39% of the alpine meadows converted to woody shrubs. The patterns of change suggest that a regime shift is occurring. Despite multiple perturbations to the climate and land use systems starting in the 1950s, alpine meadows remained resilient to shrub expansion until the late 1980s. Shrublands rapidly expanded then due to feedback mechanisms involving climate, woody cover, and grazing. Fire is no longer an effective tool for controlling shrub expansion. This regime shift threatens both endemic meadow biodiversity and local livelihoods. More generally, these trends serve as a warning sign for the greater Himalayan region where similar vegetation changes could greatly affect livelihoods, hydrology, and climate.

Introduction

      Worldwide, shrubs are encroaching in grasslands, affecting biodiversity, ecosystem function, and carbon storage (Knapp et al. 2008). Climate change, overgrazing, and land use all contribute to shrub encroachment (Walker and Wahren 2006). When multiple interacting factors reach a critical threshold, a relatively small perturbation can trigger a regime shift, i.e., a sudden, and potentially irreversible, transition to an alternate state (Scheffer 2009). To conserve grassland biodiversity, the drivers of shrub encroachment need to be identified and their critical thresholds determined. Untangling these factors, however, is challenging in coupled natural and human systems (Brock and Carpenter 2010).

      Shrub encroachment into alpine meadows represents a particular grave conservation threat (Montane et al. 2007; Xu and Wilkes 2004). Alpine meadows often harbor many endemic plants adapted to harsh conditions, and orogenies have resulted in high levels of both paleo- and neo-endemism (Wu et al. 2007). With the largest alpine ecosystems in the world, alpine meadows in the Greater Himalayan region are of particular concern. Northwest Yunnan Province in southwest China represents a global biodiversity hotspot (Myers et al. 2000), and meadows here have higher species richness, beta diversity, and endemism than elsewhere in the Himalayas (Salick et al. 2009; Xu et al. 2009).

      Historically, Himalayan meadows have been used by indigenous agro-pastoralists whose rangeland management practices sustained both local livelihoods and biodiversity (Klein et al. 2011). The highly nutritious meadows are critical to Tibetan transhumance herding, and the replacement of meadows by unpalatable shrubs threatens their livelihoods (Yi et al. 2007). Alpine meadow species can persist in the low-intensity land use systems typical for montane regions, but even subtle environmental changes may threaten them (Galop et al. 2011; Thuiller et al. 2005). For example, when climate change shifts woody vegetation to higher elevations,

species of alpine mountaintop meadows may not be able to migrate to other suitable environments (Parmesan 2006). Likewise, the abandonment of traditional land use practices can result in shrub encroachment (Baur et al. 2006; Laiolo et al. 2004). Indeed, climate change and land use change interact in alpine ecosystems making it difficult to identify the main driver(s) of shrub expansion.

Since the 1950s, numerous environmental changes affected Himalayan ecosystems. Climate warming rates here are higher than the global average, altering ecosystem productivity (Peng et al. 2010), phenology (Yu et al. 2010), and permafrost (Xu et al. 2009). Changing political and social structures have led to economic development and abandonment of traditional land use practices (Klein et al. 2011; Yeh and Gaerrang 2010). However, despite grassland degradation throughout the Himalayas (Harris 2010), rates of shrub encroachment have not been quantified, and its drivers are not well understood.

Our goals were a) to measure rates of shrub expansion into alpine meadows in Northwest Yunnan and b) to identify the likely mechanisms driving these changes. We used Landsat TM/ETM+ satellite image analysis and dendrochronology to map land-cover distribution and change in the forest/shrub/meadow ecotone of the alpine zone (3,800 - 4,500 m) in 1974, 1990, and 2009. In addition, we reconstructed changes since the 1950s using interviews, livestock records, and climate data. We then tested the following hypotheses:

H1.   *Climate change*: We hypothesized that temporal patterns of shrub establishment and expansion were caused by changes in temperature and precipitation. Warming alters phenology (Sturm et al. 2005; Yu et al. 2010) and caused shrub encroachment in other alpine (Harte and Shaw 1995; Klein et al. 2007) and arctic (Elmendorf et al. 2012a; Elmendorf et al. 2012b; Molau 2010) environments. Snowpack variability can alter

productivity of high-elevation systems (Peng et al. 2010) and cause shrub encroachment (Bjork and Molau 2007; Wipf and Rixen 2010). In the Himalayas, temperature, precipitation, snowpack, and phenology changed rapidly since the 1950s (Gao et al. 2012; Xu et al. 2009), and NW Yunnan represents a hotspot of change even within the Greater Himalayas (Haynes 2011), resulting in receding glaciers and advancing tree lines (Baker and Moseley 2007; Wong et al. 2010).

H2.   *Burning cessation*: We hypothesized that the 1988 region-wide burning ban triggered shrub establishment, and that areas where burning continued irrespectively suffered less shrub encroachment. Burning cessation has triggered shrub encroachment world-wide (Roques et al. 2001). In NW Yunnan, herders historically burned shrubs to improve meadows, but the 1988 burning ban may have fostered shrub encroachment (Sherman et al. 2008).

H3.   *Shrub autocatalysis*: We hypothesized that shrub autocatalysis, where existing shrubs facilitate further shrub expansion due to feedbacks (D'Odorico et al. 2010; Ratajczak et al. 2011; Sturm et al. 2005), was an important driver of shrub expansion. Feedbacks are critical components of regime shifts, because they push the original ecosystem towards an alternate stable state from which reversion to the original state is difficult or impossible (Scheffer 2009).

H4.   *Overgrazing*: We hypothesized that areas of high grazing intensity had more shrub encroachment, because shrubs establish more easily when other vegetation is removed (Eldridge et al. 2011; Schlesinger et al. 1990).

H5.   *Abandonment*: We hypothesized that territories where alpine yak herding was abandoned have particularly high shrub encroachment rates because activities associated with

humans (e.g., clearing of woody vegetation) may facilitate encroachment. Abandonment was the major driver of 20th century shrub encroachment in the European Alps (Galop et al. 2011; Montane et al. 2007). In our study area, economic development integrated rural areas into the regional economy of western China since the 1980s (Yeh and Gaerrang 2010), leading to abandonment of yak herding in some villages (Yi et al. 2007).

Materials and methods

Study area

Northwest Yunnan Province is at the southeast edge of the Qinghai-Tibetan Plateau (QTP), bordering Tibet and Sichuan Province (Fig. 9a), and an IUCN biodiversity hotspot (Myers et al. 2000). Three major rivers (the Yangtze, Mekong, and Salween) create steep gorges, with elevations ranging from 1,800 to 6,740 m. The alpine zone occurs between 4000 and 5000 m. Climate in the alpine zone is cold with near-constant rain during the monsoon season (June-September) and sporadic snowfall from October through May. The mean annual temperature above 4,100 m is < 0° C (Sherman et al. 2008).

The alpine zone consists of shrub, meadow, and scree ecosystems. Meadows exhibit the highest species richness and support the most rare and endemic plant species (Salick et al. 2009; Sherman et al. 2008). Alpine meadow communities are dominated by *Polygonum viviparum*, *Potentilla fulgens*, *Fragaria nilgeerensis*, *Anemone narcissiflorioides*, *Cyananthus flavus*, and *Festuca ovina* and include *Pedicularis dolichoglossa*, *Viola szetchuanensis*, *Agrostis limprichtii*, and *Primula* sp. (Li and Walker 1986), and beta diversity is high (Salick et al. 2009; Sherman et al. 2008).

Alpine meadows are crucial to local Tibetans' yak husbandry because meadows provide the highest nutritional value (Yi et al. 2007). When interviewed, herders confirmed the increase

in shrubs, and cited it as a major threat to livelihoods (Haynes 2011). The shrub invaders include

Rhododendron spp., *Juniperus* spp., *Berberis* spp., *Potentilla fruticosa* and *P. glabra*, all of

which are either noxious or poor forage for grazers (Haynes et al. In press).

Satellite Image Analysis

General Approach

We used Landsat TM/ETM+ images and a multi-temporal change classification

technique to quantify land use and land cover change in the alpine zone (> 3800 m) in two time

periods: 1974–1990 and 1990-2009. We then summarized land cover patterns and encroachment

rates to determine temporal and spatial patterns of shrub encroachment, and test hypothesized

drivers of the encroachment. A detailed description of the satellite image analysis is included in

Brandt et al. 2012.

Satellite imagery and image pre-processing

The study area is covered by two Landsat footprints (path/row 132/040 and 132/041). We

acquired Landsat MSS images from 1974, and Landsat TM/ETM+ images from circa 1990,

2000, and 2009, and co-registered all images to the orthorectified Landsat 2000 GeoCover

Dataset. Positional uncertainty was < 0.4 pixels (<12 m). Clouds and cloud shadows were

masked manually.

Ground-truth data collection

We collected field data to train and validate the satellite classifications in July-November

2008, August-October 2009, July-September 2010, and May-July 2011. Due to the ruggedness of

the study area, a random sampling design was not feasible. We collected field data in nine alpine

territories prior to image analysis, and nine different alpine territories thereafter (Table 4). We

hired local guides, conducted informal interviews about land-use, and recorded land use for at

least 40 locations within each land cover type and took photographs of the surrounding 1 ha

(Justice and Townshend 1981). To supplement the field data, we gathered additional ground-truth data from high resolution imagery in GoogleEarth[TM] (approximately 20% of the ground truth dataset). In total, our ground truth dataset included 1,573 polygons (93,300 pixels).

Image classification

To classify land cover change, we used a composite analysis approach. Composite analysis uses multi-date imagery, i.e. satellite images from multiple seasons and different years are combined into a single image stack. The added phenological and temporal information of the multi-date imagery allows more detailed land cover classification (Wolter et al. 1995) and more accurate classification of land cover change (Brandt et al. 2012; Kuemmerle et al. 2006). To separate the classes, we used Support Vector Machines (SVM). SVM is a non-parametric classifier that places hyperplanes to separate different classes (Foody and Mathur 2004). SVM are well-suited for composite analysis in complex environments because they can accommodate the non-normal and multi-modal class distributions of multi-date imagery (Brandt et al. 2012; Huang et al. 2002).

We assessed two time periods, 1974-1990 (historic period) and 1990-2009 (recent period). For the historic period, we combined 1974 MSS images, circa 1990 TM images, and elevation and hillshade (corresponding to the illumination of the November 19, 1990 Landsat TM image) and separated four classes: Grassland, Shrubland, Forest, and Snow. Similarly, for the recent period, we combined TM/ETM+ imagery from 1990, 2000 and 2009, along with elevation and hillshade data (October 28, 1999 image) to classify the same land covers, plus the change class "shrub encroachment", i.e., those areas that converted from grassland in 1990 to shrubland in 2009. To fill cloud and snow gaps, we carried out a classification excluding the spring images (where snow is more extensive). To train and validate our SVM, we randomly

selected approximately 1000 points from each class in our ground truth dataset and used ten-fold

cross-validation(Brandt et al. 2012) . We used a minimum mapping unit of 6 pixels (~ 0.65 ha).

Accuracy assessment

To validate our change maps, we calculated a confusion matrix, overall, user's and

producer's accuracies, plus area-adjusted estimates of land cover proportions and their

confidence intervals (Card 1982). For the accuracy assessment, we used a total of 231

independent ground truth points, including 153 field points from 11 *post-hoc* field visits in 2010

and 2011. We also randomly sampled 78 points using GoogleEarth high-resolution imagery. For

the shrub encroachment class, we relied solely on field data. Acquiring independent data for the

historic shrub encroachment class was not possible retrospectively and we report the cross-

validation accuracies only.

Temporal and spatial patterns of encroachment

We estimated shrub encroachment first as the encroachment rate (ER), i.e., the

proportional (%) area of grassland in 1990 that converted to shrubland by 2009.

$ER = 100 * E/(E + PG)$ *Eq. 1*

Here, E is the number of pixels in the encroachment class, and PG is the number of pixels

in the Permanent Grassland class. This measure is a slight overestimate, because most snow-

covered areas in the imagery were grasslands. Therefore, we also calculated a snow adjusted

encroachment rate (ERA) which assumes that all of the snow-covered areas were grassland:

$ERA = 100 * E/(E + PG+S)$ *Eq. 2*

where S is the number of snowy pixels. This represents a conservative rate of shrub

encroachment, because a small percentage of the snow-covered areas are shrub, bare ground,

scree, or bedrock.

We summarized encroachment rates and land cover for 1990-2009 at several different spatial scales. First, we summarized alpine land cover and change for the entire study area, and inside and outside of the Baimaxueshan National nature reserve, where burning prohibitions are most strictly enforced. Second, we summarized land covers for zones of 100-m elevation, 5° slope, and 45° aspect. Third, we summarized land cover change at the township level. Finally, we summarized encroachment and land cover within the alpine "territory" of each village where we had conducted interviews with herders (see below).

Dendrochronology

Data collection

To provide greater insight into the timing of shrub establishment we collected shrub cuttings from 125 shrubs in 13 sites and five territories. Prior to satellite image classification, we collected shrub cuttings in areas of mixed meadow and shrub land cover in the summer of 2008, for use in training the image classification. Following image analysis, we sampled areas mapped as encroachment in the summers of 2009 and 2010 for the accuracy assessment.

Analysis

Alpine shrubs of the southeastern Tibetan Plateau produce latewood, have clear growth rings, and can be used for detailed dendrochronological analysis (Liang and Eckstein 2009; Liang et al. 2012). It was beyond the scope of our study to perform detailed dendrochronological analysis, but we used standardized growth ring counting techniques to obtain estimates of the oldest and average ages of the shrubs at each site (Cook and Kairlukstis 1990; Montane et al. 2007). At each site, we cut discs from the base of at least 3 of the largest individuals of the dominant shrub species. Samples were sanded and digitally photographed on a ruler to enable

thorough ring counting. A ring was indicated by a section of earlywood followed by a section of latewood. Proper training and magnification of microsections enabled false rings to be identified.

Climate Data

Data Collection

We acquired meteorological station data from 1960 to 2008 from the two National Meteorological Administration of China stations in our study area, Zhongdian and Deqin counties.

Analysis

We calculated local variation in the rates and seasonality of change over the last half century (1960-2008) using the cumulative method (Lozowski et al. 1989) to filter out noise. We calculated 24- and 48-year rates of change for precipitation, annual daily low, annual daily high, growing season daily low, growing season daily high, winter daily low, and winter daily high (Haynes 2011).

Alpine vegetation is vulnerable to snowpack and snowfall variability. Ideally, our climate data would have included long-term data on snowpack and snowfall change in the alpine zone. Lacking such data, we estimated alpine zone temperature changes from 1960 to 2009. We were especially interested in periods when average daily low temperatures changed from sub-freezing to above-freezing temperatures.

To estimate temperature changes at alpine elevations, we used 48-year temperature data at the Deqin County station (3320 m), and data from 13 stations ranging from 1646 to 4292 m within Deqin County based on at least 20-year means (Le'anwangdui 2001). We calculated the linear lapse rate adjustment for each month (Dodson and Marks 1997) since this technique provides more detail than the global mean lapse rate of -6.5°C km^{-1} (Barry and Chorley 1987),

does not require interpolation which is often inaccurate for the Himalayas (Leemans and Cramer 1991; Rolland 2003), and was spatially detailed enough for our analysis. The linear lapse rates fit well within global estimates and followed the expected trend from months of lower moisture to higher moisture (Barry and Chorley 1987; Dodson and Marks 1997; Rolland 2003) (February, -6.65°C km^{-1}; March, -6.35°C km^{-1}; April, -6.25°C km^{-1}; May, -5.91°C km^{-1}; June, -5.59°C km^{-1}, all r^2 > 0.97). Average daily low and high temperatures, as recorded at Deqin climate station, were then used to calculate low and high temperatures at all elevations in the alpine zone (>3800 m) for February through June using our DEM and the lapse rate adjustments.

Formal Interviews and Livestock Records

Data Collection

From 2006 to 2010, we performed informal and formal interviews to determine alpine land use history and land cover change since the 1950s (Haynes 2011). In the summer of 2006 we held open-ended interviews with local officials and with villagers during house stays. In the summers of 2007 and 2008 we conducted preliminary interviews at the alpine rangelands. Ethnographic investigations were conducted in 2009 and 2010, taking extended trips with Tibetan herders to alpine rangelands to discuss ecological and livelihood changes and to collect ground-truth data for the satellite image analysis. Formal, semi-structured interviews were conducted with 37 herders in six villages during the winter of 2010, before the spring festival holiday during a time when villagers had a break from harvesting and had returned from herding in the distant summer pastures. The survey instrument contained 7 sections: background of the interviewee, animal husbandry, burn history, village history, livestock health, ecology, and future expectations. In response to initial interviews, we modified the survey instrument to include additional sections on village history and detailed questions about traditional burning practices.

We collected data on general burning practices in five time periods: feudal (prior to 1958), collectivization (1959-1982), decollectivization (1983-1987), post burning restrictions (1988-1999), and present time (2000-2010). Using the snowball method, we sampled households with experienced herders to gather information on the depth of knowledge from those with the longest history in rangeland management in the area. To assess additional village level characteristics and the history of administrative decisions, we also interviewed officials from the grassland monitoring station and animal husbandry bureau.

Livestock data were collected from published literature, including the Deqin County and Diqing Prefecture Almanacs, and annual statistical almanacs (Deqin 1997; Le'anwangdui 2001).

Analysis

From the formal interviews, we calculated the percent of respondents who participated in, or had heard of, burning during each of the five time periods included in the survey instrument.

Results

Changes in Alpine Land Cover

Land use and land cover in the alpine zone (Fig. 9b) were mapped with an overall accuracy of 94% and 93% in the recent and historic time period, respectively (Table 5). The overall accuracy of the shrub encroachment class was 91%, and the minimum accuracy of any class was 80%.

Changes in the proportions of grass and shrub between 1974 and 1990 were negligible, and forest cover remained largely unchanged from 1974 to 2009 (Fig. 9c). However, from 1990 to 2009, meadows shrank from 20% to 7%, representing a shrub encroachment rate of 65%. Even the conservative adjusted encroachment rate (which assumes snow-covered areas to be

unchanged grassland) was 39%, representing an annual encroachment rate of 2.1%. All rates reported in the following are adjusted encroachment rates.

Spatial patterns of Shrub Encroachment

Shrub encroachment rates varied across the study area, with low rates in the western and southern townships (~5%) and high rates in the northern and eastern townships (>65%) (Fig. 10a). Encroachment rates, summarized for each of the village territories where we conducted interviews, were negatively associated with the proportion of spring snow cover from the image classification (Pearson's r = -0.687) and positively correlated with the proportion of woody cover in 1990 (Pearson's r = 0.692, Fig. 10b).

Meadows at the lower elevations of the alpine zone (between 4000 m and 4200 m) were encroached most rapidly (>40%), whereas encroachment rates in the sub-alpine (3800-4000m) and upper alpine meadows (4300-4500m) were lower (Fig. 10c). Meadows on the sunnier south, SE, and SW facing slopes were encroached twice as fast (40-50%) as those on north-facing slopes (18-23%) (Fig. 10d). Encroachment rates did not vary among different slope zones.

Encroachment rates near the national highway were highest (~60%) and declined further away (to about 40%) (Fig. 11a). Encroachment rates within the Baima Reserve (26%), where the burning ban was strictly enforced, were lower than outside the reserve (42%) (Fig. 11b). Remote villages where patchy burning was still practiced had some of the highest rates of encroachment (>50%) compared to <41% in villages where burning was no longer practiced. The two territories that were abandoned exhibited both one of the lowest (12%) and the highest (72%) encroachment rates (Fig. 11b).

Temporal Trends in Shrub Establishment

According to the satellite classification, eight of the 13 sites sampled for the dendrochronological analysis converted from grass to shrub from 1990 to 2009, three sites were stable grasslands, and two sites were already shrub-dominated before 1990 (Table 6). Seven of the eight converted sites had > 50% shrub cover according to field visits. All converted sites contained at least three different shrub genera, but dwarf rhododendron was dominant in seven of the eight converted sites. The oldest shrub in each site (typically *Juniperus spp.*) established around 1980 (age = 29 years (SD 4.2)) and the oldest rhododendron shrubs established in 1988 (age = 21 years (SD 8.1)).

Climate Change

Deqin and Shangri-la counties experienced substantial changes in temperature and precipitation from 1960 to 2008. At the Deqin County station the rate of daily high temperature change over the past 24 years was 7.2°C/100 years and the rate of change in daily low temperatures was 1.4°C/100 years. At the climate station and at higher elevations, average estimated daily high and low temperatures generally increased from 1960 to 2008 (Fig. 12a and 12b). At 4000 m, the most dynamic oscillation around the 0° mark occurred in May between 1980 and 1990, with minimum temperatures rising consistently above freezing by the mid 1980s (Fig. 12b). In the alpine zone overall, average daily low May temperatures were generally below freezing at the beginning of our study period (1959 to 1969) (Fig. 12e), but above freezing for the lower elevations of the alpine zone (i.e. 3800 to 4200 m) at the end of our study period (1999 to 2008) (Fig. 12f). Precipitation changes were especially pronounced in spring (February through May) after 1980 (Fig. 12c and 12d). The overall amount of precipitation during these months did not change considerably, but there was increased rainfall (Fig. 12c) and no snowfall (Fig. 4d) after 1980 at the climate stations.

Changes in Land-use Practices

Our interviews and official livestock records highlighted that the period from 1950 to 2009 was delineated into three major eras of policy shift and land tenure: Feudal, Collectivization and Decollectivization (Fig. 13). Alpine herding practices, including yak herd size and burning practices, varied greatly among eras. During the Feudal era (pre-1958), village chiefs or monasteries owned and managed the livestock, and yak herds were small (< 50,000 total head of yak in Diqing prefecture in 1952). Grasslands were abundant and burning was limited (only 11% of respondents reported burning). During the Collectivization era (1958-1983), livestock and land were collectivized, with incentive to increase production. Total herd sizes grew to >150,000 yaks by 1983, and alpine burning was at its peak (54% of respondents reported burning). Following decollectivization (1983-present), families for the first time owned and managed livestock and land. Total head of yak grew to a peak of almost 250,000 in 2001. Burning diminished (to 40%) immediately after decollectivization, and decreased further after the 1998 burning restrictions (to 22% from 1988 to 1999 and then to only 11% from 2000 to 2009).

Synthesis of land use, climate and shrub establishment from 1950 to 2009

The synthesis of our satellite, dendrochronology, climate, and land use data (Fig. 13) indicated that alpine ecosystems were subject to mounting perturbations in both the land use and the climate systems from 1950 to 2009 (Fig. 14). During the feudal era (Fig. 14a), alpine land use, climate, and land cover were stable. Following collectivization (Fig. 14b), climate became slightly warmer and wetter, and land use practices shifted due to incentives for increased production under the communal system. Alpine land cover remained stable. Following decollectivization, burning prohibitions were enacted and yak herds grew. Grazing pressure

increased throughout the alpine zones, and especially along major transportation routes.

Perturbations in the climate system, including rising temperatures and decreasing snowfall, also

mounted. The first dwarf rhododendron shrubs established in 1988, and expanded rapidly (Fig.

14).

Discussion

Implications of Shrub Encroachment for Biodiversity

Alpine meadows remained unchanged from 1974 to1990 despite changes in climate and

land use, but an abrupt shift occurred from 1990 to 2009 when at least 39% of all meadows were

encroached by shrubs. The annual encroachment rate of 2.1% is among the highest reported in

the literature (0.1%-2.3% per year) for other areas of broad-scale shrub expansion (Briggs et al.

2005; Coop and Givnish 2007; Sankey and Germino 2008; Thompson 2007).

Given the exceptionally rich flora with many endemics, this shrub encroachment is likely

to seriously deplete plant diversity in the region . The highest plant diversity of this region is

found in alpine meadows (Sherman et al. 2008) between 4200-4500m (Salick et al. 2004). Our

results showed that meadows in this elevation zone disappeared at a rapid rate, and the shrinking

habitat area represents a major conservation threat (MacArthur and Wilson 1967). Each territory

has distinct species assemblages with little similarity of species among sites (Sherman et al.

2008). With shrub expansion rates approaching 70% in some townships, it is likely that such

meadow contraction is leading to a reduction in endemic plant biodiversity locally (Rejmanek

and Rosen 1992) and regionally (Eldridge et al. 2011; Ratajczak et al. 2012).

4.2 Evidence for a Regime Shift

The observed patterns of shrub encroachment suggested that the alpine zones of

Northwest Yunnan are shifting from an herbaceous to a shrub-dominated ecosystem. Regime

shifts occur when an ecosystem shifts suddenly from one state to the other, and the shift cannot easily be reversed even when the original environmental conditions are restored (Brock and Carpenter 2010; Groffman et al. 2006; Scheffer 2009).

There were three lines of evidence suggesting that a regime shift occurred. First, hypothesis testing revealed that shrub encroachment was influenced by multiple factors.

H1. Climate change: Our results indicated that increasing temperatures since the 1970s in our study area contributed to shrub encroachment. This was not surprising, because climatic change has been linked to shrub encroachment in alpine and arctic ecosystems around the world (Elmendorf et al. 2012a; Elmendorf et al. 2012b; Harte and Shaw 1995; Klein et al. 2007). In particular, decreasing snow cover gives a competitive advantage to shrubs over herbaceous species in alpine and arctic environments (Bjork and Molau 2007; Wipf and Rixen 2010), and our results indicated that snow cover and shrub encroachment were highly correlated. Furthermore, our alpine temperature estimates indicated that the most dynamic temperature changes occurred during late spring (May) in the mid 1980s when average daily low temperatures rose above freezing, which may have triggered the initial establishment of dwarf rhododendrons in 1988.

H2. Burning cessation: The results of our dendrochronological analysis suggested that the region-wide burning ban in 1988 may have fostered initial establishment of dwarf rhododendrons that then spread rapidly. However, contrary to our expectations, burning does not appear to have driven patterns of shrub encroachment. Rates of shrub expansion were higher in areas where burning continued relative to those that did not burn. Studies in other regions have demonstrated that following a shift from grassland to shrubland, shrub cover increases regardless of fire frequency, and some shrub species actually spread faster with burning (Briggs et al. 2005), likely

due to fundamental changes in ecosystem structure and function that accompany such an ecosystem shift (Bond and Keeley 2005).

H3. Shrub autocatalysis: Our results suggested that a strong feedback mechanism influenced shrub encroachment rates and patterns, because encroachment rates were higher in areas where woody vegetation was already prevalent. Shrub autocatalysis is a result of positive feedbacks, and common in shrub expansions worldwide (Sturm et al. 2005). It is not possible to determine the exact processes at play in our study area, but spatially-structured (Coop and Givnish 2007), micro-climatic (D'Odorico et al. 2010) and biotic (Dullinger et al. 2003) feedback mechanisms seem all plausible (D'Odorico et al. 2011).

H4. Overgrazing: Overgrazing appears to have accelerated shrub expansion. However, the temporal and spatial relationships between grazing intensity and shrub expansion suggest that grazing effects were not linear, because although grazing intensity increased gradually since the 1950s, rapid shrub encroachment did not occur until after 1990.

H5. Abandonment: We found no evidence that land abandonment influenced shrub encroachment. However, land abandonment has, as of yet, been a local and recent phenomenon, unlike the widespread rural exodus that resulted in shrub encroachment in the European Alps.

In summary, our results indicated that 4 out of 5 of our hypothesized drivers influenced shrub establishment and encroachment rates. Multiple causality is the rule in regime shifts, with grassland ecosystems notoriously vulnerable to state changes when both the natural and human systems that affects them change. The presence of multiple drivers of shrub encroachment in our study area is the first line of evidence suggesting a regime shift.

The second line of evidence for a regime shift is the presence of a critical threshold. Typically, prior to a regime shift, perturbations accumulate and start to interact, gradually

reducing system resilience before changes arise. After a critical threshold is reached, even a small perturbation can trigger a rapid shift to an alternative stable state. In NW Yunnan, despite increasing stress, we found no record of change in the alpine grasslands from 1950 to the 1980s. However, in the mid- to late 1980s dwarf rhododendron shrubs suddenly established and then spread rapidly.

Initial rhododendron establishment across several alpine territories appears to correspond to two potential triggers. First, May daily minimum temperatures at 4000 m shifted from sub-zero to above-freezing levels in the mid 1980s, likely reducing snowpack and snowfall. Increases in late-spring soil temperature and moisture can provide a competitive advantage for shrubs (Bjork and Molau 2007; Wipf and Rixen 2010). Second, the 1988 burning ban immediately reduced burning by about 20%, providing another potential trigger.

A final indicator of a regime shift is evidence for a strong feedback mechanism. A regime shift requires a strong feedback to push a shifting system towards the alternative stable state from which reversion to the original state is difficult. Our results indicated that shrubs spread most rapidly in areas with some prior woody vegetation (shrub autocatalysis). Although burning apparently served historically to effectively control shrubs, burning may no longer do so. In fact, dwarf rhododendrons quickly established and colonized many recently burned (<3 years) plots regardless of the original vegetation, supporting the idea that a regime shift occurred.

Broader Impacts

Shrub encroachment has major implications for ecosystem processes, structure and function, including reduced herbaceous plant biomass and species richness (Ratajczak et al. 2012), altered patterns of soil resource availability and distribution (D'Odorico et al. 2011; Schlesinger et al. 1990) and changes in ecosystem net primary productivity and nutrient balances

(Barger et al. 2011; Knapp et al. 2008; Montane et al. 2007). Shifts from one ecosystem to another often start in ecotones, making ecotones important sentinels of change (Hufkens et al. 2009). Our study area straddles the forest-shrub-grassland ecotone at the southern edge of the Himalayas, and may represent a sentinel for the rest of the region. Vegetation shifts at the scale of the Greater Himalayas would have major implications. The high mountains and plateaus of this region regulate the region's climate while serving as the headwaters of 3 major rivers in Asia. Shrub encroachment alters regional climate systems (Swann et al. 2010) and has significant effects on ecosystem hydrology and biogeochemistry (Knapp et al. 2008). This region is a center of diversity for endemic plants and mammals (Xu et al. 2009), and shrub invasion often leads to a decrease in diversity (Ratajczak et al. 2012). In addition, shrub encroachment forces grazers to rely more on forests, with negative consequences for forest ecosystem diversity (Yi et al. 2007).Therefore, although the exact consequences of shrub encroachment on ecosystem functioning in NW Yunnan alpine ecosystems is not well understood, it is likely that the observed changes have far-reaching implications at multiple spatial scales.

Management recommendations

Traditional herding systems in NW Yunnan sustained both local livelihoods and endemic biodiversity. However, the socio-economic and climatic conditions have changed dramatically. In the past, grazing and burning both appeared to be compatible with sustaining alpine ecosystems. Presently, burning and grazing may be less sustainable, given climate change and heavy shrub encroachment (Bond and Keeley 2005). For example, although fire was historically the primary tool for shrub control, our results indicated that it no longer slows shrub expansion. In addition, although our results indicated that areas with the highest grazing pressure had accelerated shrub encroachment rates, experimental studies on the Tibetan Plateau show that

moderate levels of grazing can mitigate warming-induced shrub expansion (Klein et al. 2007).

This leaves it unclear how yak herding is affecting current alpine environments. Herders,

officials, and scientists should together perform *in-situ* experimental research to understand

grazing thresholds, post-fire regeneration processes, and alternative shrub control strategies.

Furthermore, seed collection and seed bank storage, coupled with *ex situ* propagation in

botanical gardens throughout the region (Sang et al. 2011), may be needed to preserve threatened

endemic plants for future alpine meadow restoration.

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Table 4. Alpine territories visited from 2007-2011. Types of data collected at each site include:

G=Ground truth, D=Dendrochronology, FI=Formal Interview, II=Informal Interview

Site	Number of Visits	Timing of Visit	Data Collected
AD	5	Pre-classification	G, D, FI, II
BM	4	Pre-classification	G, D, FI, II
ML	3	Pre-classification	G, FI, II
XD	1	Pre-classification	FI, II
SS	1	Pre-classification	G, FI, II
YR	1	Pre-classification	G, FI, II
HP	1	Pre-classification	G, II
GZ	1	Pre-classification	G, II
YB	1	Pre-classification	G, II
MY	1	Pre-classification	G, II
HS	1	Pre and Post-classification	G, II
QH	2	Pre and Post-classification	G, II
SK	5	Post-classification	G, D, II
AB	1	Post-classification	G, II
TB	1	Post-classification	G, D, II
ZH	1	Post-classification	G, D, II
TC	1	Post-classification	G, II
DX	1	Post-classification	G
LE	1	Post-classification	G
NP	1	Post-classification	G, II
NL	1	Post-classification	G, II

Table 5. Alpine land cover/land use classification accuracy assessment for the Historic (1974-1990) and Recent (1990-2009) classifications.

HISTORIC CLASSIFICATION (1974-1990)					
Class	**PA**	**UA**	**Adj. Area (ha)**	**±CI (ha)**	**±CI (%)**
Grassland	94%	94%	94566	2245	2%
Shrubland	92%	86%	77296	2962	4%
Forest	99%	95%	257203	3949	2%
Snow	94%	93%	107379	2425	2%
Overall accuracy =			93%		
Khat =			0.93		
RECENT CLASSIFICATION (1990-2009)					
Class	**PA**	**UA**	**Adj. Area (ha)**	**±CI (ha)**	**±CI (%)**
Encroachment	93%	90%	69999	9624	14%
Grassland	80%	90%	43217	9091	21%
Shrubland	90%	86%	109362	14373	13%
Forest	97%	99%	311401	11290	4%
Overall accuracy =			94%		
Khat =			0.94		

Table 6. Summary of dendrochronological shrub analysis taken from 13 different sites in 5 different alpine territories.

Territory	Site	Land Cover Classification	Dominant Shrub Type	Total % Shrub Cover	Age of All Shrubs Average	SD
Visited Pre-Classification						
BM	B1	Permanent Grass	Rhododendron	50	16	2
	B2	Encroachment	Juniper	60	18	6
	B3	Permanent Shrub	Rhododendron	50	21	4
AD	A1	Permanent Grass	Juniper	6	24	14
	A2	Encroachment	Rhododendron	35	22	8
	A3	Permanent Grass	Juniper	3	18	14
Visited Post-Classification						
SK	S1	Encroachment	Rhododendron	65	4.7	2
	S2	Permanent Shrub	Rhododendron	100	23	8
	S3	Encroachment	Rhododendron	70	17	8
TB	H1	Encroachment	Rhododendron	100	15	7
	H2	Encroachment	Rhododendron	90	20	9
	H3	Encroachment	Rhododendron	90	14	2
ZH	T1	Encroachment	Rhododendron	75	14	6
Average age of all shrubs					**19**	**11**

Figure 9. a) The location of the study area. b) Close-up of land cover/land use change from 1990 to 2009 in one alpine territory. c) Land cover was stable from 1974 to 1990, but grasslands shrank dramatically from 1990 to 2009 while shrublands expanded.
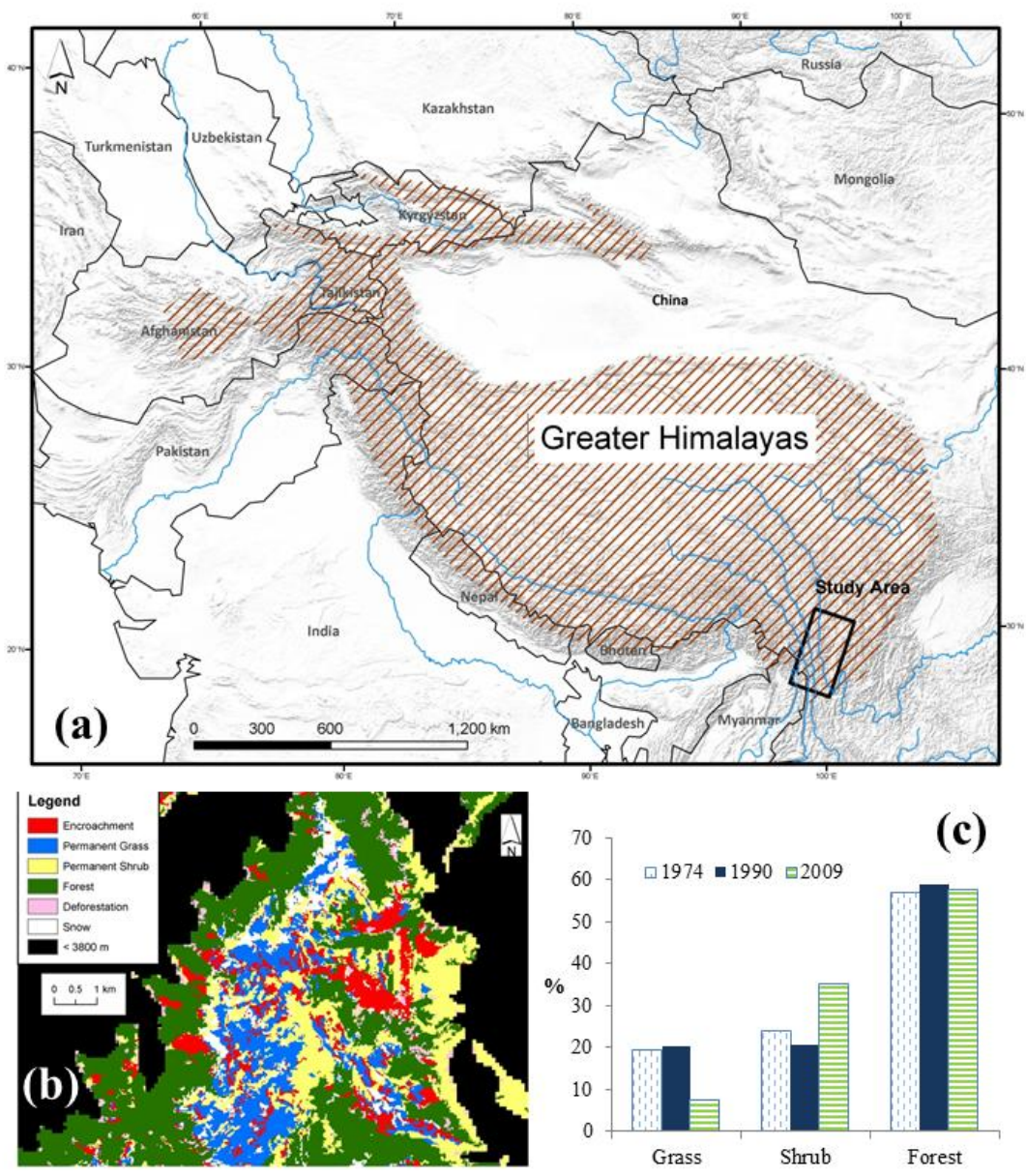
Figure 10. a) Encroachment rates were highly variable throughout the study area, with the northern and eastern regions suffering the highest encroachment rates. b) Shrub encroachment rates were negatively correlated with the proportion of spring snow cover and positively correlated with proportions of 1990 woody vegetation cover. Encroachment was related to c) elevation and d) aspect, with meadows in lower elevations of the alpine zone (4000-4200 m) and drier south facing slopes more subject to encroachment.
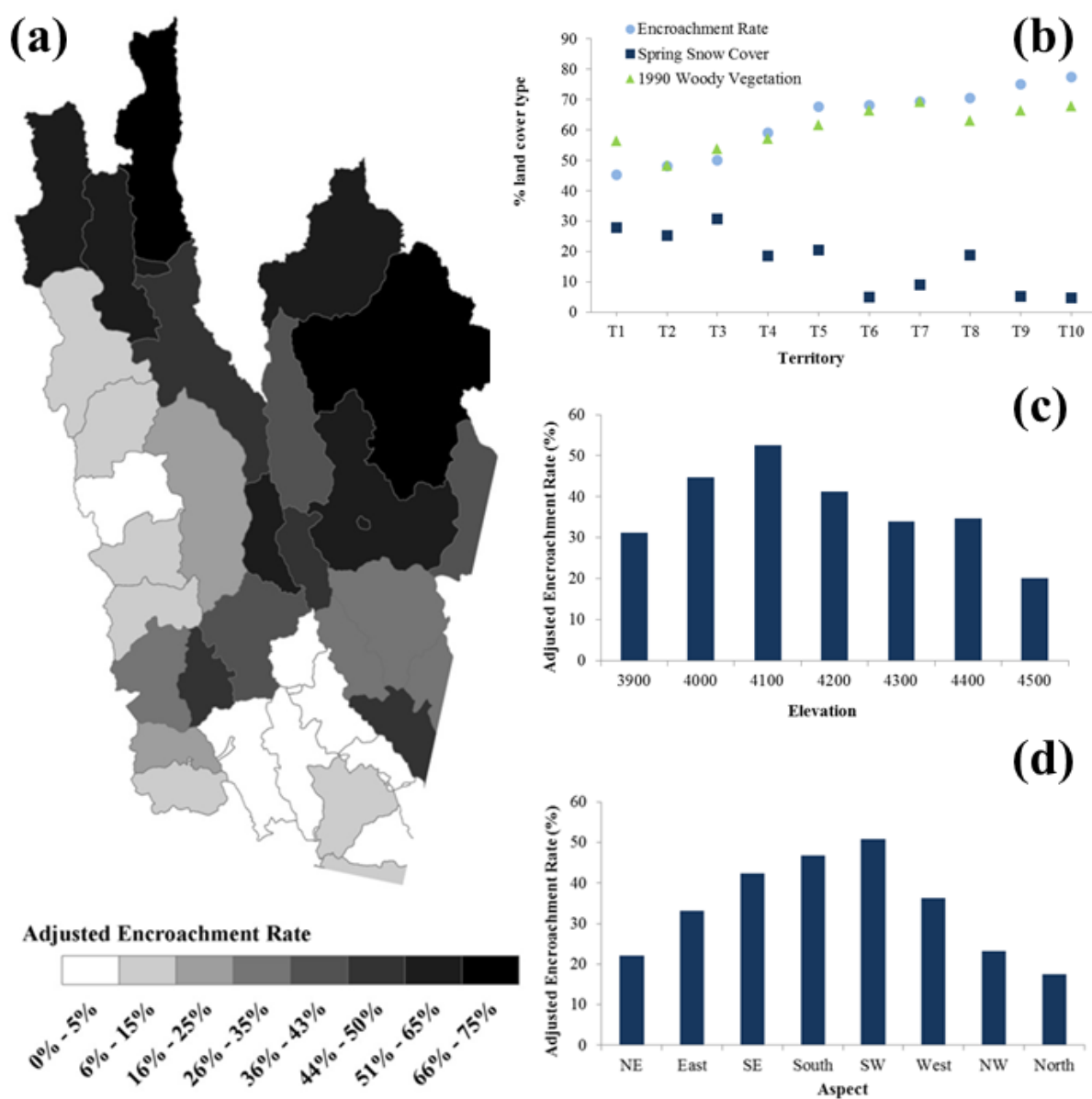
Figure 11. a) Higher grazing intensities close to the national highway increased shrub encroachment rates; b) Relationships between encroachment and burning, and encroachment and abandonment indicate that recent local-scale burning and pasture abandonment did not influence regional patterns of shrub encroachment.
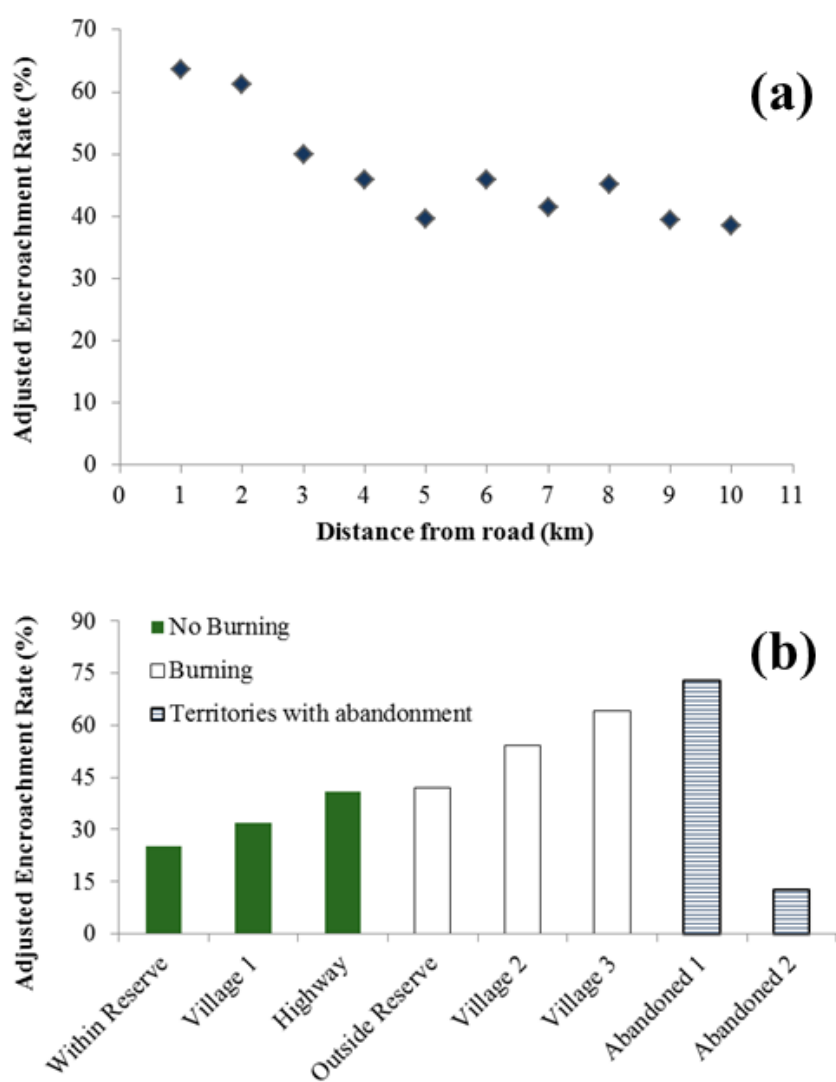
Figure 12. Average a) daily low and b) daily high temperatures (°C) at 3320 m and 4000m.Total c) rainfall (mm) and d) snowfall (mm) measured at Deqin climate station. May average daily low temperatures in the alpine zone from (e) early in the study period (1959-1968) and (f) late in the study period (1999–2008).
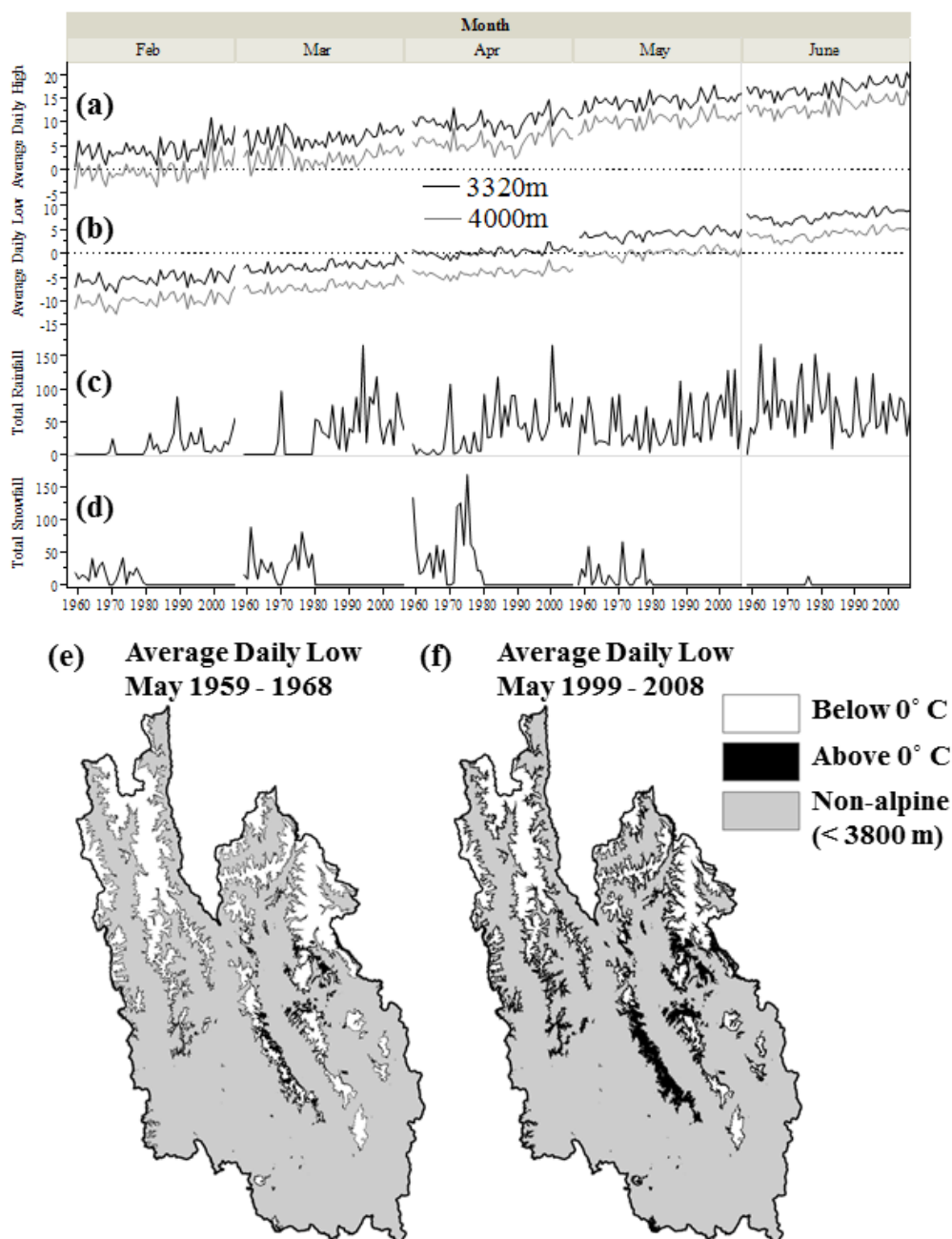
Figure 13. Synthesis of land cover, land use, and climate change from 1951 to 2009.
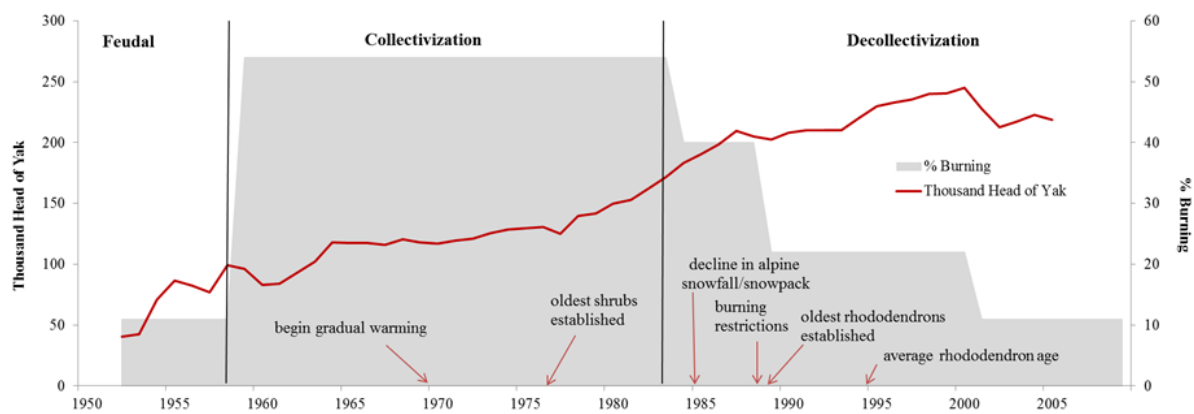
Figure 14. Interactions between social, climate and alpine sub-systems during a) the feudal era,

b) the collectivization period and c) following decollectivization.
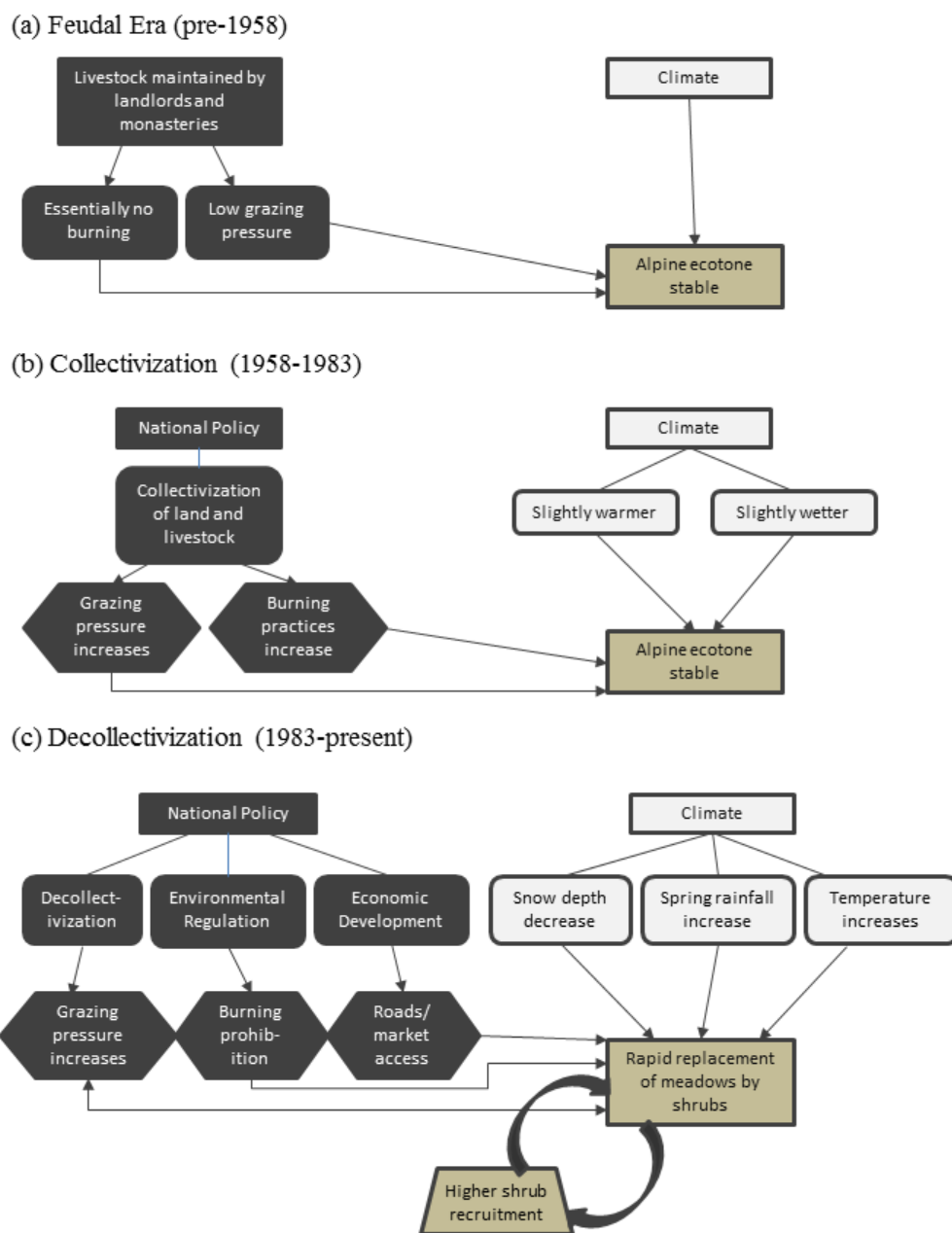
Chapter 3: Sacred forests are keystone structures for forest bird conservation in southwest China's Himalayan mountains

Abstract

Identifying and protecting "keystone structures" is essential to maintain biodiversity in an increasingly human-dominated world. Sacred forests, i.e. natural areas protected by local people for cultural or religious regions, may be keystone structures for forest birds in the Greater Himalayas, but there is limited understanding of their use by bird communities at different spatial scales. We surveyed birds and their habitat in and adjacent to six Tibetan sacred forests in northwest Yunnan China, a biodiversity hotspot. Our goal was to understand the ecological and conservation role of these remnant forest patches for forest birds. We found that sacred forests supported a significantly different bird community than the surrounding matrix, and had higher bird species richness at plot, patch, and landscape scales. Furthermore, while we encountered a single matrix bird community outside the scared forests, the sacred forests themselves exhibited high within- and between-patch heterogeneity, and supported at least two distinct sacred forest bird communities. Finally, we found an increased use of the sacred forests and their edges during 2010, a severe drought year in Yunnan Province, indicating that sacred forests may serve as refuges during extreme weather years. While bird community composition was primarily driven by the vertical structure of the vegetation, plots with the largest diameter trees and the most bamboo coverage had the highest bird diversity and abundance, indicating the importance of protecting old-growth forest ecosystems for Himalayan forest birds. Old-growth forest clearing and degradation have accelerated throughout the Himalayas, and our results offer hope for forest birds, in that existing sacred forests do protect a variety of habitat niches and increase bird diversity at multiple spatial scales. As population growth and rapid economic development

continues throughout the Himalayas, sacred areas can represent an important opportunity for

biological conservation at the local, landscape and regional scales.

Introduction

As humans consume an ever-increasing proportion of the Earth's resources, biodiversity declines at an accelerating rate (Chapin et al. 2000; Foley et al. 2005), making the protection of "keystone structures", i.e., discrete spatial features that maintain biodiversity at multiple spatial scales, evermore important (Belsky & Canham 1994; Tews et al. 2004; Manning et al. 2006; Stagoll et al. 2012). For example, forest gaps, large trees, and temporary wetlands are keystone structures whose presence adds heterogeneity to the resources available in the landscape, facilitating greater species richness. The question is how to identify such keystone structures, and how to protect them.

Sacred forests, i.e., natural areas protected by local people for cultural or religious reasons (Dudley et al. 2009), may be keystone structures for biodiversity in traditional landscapes around the world. Sacred forests are numerous, dispersed across a broad range of topographic and micro-climatic conditions, and range in size from a single hectare to thousands of square kilometers (Ormsby 2011). As such, they likely serve multiple ecological functions, including as corridors, refugia, and source habitats (Bhagwat & Rutte 2006). Sacred forests may be critical components of protected area networks, but we have little understanding of their potential role for biodiversity conservation, especially in the less-studied biodiversity hotspots.

The traditional land management systems that sustain sacred forests may create optimum conditions for species diversity at multiple spatial scales. Sacred forests are typically managed by communities (Dudley et al. 2009) and often experience a gradient of human disturbance (UNESCO-MAB 2003), where a variety of organisms can respond to and thrive in variable resource conditions (Belsky & Canham 1994). In addition, sacred forests are typically embedded in landscapes with matrix habitats that are hospitable to at least some species, and thus conventional assumptions of patch size and fragmentation effects (MacArthur & Wilson 1967)

may not apply (Prugh et al. 2008). Furthermore, the edges between sacred forests and their matrix are often not abrupt barriers, but a gradient of disturbance to levels characteristic of the surrounding matrix. These edges may serve as "ecotones", facilitating ecological interactions between the patch and the matrix, and offering supplementary resources not available in the core habitats (Ries et al. 2004). However, despite their potential importance for species dispersal and persistence, we have little understanding of how sacred forests are influenced by patch size, edge effects, and interactions between patch and matrix habitats.

One region where sacred forests are relatively common are the Himalayan mountains (Peng et al. 2003; UNESCO-MAB 2003; Xu et al. 2005; Salick et al. 2007; Mallarach 2008; Barbhuiya et al. 2010). Several ethnic minority groups recognize sacred areas as part of their religion, including sacred beyuls (which protect entire valleys), sacred mountains (10s to 100s of km^2), and village-level sacred forests (1 to 1000 ha). The Himalayan mountains also contain three biodiversity hotspots (Myers et al. 2000) and forest birds are of special conservation concern (Renner 2011). The region exhibits high levels of bird diversity and endemism (Acharya et al. 2011; Renner & Rappole 2011), and rank highest in global assessments of threatened bird species richness (Grenyer et al. 2006). Many forest bird species in the Greater Himalayas follow a sino-Himalayan distribution (Renner 2011; Renner & Rappole 2011), which includes the Himalayan range, the mountains of southwest China, and the Qinghai Tibetan plateau (Fig. 15a). Forest degradation has accelerated throughout this region in recent decades (Spehn et al. 2010; Brandt et al. 2012), destroying bird habitats (Dumbacher et al. 2011). Sacred areas may be critical for bird conservation throughout this rapidly changing region, but their importance for Himalayan forest bird communities across multiple spatial extents is not well understood.

Our overarching objective was to understand the role of sacred forests for the conservation of Himalayan forest birds. We studied bird communities within and outside of Tibetan sacred forests in northwest Yunnan, China, with the following specific objectives:

1. determine whether bird community composition and diversity is different within sacred forests compared to the surrounding matrix,

2. identify the critical habitat characteristics structuring bird diversity, abundance, and community composition, and

3. investigate how patch size and edge habitats influence bird community composition, diversity and abundance patterns.

Study Area

Our study area is in Shangrila, northwest (NW) Yunnan Province, China (Fig. 15a). NW Yunnan is a biodiversity hotspot in the southeastern sub-Himalayan mountains, bordering Myanmar, Tibet and Sichuan Province. Three major rivers (the Yangtze, Mekong, and Salween) create steep gorges, with elevations ranging from 1,800 to 6,740 m, creating a large array of ecological niches in a relatively small area.

NW Yunnan has great importance for local, regional, and global bird diversity. First, it is a center of bird endemism (Lei et al. 2003). Second, it is part of the East Asian migratory flyway, providing important stop-over habitat for long-distance migrants (Cheng 1987). Third, it lies at the confluence of the Palearctic, Himalayan, and Indo-malay zoogeographic regions, and thus provides habitat for birds with distinct ecological and evolutionary histories (Renner 2011).

NW Yunnan's avifauna is one the poorest understood on Earth (Renner & Rappole 2011), and it is likely that forest birds face serious threats. Large expanses of NW Yunnan's forests were clear-cut by state logging companies from the 1960s through the 1990s to fuel

China's national development. Despite a ban on commercial logging in 1998 and heavy investment in reforestation and protected areas (Liu et al. 2008), old-growth forests continue to be logged and the ecological integrity of the new forests is unclear (Xu 2011; Brandt et al. 2012).

NW Yunnan is home to several ethnic minority groups that recognize sacred areas as part of their religion (Xu et al. 2005). In particular, Tibetans have a complex sacred site system that includes large Tibetan sacred mountains (tens to hundreds of square kilometers) and hundreds of smaller community-based sacred forests (1 to 1,000 ha) at lower elevations (Peng et al. 2003; Shen et al. 2012). Vegetation communities in Tibetan sacred forest sites have higher vegetation species richness, diversity, and endemism than randomly selected non-sacred sites (Anderson et al. 2005), and larger and denser trees (Salick et al. 2007). However, little is known about the importance of Tibetan sacred forests for taxa other than plants.

Methods

Avifaunal sampling

We conducted breeding bird point count surveys at six sacred forest sites that ranged in size from 13 to 75 ha (Fig. 15b). We surveyed a total of 62 plots, including 35 within the sacred forests, 9 edge plots (60 m away from the sacred forest boundary), and 18 matrix plots (260 and 520 m from the boundary) (Fig. 15c). Plots were placed at least 200 m apart, along walking paths when possible. At the plot center, we surveyed birds at least twice per year during the breeding season (May 18-June 30) in 2010 and 2011. Surveys consisted of 50-m radius, 10-minute point counts following standardized methods (Ralph et al. 1993), and included an estimate of distance to bird using a hand-held laser rangefinder (Buckland et al. 2001). All point counts were conducted by JSB and EMW.

Habitat structure

Vegetation composition and structure was measured at each point-count station according to standardized protocols (Ralph et al. 1993; Martin et al. 1997) from June to August of 2010. Within each point-count station, we measured four 5-m radius subplots (Ralph et al. 1993). The initial sub-plot was located at the center of the point-count station, and the remaining three subplots were located 30-m away at 0º, 120º and 240º. Slope, aspect and basal area (using a 10- or 20-factor basal area per ft^2 prism) were measured at the center point of each subplot. Canopy coverage (using a densitometer) and foliage height diversity (in 0.3-m sub-sections) was measured at the north, east, south, and west edge of each of the four subplots. Ocular estimates for the sub-canopy layer (0.5-5 m) and the ground layer (0-0.5 m) were collected at each subplot. Finally, we recorded all species of trees and shrubs, and the heights and dbh of the three tallest and three largest-diameter trees, encountered in the entire 50-m radius plot.

Data Analysis

Differences between sacred forest and matrix habitats

We estimated differences in detection probabilities among habitats, and between years based on our distance measurements and made density adjustments for those species for which we had sufficient observations (>75) in each year (Buckland et al. 2001). We lumped edge plots with matrix plots to estimate a species detection curve for sacred or non-sacred (i.e., edge and matrix plots) habitats because matrix and edge habitat characteristics were similar in bird detectability. There was a single species with sufficient observations in both 2010 and 2011 (Blyth's Leaf Warbler (*Phylloscopus reguloides*)), and an additional species with sufficient observations in 2010 only (Hume's Leaf Warbler (*Phylloscopus humei*). Three models were used to fit the detection function (Buckland et al. 2001) and the best model was selected using the Akaike's Information Criterion (AIC) (Burnham & Anderson 2002).

We compared bird diversity and abundance among habitat types and between years at three different spatial scales: plot, patch and landscape. At the plot scale, we compared raw values of observed bird species richness, Shannon index, and absolute abundance in sacred, matrix and edge habitats. Differences among habitat types were tested using a one-way analysis-of-variance (ANOVA) and pairwise comparisons (Tukey multiple comparisons of means). At the patch scale (n=6), we compared sacred and matrix/edge (lumped together for rarefaction) habitats using observed species richness, rarefied species richness, and rarefied Shannon index, all standardized by the number of individuals, derived from sample-based rarefaction curves constructed in EstimateS v.7 (Colwell 2009). Differences at the patch scale were tested using paired two-sample student's t-tests. At the landscape scale, we calculated rarefied species richness, rarefied Shannon index, and estimated total species richness (using the Jackknife 1 estimator) (Colwell 2009; González-Oreja et al. 2010). Patterns of bird diversity according to the Shannon Index were consistently similar to raw and rarefied species richness, and therefore only raw and rarefied species richness were reported here.

To determine whether bird species assemblages differed among habitats and sacred forests, we removed rare species (less than 3 observations per year) from our multivariate dataset and computed a Bray-Curtis similarity index on square root-transformed abundance data (Carr 1997). We then used non-metric multidimensional scaling (NMDS) to create a graphical representation of the resemblance matrix (Kruskal 1964). Bird assemblage differences among a) habitats and b) sacred forests were tested for using an analysis of similarity (ANOSIM). We used a Bonferonni adjusted alpha value for pairwise comparisons among the three habitats ($p = 0.05/3 = 0.016$). NMDS and ANOSIM analyses were conducted using PRIMER v6 (Clarke & Gorley 2006).

Habitat selection

We used step-wise multiple linear regression to determine the most important environmental variables influencing bird diversity and abundance at the plot scale. The best model was selected using the Akaike's Information Criterion (AIC) (Burnham & Anderson 2002). To investigate the importance of patch size on species richness, we calculated Pearson's correlations between patch size and raw species richness. These analyses were performed in the statistical package R version 2.8.1. To identify the most prominent habitat gradients and the most important variables driving those gradients, we performed principal components analysis (PCA, using PRIMER v6 (Clarke & Gorley 2006)) on the habitat variables that were both uncorrelated and known to be important for bird communities according to the regression analysis. To understand the relationship between the prominent habitat gradients and bird community composition we performed canonical correspondence analysis (CCA in PC-ORD 6.04), which constrains habitat gradients by the bird species data.

Results

Differences between sacred forest and matrix habitats

Habitat

We surveyed 62 plots that captured a wide range of variability in vegetation disturbance, structure and species composition (Appendix 3). PCA identified two prominent habitat gradients in our study area (Fig. 16a). The first axis (eigenvalue=3.59, explaining 44.8% of the variance) corresponded to differences between sacred and matrix habitats, which had significantly different vegetation composition and structure in the canopy, sub-canopy and ground layers (Appendix 4). The first axis had high vertical structure (foliage height diversity), canopy cover and coarse woody debris on at low values on Axis 1, and high proportions of bare soil and multiple-

stemmed woody vegetation in the ground layer (0 – 0.5 m) at high values on Axis 1. The second axis of the PCA (eigenvalue=1.51, explaining 18.9% of the variance) represented a within-sacred forest gradient, with dense understory vegetation (i.e., high proportions of sub-canopy coverage and bamboo) corresponding to high values of Axis 2, while those with a more open understory (high herbaceous cover and coarse woody debris in the ground layer) corresponding to low values.

Birds

We observed a total of 81 species exhibiting breeding behavior (Appendix 5), ranging from a few very common species (a total of 7 species detected > 100 times) to several rarely-detected species (a total of 35 species observed 10 times or less). Detection probability was 5% to 21% higher in the matrix than in the sacred forests. Detection probability was 10% to 17% lower in 2010 than in 2011, and therefore we performed all analyses separately for the two years. We used raw counts for the statistical analyses because sample size was too low to estimate density for most species.

Species composition of the bird communities overlapped between the sacred, edge, and matrix habitats (Fig. 16b), but still exhibited statistically significant patterns (NMDS, 2D stress=0.21, ANOSIM Global R=0.254, p=0.001). Edge and matrix plots shared the same bird community (p=0.51), while sacred forest bird communities were distinct from edge (R=0.227, p=0.005) and matrix (R=0.37, p=0.001) communities. Furthermore, different sacred forests supported distinct bird assemblages. Species composition was significantly different in five of 15 pairwise comparisons (ANOSIM, Global R=0.22, p=0.001), indicating that the sacred forests as a whole provided habitat for more than one bird community.

We measured differences in bird species richness at three spatial scales. At the plot scale, mean species richness was higher in sacred forests (mean (SD) = 13.3 (3.1)) than in edge (mean = 11.1 (2.9), $p = 0.084$) and matrix (mean = 9.64 (1.9), $p < 0.001$) (Fig. 17a). Bird abundance was slightly higher in sacred than in edge or matrix, but these differences were not significant ($p = 0.53$ and 0.33, respectively).

Since edge and matrix were always similar in terms of bird species composition and diversity, we aggregated edge and matrix plots into a single "matrix" class at the patch and landscape scales, which allowed us to build rarefaction curves and thereby adjust for differences in sampling effort and observed individuals. At the patch scale, sacred forest patches had higher mean rarefied species richness (mean (SD) = 28 (6.8)) than the matrix (mean = 21 (5.8) ($p < 0.001$)) (Fig. 17b). At the landscape scale, bird species accumulated fastest in the sacred forest habitat (Fig. 17c) and rarefied species richness (rarefied to 824 individuals) was higher in the sacred (mean (SD) = 59 (4.1)) than the matrix (mean = 53(4.1)).

Habitat Selection

Four variables were selected among the candidate variables in the stepwise regression (Appendix 4) as important predictors of species richness: the diameter of the largest tree, percent bamboo, percent ground cover of coarse woody debris, and percent sapling cover (Stepwise Regression AIC=112, Adj. R^2=0.46, $p<0.0001$). In simple linear regression models to predict bird abundance, only one variable, the diameter of the largest tree, was a significant predictor of abundance (Adj. R^2=0.20, $p=0.00018$).

The canonical correlation analysis indicated that habitat gradients and species composition were highly correlated (Axis 1 Pearson's $r >0.95$, Axis 2 Pearson's $r =0.718$, Fig. 18). While several common generalist species (e.g., Hume's and Blyth's Leaf Warblers) were

detected in all habitats, many species were clearly associated with either sacred forests or matrix.

Axis 1 (Eigenvalue=0.480, explaining 14 % of the variance in the species data) captured a gradient between birds associated with the matrix habitats at high values (e.g., White-bellied Redstart (*Hodgsonius phaenicuroides*), White-tailed Rubythroat (*Luscinia pectoralis*), and Common Stonechat (*Saxicola torquata*), and those associated with the sacred forests at low values (e.g., Mrs Gould's Sunbird (*Aethopyga gouldiae*), Blood Pheasant (*Ithaginis cruentus*), Chinese Thrush (*Turdus mupinensis*), Grey-crested Tit (*Pyrrhula erythaca*), and Giant Laughingthrush (*Garrulax maximus*). Foliage height diversity had the highest correlation with Axis 1 ($r = -0.525$), indicating that it explained the highest variance in the species data. Axis 2 (Eigenvalue=0.114, explaining 3.3% of the variation in the species data) captured a gradient of within-sacred forest habitats, and birds associated with dense understory cover (e.g., Giant Laughingthrush, Lady Amherst's Pheasant (*Chrysolophus amherstiae*), and Yellowish-bellied Bush Warbler (*Cettia acanthizoides*)) had high values of Axis 2, while birds associated with large trees, high canopy cover and coarse woody debris (e.g., Yunnan Nuthatch (*Sitta yunnanensis*), Great Spotted Woodpecker (*Dendrocopos major*), and several tit species) had low values.

Edge effects and patch-matrix interactions

To investigate whether edges influenced bird diversity patterns, we regressed bird richness and abundance against distance from the edge of a sacred forest. Within sacred forest patches, species richness increased with a plot's distance to the edge of the sacred forest patch (R^2=0.11, p=0.06). For the matrix, we found the opposite relationship. Matrix bird diversity was highest at the edge, but decreased with distance from the sacred forest (R^2=0.17, p=0.03). There was no relationship between bird abundance and distance from the edge.

The correlation between patch size and bird species richness was positive and significant for patch size and raw species richness in the sacred forest patches (r=0.79, p=0.03) and in the matrix plots associated with each sacred forest patch (r=0.80, p=0.05). However, when standardizing for sample effort and number of individuals, the correlations between patch size and rarefied species richness were not significant.

Differences between 2010 versus 2011

We encountered significantly more birds in 2010 than in 2011 ($p < 0.001$) in all three habitats (sacred, matrix, and edge). There were a total of 15 species (including Greenish Warbler (*Phylloscopus trochiloides*), Bar-tailed Treecreeper (*Certhia himalayana*) and Grey-chinned Minivet (*Pericrocotus solaris*)) that were observed in 2010 but not 2011, and another 9 species (including Lady Amherst's Pheasant, Chinese Thrush, Giant Laughingthrush, and Chestnut-vented Nuthatch (*Sitta nagaensis*)) that were observed in both years, but were considerably (> 3x) more abundant in 2010 than 2011. Plot-scale bird richness was significantly higher in 2010 than in 2011 in sacred and edge, but not in matrix (Fig. 19a). Estimated total species richness curves indicated that species accumulated at the same rate in both years in both the matrix and sacred habitats, but species accumulated at a much faster rate in edge habitats in 2010 versus 2011 (Fig. 19b).

Discussion

Sacred Forests as Keystone Structures

Our results indicated that Tibetan sacred forests conserved old-growth forest characteristics and protected unique forest bird communities in the Chinese Himalayan mountains. In addition, sacred forests had the highest bird diversity of all habitats at multiple spatial scales and in both years. Since detection probabilities were considerably lower in the

sacred forests compared to their matrix, it is likely that our estimates of differences are conservative, and that sacred forests are even more important than indicated by the raw data.

Sacred forests exhibited several characteristics of keystone structures (Tews et al. 2004). First, sacred forests maintained higher bird and vegetation diversity despite being small in proportion to the adjacent matrix habitats that make up the majority of the Shangrila landscape. Second, the bird diversity was not dependent on a particular tree species or forest community, but instead associated with structural characteristics that increased habitat heterogeneity. Finally, the positive relationship between habitat heterogeneity and bird diversity was consistent across multiple spatial scales.

Keystone structures maintain biodiversity because of both within-patch and between-patch heterogeneity. The Tibetan sacred forests that we studied have been protected from clear-cut logging, but do experience a range of human disturbance, including occasional selective logging, NTFP collection, and grazing. Thus, they are structurally complex and composed of a mixture of successional and old-growth forests. This within-patch heterogeneity is important to create an environment where a variety of organisms can respond to - and thrive in - the variable resource conditions of the patch (Belsky & Canham 1994).

In terms of between-forest heterogeneity, although the sacred forests were relatively close to each other (<20 km) and at similar elevation (3200 to 3800 m), they contained a variety of habitat niches due to micro-topographic and micro-climatic variability. In contrast, the surrounding matrix, which has been subject to a range of high-intensity subsistence land-use pressures including logging, non-timber forest resource collection, and grazing, exhibited a relatively homogeneous matrix habitat. As a result, while the matrix habitats had a single,

homogeneous bird community, sacred forests supported a wider range of bird species, and two distinct sacred forest bird communities.

Habitat Selection of Old-growth Forest Characteristics

Our results indicated the importance of mature forest ecosystems over secondary or disturbed forest habitats. The relatively large range in vertical complexity (i.e., foliage height diversity, MacArthur & MacArthur 1961) of our survey plots was the main characteristic structuring bird species composition, while old-growth trees, bamboo groves and coarse woody debris were the most important factors determining high species richness and abundance. In some ecosystems, bird diversity peaks in secondary growth stages (Keller et al. 2003; Schieck & Song 2006), while in other ecosystems, primary forests support unique, high-diversity bird communities (Barlow et al. 2007; Ding et al. 2008). Old-growth forests, including large trees and bamboo groves (a native understory component), have been heavily exploited for both subsistence and commercial use in this region (Xu 2011; Brandt et al. 2012), Our results suggest that the protection of forests that retain old-growth characteristics should be a high priority for forest bird conservation in this biodiversity hotspot.

Bird diversity at the plot scale was also positively associated with high proportions of sapling cover. Post-logging tree regeneration in the matrix is limited due to logging practices that leave no mature trees as sources for natural regeneration, and due to grazing which destroys any seedlings and saplings which do grow, allowing shrub and scrub-forest communities to persist for decades following forest clearing (Xu 2011). Land management practices that encourage tree regeneration in the matrix would benefit forest bird communities.

Influence of edge habitats and patch size on bird community patterns

In some ecosystems, edges serve as an ecotone, providing supplementary resources that are not present in the core or matrix habitats, resulting in relatively high species richness and abundance and distinct species assemblages along edges (Ries et al. 2004). Surprisingly, our results suggested that sacred forest edges were not a distinct habitat, but rather an intermediate and overlapping zone between sacred and matrix habitats. In addition, species richness increased moving deeper into the core of the sacred forests, indicating that interior forests contained higher quality habitat than edges.

Thus, large remnant old-growth forest patches are especially important for birds in our study area. Generally speaking, the larger the patch the higher the ratio of core forest to edge habitats (Turner et al. 2001). Furthermore, while even the smallest sacred forest patch that we surveyed (13 h) had a bird community that was distinct from - and more diverse than - the surrounding matrix, large patches supported more bird species, likely because they contained more habitat niches (MacArthur & Wilson 1967) and supported more individual birds (More Individuals Hypothesis (Srivastava & Lawton 1998)).

Differences between 2010 versus 2011

We found clear inter-annual differences in bird presence, abundance, and richness. Bird abundance was higher in all habitats in 2010. In sacred and edge plots we also encountered higher bird diversity in 2010, and the edge habitat had a higher rate of species accumulation. Yunnan province as a whole experienced a severe drought in 2010, receiving 60% less rainfall than normal during the 6 months leading up to the 2010 breeding season (Qiu 2010). However, Shangrila weather station data indicated that the drought was less severe in our study area. The typical effect of a drought is to reduce bird abundance and diversity in some habitats while other

habitats act as refugia (Albright et al. 2010). Our results indicated that sacred forests, and especially their edges, may serve as refuges during extreme weather years.

Management Implications

Although in the past, sacred forests have proven to be remarkably resilient to social change (Dudley et al. 2009), the current trend is towards cultural assimilation and the degradation of sacred forests (Rutte 2011), and efforts to understand the underlying cultural values and management mechanisms may be necessary if sacred forests are to persist. For example, incorporating sacred forests into official protected area networks may not be desirable from the community perspective, as it leads to a loss in legal ownership and property rights (Bhagwat & Rutte 2006). Furthermore, as ecotourism expands, many communities exploit sacred forests for commercial use as touristic destinations, which can lead to a fundamental change in their meaning, management and ecological function (Barbhuiya et al. 2010)

Sacred forests are apparently keystone structures for forest birds in NW Yunnan, and, potentially, throughout the Himalayas. Faced with rapid land use and climate change, it is important to establish reserve networks that cover the entire range of elevations and aspects (Wu et al. 2010), but establishing large, contiguous protected areas is challenging in this densely inhabited landscape. Although China's protected area system has expanded greatly since the 1980s, its effectiveness is limited (Tang et al. 2006). Sacred forests throughout the Greater Himalayan region provide an existing network of native vegetation patches that protect a variety of habitat niches, maintain biodiversity at multiple spatial scales, and may even function as refugia during extreme weather years.

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Figure 15. a) Location of Shangrila within the Greater Himalayan region, b) the six sacred forest patches that were surveyed, and c) sampling plots within and outside of sacred forests. Matrix plots were placed on transects at approximately 60, 260, and 510 m away from the edge of the sacred forest.
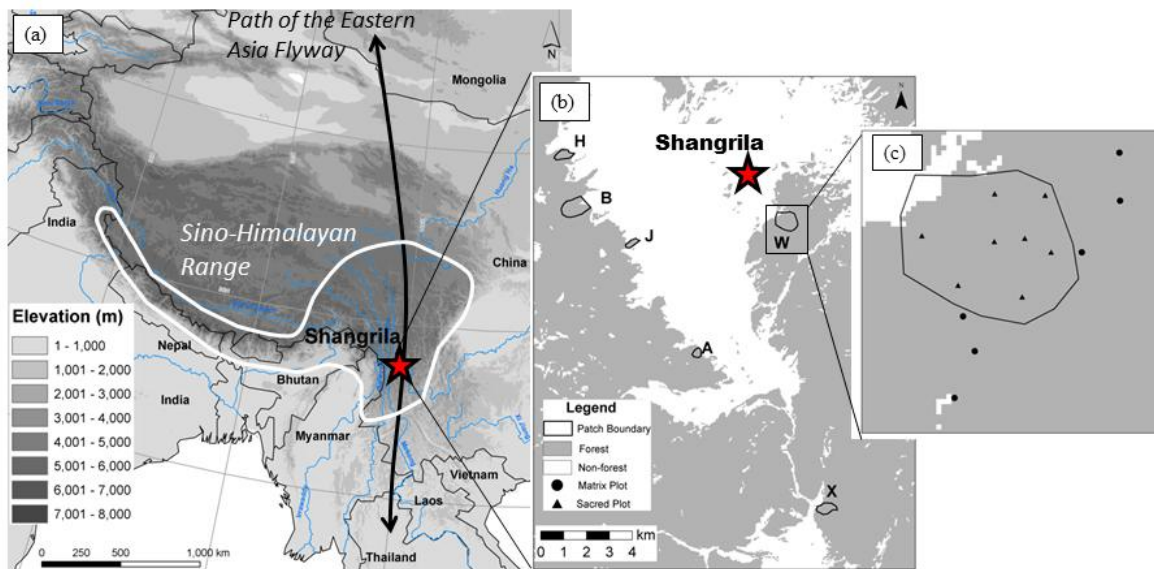
Figure 16. Multivariate analyses of a) habitat gradients (PCA) and b) bird community composition (NMDS).
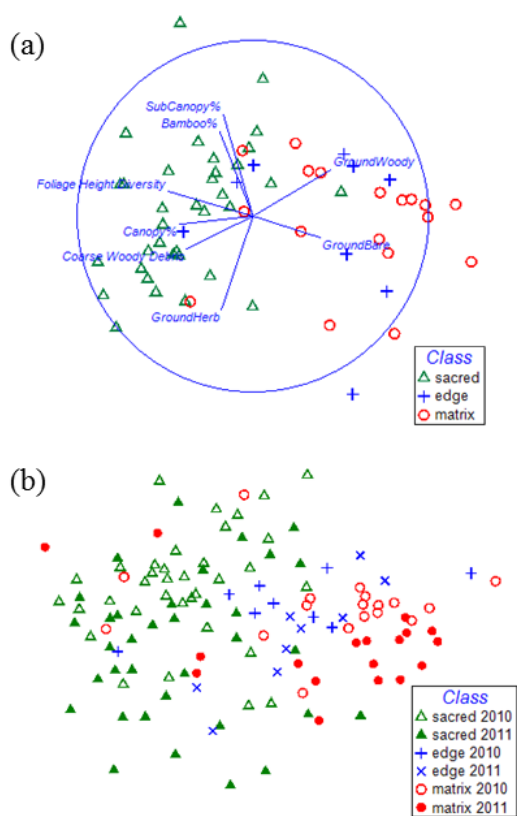
Figure 17. Box plots of a) plot-scale bird species richness, b) patch-scale rarefied bird richness, and c) rarefied species richness accumulation curves at the landscape scale (dotted lines are 95% confidence intervals).
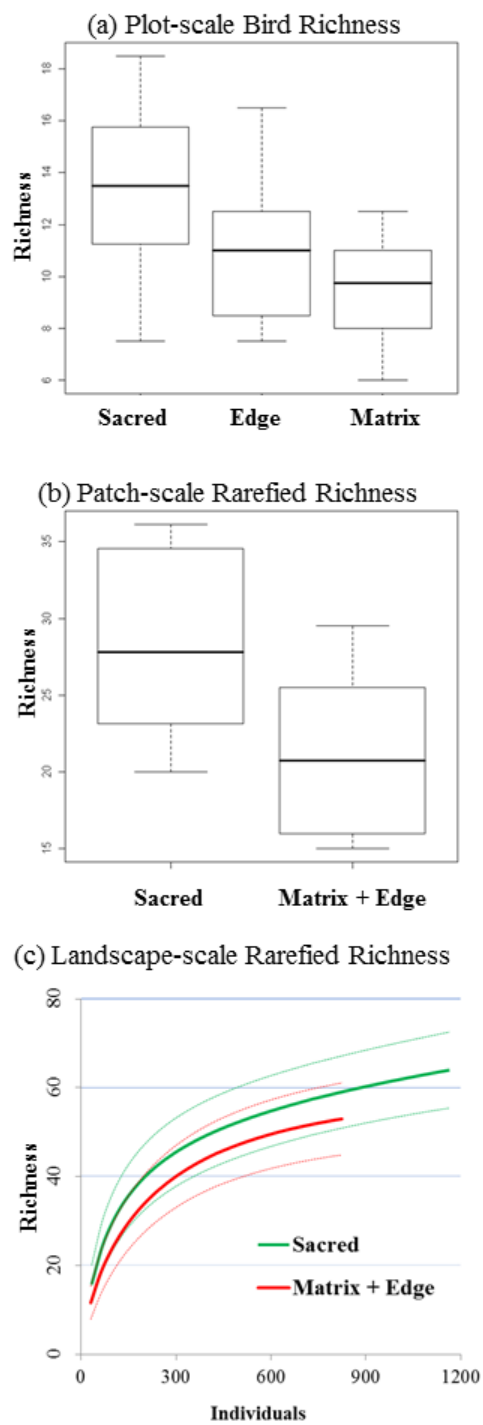
Figure 18. Canonical Correspondence Analysis demonstrates that Foliage Height Diversity was the main characteristic structuring bird communities along Axis 1, while Axis 2 showed the separation between two distinct sacred forest bird communities. Bird species indicated with 4-letter species code. Full species names can be found in Appendix 5.
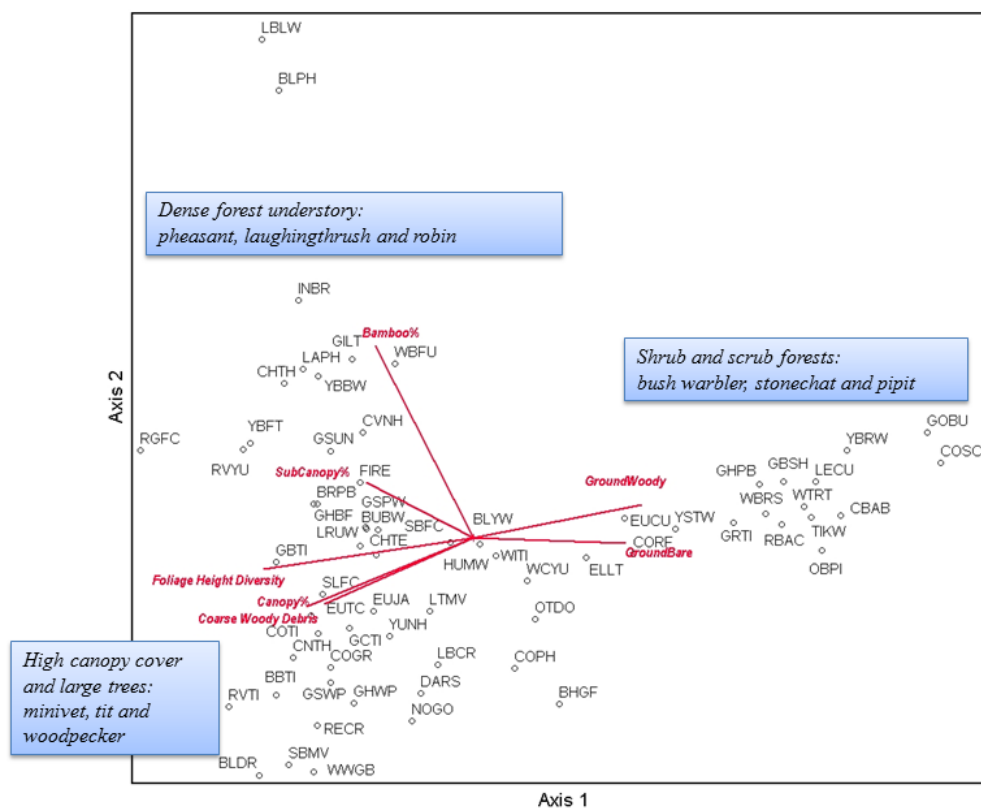
Figure 19. Inter-annual variability in a) plot-scale species richness and b) estimated total species richness at the landscape scale.
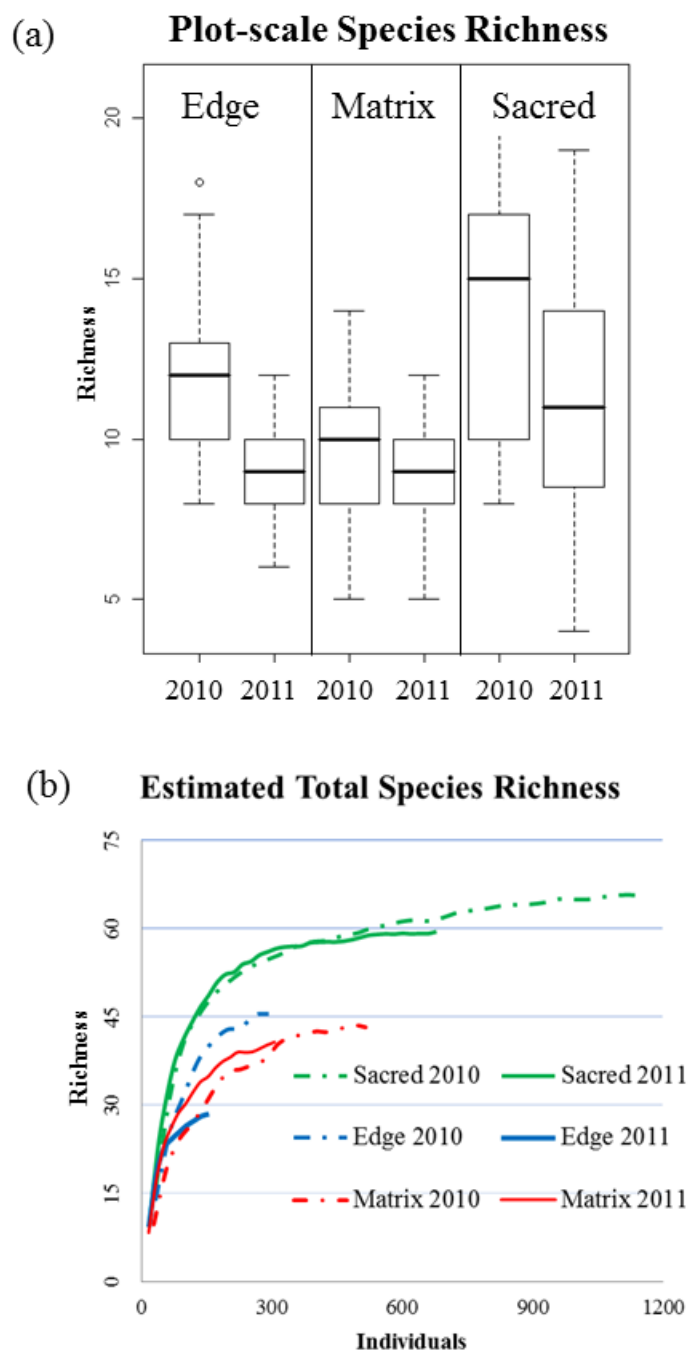
Appendix 3**.** Description of the 62 plots sampled during the study.

Site	Class	Plot	General Habitat Type	Dominant Tree Species	Foliage Height Diversity	Tree Species Richness	Shrub Species Richness
A	Sacred	AA1	Mid-successional forest	*Pinus densata*	2.8	4	10
A	Sacred	AA2	Primary forest	*Quercus aquifolioides*	3.0	7	12
A	Sacred	AA3	Scrub and saplings	*Pinus densata*	2.7	6	12
A	Sacred	AA4	Primary forest	*Quercus aquifolioides*	2.7	7	9
A	Matrix	AT1-260	Scrub forest	na	1.1	4	7
A	Matrix	AT1-510	Scrub forest	na	1.1	2	10
A	Edge	AT1-60	Scrub and saplings	na	1.5	5	11
B	Sacred	BA1	Mid-successional mixed	*Betula platyphylla*	2.7	8	11
B	Sacred	BA2	Primary forest	*Picea likiangensis var. linzhiensis*	2.5	6	13
B	Sacred	BA3	Primary forest	*Picea likiangensis var. linzhiensis*	2.6	6	16
B	Sacred	BA4	Primary forest	*Picea likiangensis var. linzhiensis*	2.4	2	17
B	Sacred	BA5	Primary forest	*Sorbus multijuga*	2.3	3	9
B	Sacred	BA6	Primary forest	*Picea likiangensis var. linzhiensis*	3.5	4	10
B	Sacred	BA7	Primary forest	*Picea likiangensis var. linzhiensis*	3.1	6	12
B	Sacred	BA8	Mid-successional mixed	*Tilia chinensis*	2.4	5	15
B	Sacred	BA9	Mid-successional birch	*Betula platyphylla*	2.8	6	14
B	Matrix	BAT1-260	Scrub forest	na	1.0	2	14
B	Matrix	BAT1-510	Scrub forest	na	1.3	3	17
B	Matrix	BAT2-260	Scrub forest	na	0.7	2	9
B	Matrix	BAT2-510	Scrub forest	na	0.4	4	14
B	Edge	BAT1-60	Scrub and saplings	*Larix potaninii var.macrocarpa*	1.3	5	13
B	Edge	BAT2-60	Scrub and saplings	na	1.7	3	12
H	Sacred	HA1	Early successional birch	*Betula platyphylla*	2.4	6	12
H	Sacred	HA2	Mid-successional mixed	*Picea likiangensis var. linzhiensis*	2.3	9	15
H	Sacred	HA3	Primary forest	*Picea likiangensis var. linzhiensis*	2.7	7	13
H	Sacred	HA4	Primary forest	*Picea likiangensis var. linzhiensis*	3.1	7	12
H	Matrix	HAT1-260	Scrub forest	na	1.5	5	11
H	Matrix	HAT1-510	Scrub forest	na	1.0	2	8
H	Edge	HAT1-60	Scrub and saplings	na	1.4	6	17
J	Sacred	JA1	Mid-successional mixed	*Larix potaninii var.macrocarpa*	1.4	3	10

J	Sacred	JA2	Early successional birch	*Betula platyphylla*	2.8	7	14
J	Sacred	JA3	Early successional birch	*Betula platyphylla*	2.7	5	12
J	Matrix	JAT1-260	Scrub forest	na	0.0	2	8
J	Matrix	JAT1-510	Scrub forest	na	0.5	3	15
J	Edge	JAT1-60	Scrub and meadow	na	0.5	3	12
W	Sacred	WF1	Mid-successional birch	*Betula platyphylla*	2.4	3	14
W	Sacred	WF2	Primary forest	*Larix potaninii var.macrocarpa*	2.7	4	17
W	Sacred	WF3	Primary forest	*Quercus pannosa*	2.8	4	10
W	Sacred	WF4	Primary forest	*Quercus pannosa*	2.8	5	12
W	Sacred	WF5	Primary forest	*Quercus pannosa*	3.1	4	13
W	Sacred	WF6	Primary forest	*Quercus pannosa*	2.8	3	14
W	Sacred	WF7	Primary forest	*Larix potaninii var.macrocarpa*	1.8	4	16
W	Sacred	WF8	Primary forest	*Quercus pannosa*	2.5	4	14
W	Matrix	WAT1-260	Scrub and saplings	*Pinus densata*	1.2	6	10
W	Matrix	WAT1-510	Scrub forest	na	1.0	3	7
W	Matrix	WAT2-260	Scrub forest	na	0.8	4	8
W	Matrix	WAT2-510	Scrub forest	na	0.9	4	9
W	Edge	WAT1-60	Scrub and saplings	*Larix potaninii var.macrocarpa*	1.5	4	8
W	Edge	WAT2-60	Scrub and saplings	*Larix potaninii var.macrocarpa*	2.2	2	15
X	Sacred	XA1	Primary forest	*Picea likiangensis var. linzhiensis*	2.4	6	18
X	Sacred	XA2	Primary forest	*Populus davidiana*	2.2	6	11
X	Sacred	XA3	Primary forest	*Picea likiangensis var. linzhiensis*	2.0	6	11
X	Sacred	XA4	Primary forest	*Salix delavayana*	3.9	5	16
X	Sacred	XA5	Primary forest	*Acer caesium*	2.5	7	12
X	Sacred	XA6	Primary forest	*Acer pectinatum*	2.9	6	9
X	Sacred	XA7	Primary forest	*Salix delavayana*	2.5	6	8
X	Matrix	XAT1-260	Mid-successional mixed	*Betula platyphylla*	2.5	6	18
X	Matrix	XAT1-510	Mid-successional pine	*Pinus densata*	2.3	6	18
X	Matrix	XAT2-260	Early successional mixed	*Pinus densata*	2.2	3	11
X	Matrix	XAT2-510	Early successional pine	*Pinus densata*	2.4	3	9
X	Edge	XAT1-60	Mid-successional pine	*Pinus densata*	2.3	4	7
X	Edge	XAT2-60	Early successional pine	*Pinus densata*	2.7	5	10

Appendix 4. The set of candidate variables chosen for the stepwise regression, with the corresponding Adjusted R^2 and significance values in the simple linear regressions to predict plot-scale species richness; and means, standard deviations and significance values for each variable in sacred versus matrix habitats.

Variable	Simple Linear Regression Analysis		Sacred		Matrix		Difference between Sacred and Matrix
	Adj. R^2	p	Mean	SD	Mean	SD	p
Canopy Layer (> 5 m)							
Biggest Tree (dbh)	0.31	< 0.01	63.4	39.7	23.7	24.1	< 0.01
Tallest Tree (m)	0.30	< 0.00	26.7	9.7	11.7	10.4	< 0.01
Foliage Height Diversity	0.13	< 0.01	3.1	0.7	1.8	0.4	< 0.01
Tree Species Richness	0.09	0.01	5.3	1.6	3.7	1.4	< 0.01
Canopy Cover (%)	0.04	0.06	54.9	27.6	12.8	21.7	< 0.01
Basal area (sq. ft./acre)	0.04	0.06	70.1	49.0	15.2	28.6	< 0.01
Sub Canopy Layer (0.5 - 5 m)							
Bamboo Cover (%)	0.20	< 0.01	8.7	12.6	1.9	3.2	0.01
Subcanopy Cover (%)	0.07	0.02	62.4	10.5	52.0	15.2	< 0.01
Sapling Cover (%)	0.05	0.04	20.8	8.5	17.1	12.9	0.181
Ground Layer (0 - 0.5 m)							
Downed Log Cover (%)	0.12	< 0.01	1.6	1.3	0.4	1.0	< 0.01
Bare ground (%)	0.12	< 0.01	0.3	0.6	6.5	7.9	< 0.01
Live Woody Plant Cover (%)	0.05	0.05	39.7	12.0	59.6	13.4	< 0.01

Appendix 5. Breeding birds observed during the study.

Code	Common name	Latin name	Total observations 2010 + 2011	Total Sacred	Total Matrix+Edge	Proportional Difference [1]	Total 2010	Total 2011	Proportional Change [2]
BTTC	Bar-tailed Treecreeper	*Certhia himalayana*	8	8	0	NO M/E	8	0	NO 2011
BWWB	Bar-winged Wren-babbler	*Spelaeornis troglodytoides*	3	2	1	2.0	3	0	NO 2011
BLDR	Black Drongo	*Dicrurus macrocercus*	1	1	0	NO M/E	0	1	NO 2010
BBTI	Black-browed Tit	*Aegithalos bonvaloti*	44	36	8	4.5	27	17	1.6
BLPH	Blood Pheasant	*Ithaginis cruentus*	21	19	2	9.5	12	9	1.3
BFRS	Blue-fronted Redstart	*Phoenicurus frontalis*	4	2	2	1.0	4	0	NO 2011
BLYW	Blyth's Leaf Warbler	*Phylloscopus reguloides*	409	226	183	1.2	234	175	1.3
BRPB	Brown Parrotbill	*Paradoxornis unicolor*	5	3	2	1.5	3	2	1.5
BUBW	Buff-barred Warbler	*Phylloscopus pulcher*	79	64	15	4.3	54	25	2.2
CNTH	Chestnut Thrush	*Turdus rubrocanus*	24	23	1	23.0	19	5	3.8
CHTE	Chestnut-headed Tesia	*Tesia castaneocoronata*	18	9	9	1.0	10	8	1.3
CVNH	Chestnut-vented Nuthatch	*Sitta nagaensis*	16	14	2	7.0	12	4	3.0
CBAB	Chinese Babax	*Babax lanceolatus*	6	2	4	0.5	3	3	1.0
CHTH	Chinese Thrush	*Turdus mupinensis*	40	37	3	12.3	33	7	4.7
COTI	Coal Tit	*Parus ater*	54	35	19	1.8	28	26	1.1
COGR	Collared Grosbeak	*Mycerobas affinis*	9	9	0	NO M/E	6	3	2.0
EUCU	Common Cuckoo	*Cuculus canorus*	23	8	15	0.5	6	17	0.4
COPH	Common Pheasant	*Phasianus colchicus*	10	4	6	0.7	7	3	2.3
CORF	Common Rosefinch	*Carpodacus erythrinus*	238	73	165	0.4	166	72	2.3
COSC	Common Stonechat	*Saxicola torquata*	17	0	17	0.0	12	5	2.4
CBWP	Crimson-breasted Woodpecker	*Dendrocopos cathpharius*	1	1	0	NO M/E	0	1	NO 2010
DBRF	Dark-browed Rosefinch	*Carpodacus nipalensis*	2	2	0	NO M/E	2	0	NO 2011
DARS	Daurian Redstart	*Phoenicurus auroreus*	22	20	2	10.0	14	8	1.8
ELLT	Elliot's Laughingthrush	*Garrulax elliotii*	174	67	107	0.6	136	38	3.6
EUJA	Eurasian Jay	*Garrulus glandarius*	4	4	0	NO M/E	2	2	1.0
EUTC	Eurasian Treecreeper	*Certhia familiaris*	7	6	1	6.0	0	7	0.0
FIRE	Firethroat	*Luscinia pectardens*	3	3	0	NO M/E	1	2	0.5
GILT	Giant Laughingthrush	*Garrulax maximus*	34	32	2	16.0	26	8	3.3
GOBU	Godlewski's Bunting	*Emberiza godlewskii*	3	0	3	NO S	2	1	2.0
GSPW	Golden Spectacled Warbler	*Seicercus burkii*	205	152	53	2.9	132	73	1.8
GRPB	Great Parrotbill	*Conostoma oemodium*	1	1	0	NO M/E	1	0	NO 2011

Code	Common Name	Scientific Name				Prop. Diff.[1]			Prop. Change[2]
GSWP	Great Spotted Woodpecker	*Dendrocopos major*	13	11	2	5.5	7	6	1.2
GRTI	Great Tit	*Parus major*	18	12	6	2.0	15	3	5.0
GBTI	Green-backed Tit	*Parus monticolus*	8	3	5	0.6	4	4	1.0
GRNW	Greenish Warbler	*Phylloscopus trochiloides*	15	10	5	2.0	15	0	NO 2011
GBSH	Grey-backed Shrike	*Lanius tephronotus*	30	2	28	0.1	20	10	2.0
GCMV	Grey-chinned Minivet	*Pericrocotus solaris*	14	12	2	6.0	14	0	NO 2011
GCTI	Grey-crested Tit	*Pyrrhula erythaca*	56	56	0	NO M/E	34	22	1.5
GHBF	Grey-headed Bullfinch	*Pyrrhula erythaca*	62	57	5	11.4	37	25	1.5
GHPB	Grey-headed Parrotbill	*Paradoxornis gularis*	7	3	4	0.8	3	4	0.8
GHWP	Grey-headed Woodpecker	*Picus canus*	3	3	0	NO M/E	2	1	2.0
HUMW	Hume's Leaf Warbler	*Phylloscopus humei*	280	151	129	1.2	196	84	2.3
INBR	Indian Blue Robin	*Luscinia brunnea*	30	27	3	9.0	19	11	1.7
LAPH	Lady Amherst's Pheasant	*Chrysolophus amherstiae*	6	6	0	NO M/E	5	1	5.0
LBCR	Large-billed Crow (tibetosinensis)	*Corvus macrorhynchos tibetosinensis*	21	20	1	20.0	18	3	6.0
LBLW	Large-billed Leaf Warbler	*Phylloscopus magnirostris*	24	20	4	5.0	17	7	2.4
LRUW	Lemon-rumped Warbler	*Phylloscopus proregulus*	113	99	14	7.1	63	50	1.3
LECU	Lesser Cuckoo	*Cuculus poliocephalus*	4	0	4	NO S	0	4	NO 2010
LTMV	Long-tailed Minivet	*Pericrocotus ethologus*	40	34	6	5.7	24	16	1.5
GSUN	Mrs Gould's Sunbird	*Aethopyga gouldiae*	60	53	7	7.6	37	23	1.6
NOGO	Northern Goshawk	*Accipiter gentilis*	1	1	0	NO M/E	0	1	NO 2010
OBPI	Olive Backed Pipit	*Anthus hodgsoni*	15	0	15	0.0	9	6	1.5
OTDO	Oriental Turtle Dove	*Streptopelia orientalis*	57	42	15	2.8	34	23	1.5
PALW	Palla's Leaf Warbler	*Phylloscopus proregulus*	1	1	0	NO M/E	1	0	NO 2011
RECR	Red Crossbill	*Loxia curvirostra*	2	0	2	NO S	2	0	NO 2011
RTFC	Red-throated Flycatcher	*Ficedula Parva*	2	2	0	NO M/E	0	2	NO 2010
RBAC	Rufous-breasted Accentor	*Prunella strophiata*	6	0	6	0.0	3	3	1.0
RGFC	Rufous-gorgeted Flycatcher	*Ficedula strophiata*	1	1	0	NO M/E	1	0	NO 2011
RVTI	Rufous-vented Tit	*Periparus rubidiventris*	40	33	7	4.7	28	12	2.3
RVYU	Rufous-vented Yuhina	*Yuhina occipitalis*	13	9	4	2.3	4	9	0.4
RCFU	Rusty-capped Fulvetta	*Schoeniparus dubia*	10	10	0	NO M/E	0	10	NO 2010
SBMV	Short-billed Minivet	*Pericrocotus brevirostris*	2	2	0	NO M/E	0	2	NO 2010
SBFC	Slaty Blue Flycatcher	*Ficedula tricolor*	57	51	6	8.5	37	20	1.9
SLFC	Slaty-backed Flycatcher	*Ficedula hodgsonii*	103	91	12	7.6	65	38	1.7
SWGB	Spot-winged Grosbeak	*Mycerobas melanozanthos*	1	1	0	NO M/E	1	0	NO 2011
TIKW	Tickell's Leaf Warbler	*Phylloscopus affinis*	66	5	61	0.1	40	26	1.5

VIRF	Vinaceous Rosefinch	*Carpodacus vinaceus*	3	3	0	NO M/E	3	0	NO 2011
WBRS	White-bellied Redstart	*Hodgsonius phaenicuroides*	97	3	94	0.0	57	40	1.4
WBFU	White-browed Fulvetta	*Alcippe vinipectus*	37	21	16	1.3	21	16	1.3
WBRF	White-browed Rosefinch	*Carpodacus thura*	12	8	4	2.0	12	0	NO 2011
WCYU	White-collared Yuhina	*Yuhina diademata*	63	29	34	0.9	36	27	1.3
WTRO	White-tailed Robin	*Myiomela leucura*	1	1	0	NO M/E	1	0	NO 2011
WTRT	White-tailed Rubythroat	*Luscinia pectoralis*	43	0	43	NO S	29	14	2.1
WWGB	White-winged Grosbeak	*Mycerobas carnipes*	9	6	3	2.0	7	2	3.5
WITI	Willow Tit	*Parus montanus*	21	12	9	1.3	12	9	1.3
WIWR	Winter Wren	*Troglodytes troglodytes*	1	1	0	NO M/E	1	0	NO 2011
YBFT	Yellow-bellied Fantail	*Rhipidura hypoxantha*	6	6	0	NO M/E	3	3	1.0
YBRW	Yellow-browed Warbler	*Phylloscopus inornatus*	1	0	1	NO S	0	1	NO 2010
YBBW	Yellowish-bellied Bush Warbler	*Cettia acanthizoides*	52	39	13	3.0	34	18	1.9
YSTW	Yellow-streaked Warbler	*Phylloscopus armandii*	81	12	69	0.2	30	51	0.6
YUNH	Yunnan Nuthatch	*Sitta yunnanensis*	21	12	9	1.3	13	8	1.6

[1] Proportional Difference represents the total number of observations in sacred forests divided by the total number of observations in matrix and edge habitats. NO M/E = Not Observed in Matrix/Edge, NO S = Not Observed in Sacred.

[2] Proportional Change represents the total observations in 2010 divided by the total observations in 2011, to highlight interannual variability of different species. NO 2010 = Not Observed in 2010, NO 2011 = Not Observed in 2011.