

COMMUNITY DYNAMICS: LINKING LOCAL GOVERNANCE, FOREST
CHANGE, AND SPECIES RICHNESS IN THE SIERRA TARAHUMARA, MÉXICO

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Abstract

COMMUNITY DYNAMICS: LINKING LOCAL GOVERNANCE, FOREST CHANGE, AND SPECIES RICHNESS IN THE SIERRA TARAHUMARA, MÉXICO

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Managing and protecting forests is a difficult task, especially in regions with high development pressure and weak regulatory frameworks. In México, community-based forestry practices as a form of *ex situ* conservation have become widespread, and are a vital component of rural economies. However, the factors affecting its successful implementation and the resulting conservation impacts of these practices, critical for improving management strategies, have not been studied extensively. This dissertation research project was conducted in the Sierra Tarahumara region of northern México and focused on: (1) identifying the factors affecting local governance and forest cover change, and (2) assessing the impact of forest management on forest system state.

This research project entailed three inter-related studies. The first used generalized linear models to investigate forest cover change from 1976 to 2001 in 38 *ejidos*, or communally-owned land parcels, and the local and regional factors affecting forest governance. Results revealed that the regional forestry sector was unsustainable as forest loss exceeded regrowth, and that social characteristics, education, and proximity of *ejidos* to markets were significant predictors of forest cover change. Lower deforestation rates were found in *ejidos* where indigenous members comprised more than 50% of the population, and where user group size was less than 280 people.

A second study investigated the impact of timber harvesting on diurnal forest breeding bird communities using hierarchical Bayesian multi-species occupancy models. Substantial differences in species richness and turnover rates were found to be

associated with greater forest degradation caused by timber harvesting. Areas with the highest species richness and lowest turnover rates were found on national park lands.

A final study evaluated species composition and functional homogenization of bird communities in managed and unmanaged forests using multi-species occupancy models. The results produced clear evidence of functional homogenization of bird communities as a result of degradation and even-aged forest management practices. Sites characterized by dense forest stands dominated by small diameter trees were species poor, and contained mostly generalist species.

Combined, these studies identified important mechanisms and relationships between human actions and associated forest system changes that can be used to enhance local governance, forest management practices, and increase species richness. These studies also demonstrated that scientific, multi-disciplinary research is needed to inform management decisions, and improve the sustainability of forest management practices in regions where ecological and social systems are closely interconnected.

Dedication

*Dedicated
to my father Jorge
who left us too soon and
very suddenly on 8 January 2009*



Majalca, Julio 2006.

DIANA: *¿Como esta?*

CANTINFLAS: *Muy bien, gracias, solo que entre tanto loco, ¡se chivea uno!*

DIANA: *Me refiero a Raúl.*

CANTINFLAS: *¡Oiga usted, yo creo que esta peor! Lo deje leyendo un libro con su secretaria, la señorita Nelson...Ni libro, ni secretaria, ni señorita Nelson, ¿Como estará?*

CANTINFLAS, "EL SEÑOR FOTÓGRAFO"

1

If a man walks in the woods for love of them half of each day, he is in danger of being regarded as a loafer. But if he spends his days as a speculator, shearing off those woods and making the earth bald before her time, he is deemed an industrious and enterprising citizen.

HENRY DAVID THOREAU

2

Why should we honour those that die upon the field of battle? A man may show as reckless a courage in entering into the abyss of himself.

WILLIAM BUTLER YEATS

3

*Dear Ph.D. degree,
Last night I fell asleep curled up with my laptop. I can't hold a normal conversation; I haven't had a good night's sleep in weeks. All this studying is starting to seriously affect me. Are you sure you're worth all this trouble? I want my life and my brain back!*

JENNIFER DAISY KAPLAN

4

This is hard. Well, I say that, but really it is easy. Just do it...But we like to goof off and then we feel bad about ourselves. But the truth is that we are trying to do focused work on a machine that is full of distractions. Our minds are everywhere.

DAN P.

5

I almost wish I hadn't gone down that rabbit hole –and yet –and yet– it's rather curious, you know, this sort of life!

ALICE

Biographical sketch

Eduardo (Lalo) Carrillo-Rubio was born April 12, 1975 in Chihuahua, México, and was exposed to nature and anti-establishment ideas from an early age. After spending the better part of his formative years exploring the alpine solace of Majalca National Park in Chihuahua and the wildlands of the western U.S. after high school, he decided to pursue a career in conservation. He has worked as a seasonal park ranger for the U.S. National Park Service, and as a national park superintendent, researcher, and consultant for protected areas and conservation/ rural development NGOs in México. Awarded undergraduate Honors and the top 5% of his Master's program cohort at the University of Chihuahua, he began his Ph.D. at Cornell University as a Fulbright fellow.

Lalo's commitment to conservation is unrenounceable and irrevocable. He is passionate about social justice and culture, and is a supporter of all things local, small, and organic. He is a vegetarian, except in some cases involving traditional foods. Like Mexican poet J. E. Pacheco, he is proud of his cultural heritage, and admires various Mexican heroes, writers, mountains, rivers, autonomous rural communities, and old cities. He also thinks fish are awesome, and regrets not taking a fish ecology course at Cornell.

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Chapter 1

INTRODUCTION

1. Problem overview

Forest conservation is a recognized global priority as deforestation and degradation are important sources of greenhouse gas pollution, and among the main threats to biodiversity, ecosystem services, and rural livelihoods (Miles and Kapos 2008, Boucher et al. 2011). However, managing and protecting forests is a difficult task, especially in biologically rich developing regions where pressure on resources is high, and the implementation of forest policies is hampered by limited regulatory and institutional capacity (FAO 2009, 2011).

Perhaps this situation is nowhere more apparent than in México. Between 1970 and 2005, the lack of effective land management policies generated extensive deforestation, often at a rate of >500,000 ha/yr (Cairns et al. 2000, Klepeis 2003, Merino and Segura 2004), resulting in widespread habitat degradation, and extirpation and range reductions for numerous wildlife species (Fuller et al. 2007). Paradoxically, during the same period the number and coverage of spatial reserves increased from 2 to 20.5 million ha (ParksWatch 2006), but the representation of species in reserves declined dramatically (Fuller et al. 2007). This provides clear evidence that despite the benefits that spatial reserves can offer, effective *ex situ* conservation planning and management is needed to guarantee the maintenance of populations, communities, and habitats at significant spatial and temporal scales (Adams 2003, Adams et al. 2004, Fischer et al. 2006).

In México, most forest resources and biological diversity are located on *ejidos*, a legal form of communal land tenure in which user groups collectively own and manage a territory by establishing local institutions that regulate land and natural resource use

(Sarukhan and Larson 2001). These territories contain 60% of the country's land, 85% of the forests, and virtually all spatial reserves border or overlap *ejido* lands (Klepeis 2003). As land available for new reserves becomes scarcer, and because communal lands contain such a vast amount of natural resources, effective landscape-based conservation is unattainable without the inclusion of *ejido* lands and the enhancement of *ex situ*, participatory natural resource management schemes that explicitly integrate livelihood needs of local people (Bray et al. 2003, Bray et al. 2005).

Community-based forestry (CBF) is one such *ex situ* approach that has become particularly widespread in México during the past three decades as a result of government decentralization over the country's natural resources (Bray et al. 2005). CBF is a composite of actions related to forest vegetation management that provides economic opportunities for local forest inhabitants (Pokorny et al. 2010). Sustainability of such practices is based on the premise that by allowing local stakeholders to share the benefits, responsibility, ownership, and governance of natural resources, the outcome of management interventions will result in improved forest stewardship and livelihoods (Ostrom 1990, Brown et al. 2007, UNEP 2010).

Based on decades of implementation and numerous successful experiences, the Mexican CBF model has been proposed as a global model of sustainability that can be used to alleviate poverty and improve forest management in developing regions (Bray et al. 2003, Bray et al. 2005). However, there have also been numerous failures (Klooster 2000, Klepeis 2003, Honey-Roses 2004, Bray et al. 2005, Duran-Medina et al. 2005), and despite a growing body of literature the optimal ecological, social, and political conditions under which success or failure happens still elude researchers and policy makers (Perez-Cirera and Lovett 2006).

There have been a number of studies on common pool resource management that have identified the basic features of user groups and the institutional arrangements

required for effective natural resource governance, including salience or the importance of the resource to the user group, shared understanding of collective problems and of resource degradation, trust among members, community autonomy to regulate resource use, and prior organizational experience (Ostrom 1990, Agrawal 2001). While these principles have helped explain some of the outcomes of CBF in México, to better understand the underlying mechanisms that influence local governance and forest management outcomes, it is necessary to account for the social and cultural heterogeneity of *ejidos* to improve management predictions (Klooster 2000, Perez-Cirera and Lovett 2006). Moreover, *ex situ* conservation practices, including CBF, have been subject to critical reviews which argue that development/poverty alleviation and biodiversity protection objectives are incompatible (Adams et al. 2004, Brockington et al. 2006). Indeed, very little is known about the impact of CBF on wildlife populations, biological communities, and ecological functions, as most study efforts consist of case studies that focus on the social, cultural, and economic components of CBF (for a review, see Merino and Segura 2004, and Bray et al. 2005). To better manage a system, it is first necessary to assess and monitor its state using relevant vital rates that can be used to make informed management decisions and optimal use of limited conservation funds. Vital system rates, or state variables (e.g., size of wildlife populations of interest, species richness, and probability of occupancy) are those that can provide inference regarding the system's structural processes and functional dynamics, allowing managers to understand and predict how these rates respond to degradation and management interventions (Yoccoz et al. 2001, Nichols and Williams 2006).

Considering that deforestation in México continues at alarming rates (FAO 2011), and the significant role that forest communities play in the fate of forest resources and biodiversity, increasing our understanding of the social, cultural, institutional, and ecological conditions that are conducive to better forest governance

and more sustainable management practices is considered a priority (Larson et al. 2010). Effective implementation of large-scale CBF practices requires linking these multidisciplinary components of forest systems so that its state and the relationships between its multiple components can be better understood and modeled. In addition, research efforts also need to account for the governance and institutional arrangements that influence CBF outcomes within the context of local socio-ecological conditions, using data from large samples and different spatial and temporal scales (Ostrom and Nagendra 2007).

Aspects of these implementation challenges were the focus of my research conducted in the Sierra Tarahumara region (STR) of México. The STR contains 15% of the country's total forest cover, 90% of which is owned by *ejidos*. The socio-economic, cultural and political heterogeneity in the STR in many ways provides a case study with relevance for other parts of México and beyond (Guerrero et al. 2000). Specifically, this dissertation addresses two major research needs: (1) understanding the factors affecting local forest governance and forest cover change, and (2) assessing the impact of CBF practices on the state of the forest system.

2. Dissertation scope

One of the most challenging aspects of studying the interactions between the multidisciplinary elements of forest management is to find reliable information and appropriate analytical tools that allow for rigorous and meaningful statistical inference. In CBF practices, the relationships between these components are often non-linear, and to understand them researchers need to consider past and present conditions of the resource/system, and obtain reliable measures of long-term social, cultural, and institutional arrangements that affect these conditions (Ostrom and Nagendra 2007).

This dissertation advances the body of knowledge relevant to this complex field

by developing an empirical approach that used (1) satellite imagery to assess long-term forest cover changes; (2) surveys to describe long-term social, cultural and local governance structures; (3) population census data to describe forest owner/user groups; and (4) novel sampling and analytical techniques to biological field data to estimate vital forest system rates that reflect the influence of management practices. The final product consists of three chapters that quantify the ecological impact of CBF practices at different spatial scales and ecological levels of organization (ecosystem, communities, and species). Combined, these chapters identified important mechanisms and relationships between species and their environment, and human actions and associated ecosystem changes that can be used to inform forest management decisions. While these chapters can best be seen as representing independent studies each with a specific research focus, it should be noted that the analytical tools used here can be applied to test a wide range of hypotheses relating to community and population ecology, and to address questions relating to the impact of governance arrangements and management and policy interventions.

In the first study (Chapter 2), I investigated forest change patterns from 1976 to 2001 in 38 *ejidos* and the local and regional factors affecting local forest governance using negative binomial generalized linear models. My results show that forest loss exceeds regrowth, which indicates that the forestry sector in the region is unsustainable, and that illegal logging is a significant contributor to forest change. Greater cultural heterogeneity, larger group size, lower technical capacity, and proximity to markets were the most significant predictors of forest change. Fewer changes were found in *ejidos* where indigenous members comprised more than 50% of the population, and where user group size was less than 280 people. The results also show that the tradeoffs between livelihoods and forest change have been mostly negative, as increased levels of forest use were not associated with improved livelihoods of local people.

In the second study (Chapter 3) I used a hierarchical Bayesian multi-species occupancy model to derive biological community summaries (specifically, species richness, turnover rates, detection and occurrence probabilities) to assess the impact of timber harvesting activities on forest system state. This model was applied to data from a breeding bird survey of 32 sites in managed (*ejidos*) and protected (national parks) forests sampled 3-5 times in 2008 and again in 2009. While this modeling framework can be applied to a broad range of taxa, bird communities were selected because the large number of species in relation to other vertebrate groups makes them a practical measure of biodiversity and environmental changes (Ceballos and Marquez 2000, Manley et al. 2006). The model yielded sensible estimates of site-specific and total species richness that were positively related to tree diameter size and negatively to tree density, the variables most frequently used by foresters to estimate stocking rates and harvest quotas (Long 2005). These findings support my original hypotheses relating loss of species with forest degradation caused by human activities. Contrary to my initial expectations, sites with higher richness also had lower estimate uncertainty (i.e., were more stable), and vice versa. Finally, in this study I mention the importance of estimate uncertainty for sampling design and inference regarding biological community structure and dynamics.

In the third study (Chapter 4) I used species-specific occupancy and detection probabilities to evaluate species composition and functional homogenization of avian communities in managed and unmanaged forests. The results show clear evidence of functional homogenization of bird communities as a result of forest degradation and even-aged forest management practices. Sites characterized with denser forest stands dominated by smaller diameter trees were species-poor and contained mostly generalist species. This indicates that habitat changes caused by timber harvesting reduce species occupancy, species diversity, and ecological functionality. Results reported in Chapters

3 and 4 can be readily incorporated into *ejido* and regional forest management plans to increase site-level avian occupancy and richness.

In the last chapter (Chapter 5) I review the key findings of this research and highlight the applicability and usefulness of the techniques and the results to help further our understanding and the enhancement of CBF practices. I also provide management recommendations and suggestions for future research efforts, and conclude by providing an overview of the current state of affairs in México regarding the role of local and state governance over forests and other natural resources.

The primary motivation for this research was to better understand how *ejidos* manage their forests, and to assess the ecological impact of such management on forest systems. The results of this work illustrate the usefulness and applicability of scientific, multi-disciplinary research to enhance CBF practices, particularly in the Sierra Tarahumara region of México. It also highlights the importance of the *ejido* land tenure system in protecting and fostering the social and human capital required for effective forest governance, and its implications for enhancing sustainability and rural livelihoods in CBF practices. Lastly, it notes the grave implications of a Mexican state that has shown little interest in long-term ecological sustainability, has limited regulatory and institutional capacity to implement and enforce forest policies, is in many cases corrupt, and is losing its capacity to guarantee the safety of its citizens in rural (and some urban) areas. This is a serious threat to local and regional socio-political stability, has a direct impact on poverty and rural development, and in turn on the implementation of CBF practices and the conservation of natural resources.

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Chapter 2

MODELING DEFORESTATION RATES AND LOCAL GOVERNANCE IN THE SIERRA TARAHUMARA, MÉXICO

Abstract: As a result of numerous successful experiences, the Mexican community-based forestry (CBF) model has been proposed as a global model of sustainability that can efficiently address rural development and biodiversity conservation needs in developing regions. However, there have also been numerous failures –in Mexico and elsewhere, and despite a growing body of literature, the optimal ecological, social, and political conditions under which success happens still elude researchers and policy makers. This study, conducted in the Sierra Tarahumara region of México, investigated forest cover change patterns from 1976 to 2001 in a sample of 38 forest *ejidos*, or communally-owned parcels, and the local and regional factors affecting forest governance. The results show that forest loss exceeds regrowth, which indicates that the forestry sector in the region is unsustainable, and that deforestation from illegal logging is significant. Greater cultural heterogeneity, larger group size, lower technical capacity, and proximity to markets were the most significant predictors of forest change. *Ejidos* with a majority ($\geq 50\%$) of indigenous members suffered lower rates of forest loss. Similarly, fewer forest changes were associated with smaller *ejidos* (≤ 280 members). The results also show that the tradeoffs between livelihoods and forest change have been mostly negative, as forest loss is not associated with improved livelihoods of local people. Increasing our understanding of the factors affecting governance can help inform policy and management interventions that enhance the sustainability of CBF practices. This work can be useful in the design of management actions and policy interventions, and to assess the potential of communities to become conservation partners in protected areas and forest co-management schemes.

1. Introduction

Managing forests is a difficult task, especially in biologically-rich developing regions where pressures on resources, degradation, and deforestation rates tend to be greatest. In México during the past 30 years, the lack of effective forest conservation policies has resulted in extensive land conversion (Cairns et al. 2000, Klepeis 2003) with grave consequences for biodiversity (Fuller et al. 2007). During the same time period, the total area of protected lands increased from 2 to 20.5 million ha (ParksWatch 2006). This demonstrates that despite the benefits that *in situ* conservation offers (Bruner et al. 2001, Rodrigues et al. 2004, Andam et al. 2008), this strategy by itself cannot guarantee the maintenance of populations, communities, and habitats at regionally meaningful scales (Adams 2003, Adams et al. 2004, Fischer et al. 2006). Therefore, better planning and management actions are needed.

In México, the majorities of both natural resources and biological diversity are located on lands owned and managed by user groups organized into *ejidos*, a legal form of communal land tenure in which user groups own and manage a territory and its resources (Sarukhan and Larson 2001). The combined natural capital of *ejidos* is vast. These territories contain 60% of México's total land mass and 85% of all forests, with virtually all protected areas bordering or overlapping *ejido* lands (Wexler and Bray 1996, Klepeis 2003). For these reasons, effective landscape-based conservation is unattainable without the inclusion of communal lands and the enhancement of *ex situ*, participatory natural resource management schemes that explicitly integrate local livelihood needs (Bray et al. 2003, Bray et al. 2005).

Community-based forestry, or CBF, is considered one of such *ex situ* conservation practices that when implemented effectively can improve livelihoods and forest management (Nagendra et al. 2005, Nagendra 2007, Ostrom and Nagendra 2007, Chhatre and Agrawal 2009). In México CBF has become particularly widespread in

recent decades as a result of government decentralization and the transfer of natural resource governance rights to communities (Sarukhan and Larson 2001, Bray et al. 2005). After numerous successful experiences, the Mexican CBF model has been proposed as a global model of sustainability that can efficiently address both development and biodiversity conservation needs in developing regions (Bray et al. 2003). However, there have also been numerous failures of CBF in México (Klooster 2000, Klepeis 2003, Honey-Roses 2004, Bray et al. 2005, Duran-Medina et al. 2005), and despite a growing body of literature, the optimal ecological, social, and political conditions under which CBF succeeds or fails still elude researchers and policy makers (Perez-Cirera and Lovett 2006).

The literature on common pool resource management has identified the basic features of user groups and the institutional arrangements required for effective governance. These include: importance of the resource to the user group, shared understanding of collective problems and of resource degradation, trust among members, community autonomy to regulate resource use, and prior organizational experience (Ostrom 1990, Agrawal 2001). While the presence or absence of these requirements can help explain some of the outcomes of CBF in México, forest governance models there need to account for the uncertainty added by the social and cultural heterogeneity of *ejidos* to better understand the underlying mechanisms of local governance, and to improve management predictions (Klooster 2000, Perez-Cirera and Lovett 2006). They also need to consider the institutions that are legally responsible for governing *ejido* land and its resources.

The *Ejido* General Assembly, or assembly, is the legal entity defined by México's agrarian law responsible for the internal organization of the *ejido*. The assembly regulates land and resource use and, ideally, all major decisions concerning communal assets should be reached by consensus or majority vote in open meetings.

The *Ejido* Commissariat is an assembly-elected group consisting of a president, a secretary, and a treasurer that are responsible for all decisions regarding *ejido* social life. A special council is also elected to monitor the actions of the commissariat and its president (Perez-Cirera and Lovett 2006). In contrast to open-access resources that are susceptible to overuse (*sensu* “tragedy of the commons”), under the Mexican communal land tenure system CBF is best seen as a co-management arrangement in which the state imposes quantitative restrictions regarding commercial timber extraction based on forest productivity and existing regulations, leaving the *ejido* with the responsibility of implementing government-approved management plans and regulating internal use.

As such, a better model for large-scale and long-term implementation of CBF practices would require scientific information relating to biological, environmental, and social aspects of forest resources and users. In addition, governance and institutional structures that influence management at the local level must be evaluated within the current socio-ecological context of the region (Ostrom et al. 2007, Ostrom and Nagendra 2007). Indeed, aspects of both of these implementation challenges are addressed in the present study of CBF practices in the Sierra Tarahumara region (STR) of Chihuahua, México.

The objective of my study was to determine the effects of social structures and community cohesiveness (i.e., the degree of affinity of members and engagement in community affairs) on deforestation rates and the sustainability of CBF practices. A specific aim was to describe the functional relationships between deforestation rates and local forest governance, which is defined by *ejido* institutions and the socio-cultural characteristics of its members, as well as geographic conditions.

To achieve this objective, I focused on the governing institutions of the *ejido* and the potential sources of conflicts and divisions. As the democratic governing body of the *ejido*, the assembly’s decisions can have far-reaching impacts on forested systems

and communities, thus it is important to investigate not only the factors affecting the assembly dynamics (e.g., how many members attend assembly meetings, how often do they meet, and what percent of *ejido* decisions are made by the assembly), but also how these dynamics impact the community and the conservation of natural resources. Also, while forest management is considered a form of co-management between landholders and the state, it is the responsibility of federal and state governments to legislate, to enforce laws, and to monitor legal and illegal forest use. As in other regions of the world with weak regulatory frameworks (Smith et al. 2003, Laurance 2004, Amacher 2006), unfortunately in México neither state nor federal agencies have the capacity to carry out these duties efficiently (Szekely 1999, Guerrero et al. 2000, Buscaglia 2001, Steffan-Dewenter et al. 2007). This underscores the importance of self-sustaining local institutions in forest conservation.

In addition to *ejido* institutions, I paid substantial attention to regional-scale covariates, such as distance to markets and harvested timber prices, because these have been identified as key variables of concern for forest conservation. I also considered past management history, social models for timber extraction, and examined the social, educational, and cultural characteristics of *ejidos*. While some of these attributes cannot be controlled by managers, others such as education, road building and *ejido* organization can be addressed through adequate policy and management interventions. The intent of this study was to contribute to the design of conservation and development plans, inform management decisions, and help predict potential outcomes related to different community-based practices.

1.1. Hypotheses and covariate predictions

Rather than using null hypothesis testing, I defined several well-supported hypotheses (i.e., candidate models) based on *a priori* knowledge derived from relevant

literature, and used statistical tools to objectively rank all the models and select the one that best explained the process of forest cover change. For instance, I expected that centralized community control over forest resources, represented by measures of general assembly meeting frequency, attendance, and member participation, would be an important predictor of forest stewardship. Other anticipated predictors were social characteristics such as size and ethnic background of *ejidos*. Table 2.1 shows all covariates used in the analyses involving *ejido* institutions, forest management practices, social and spatial characteristics, as well as their predicted impact on forest system state and selected references. All the candidate models considered in the analyses are listed in Table 2.2.

2. Methods

2.1. Study area

The 1,200 km² study area, situated between -106.5 and -107.5°E and 27.8 and 28.8°N is located in the Sierra Tarahumara region of Chihuahua, México (see map in Appendix H). Elevations range from 1,400 to 2,700 m and topography is characterized by undulating valleys and rugged slopes, with several rivers carving deep gorges. Vegetation is dominated by ponderosa pine (*Pinus ponderosa*) and oak (*Quercus spp.*) forests on higher elevations, and sub-tropical forest in the lower elevations. Vegetation structure and composition shows varying degrees of disturbance caused by past and present management practices. Land ownership is roughly 90% communal in the form of *ejidos*, less than 0.1% public as national parks, and the rest in private ownership. The study area is sparsely populated, with most people living in small settlements, except for a few villages and towns of up to a few hundred residents. The average proportion of indigenous population in *ejidos* is 36.7%, but ranges from 0 to 76.5%. At the time of this study, 128 *ejidos* had government permits to harvest timber from their forests.

Table 2.1: Description of all explanatory variables used and the predicted forest system response: regrowth (+), deforestation (-), and no change (0).

Covariate	Forest response	Description and selected references
asemyr	+	Meeting frequency, Attendance, and Decisions made by assembly relate
assemat	+	to accountability and centralized community control over natural
deassem	+	resources (Wexler and Bray 1996, Perez-Cirera and Lovett 2006).
popind	+/-	Three classes: 0-25, 25-50, $\geq 50\%$ of indigenous members. Ethnic divisions can cause conflicts, marginalization, and over-appropriation by a powerful few, increasing deforestation rates (Wexler and Bray 1996, Perez-Cirera and Lovett 2006).
eysize3	+/-	Three classes: 20-150, 150-280 and ≥ 280 members. Size of user group associated with non-linear relationships in some cases of collective action (Poteete and Ostrom 2004).
extmod2	+/-	Social model for timber extraction: (1) <i>ejido</i> or work group; (0) other. Division of harvest volumes reduces community control over forest resources and economic competitiveness (Wexler and Bray 1996).
exttime	0	Neutral impact on forests if extraction does not exceed regrowth.
rulesf	+	Formal and informal rules to regulate user behavior. Sanctions and
rulesi	+	effective social control reduces deforestation (Ostrom 1990).
noread	+	Increased literacy and education allow communities to maintain control
avgschool	+	over their resources, monitor finances, and oversee the sustainability of forestry operations (Wexler and Bray 1996, Brown et al. 2007).
dist	-	Shorter distance to markets facilitates and accelerates logging, both legal and illegal (Nelson and Hellerstein 1997).
ressize3	0	Existing timber volume in Doyle feet ³ . Expected neutral if forest extraction does not exceed regrowth.
dfprice	+/-	Prices for timber can encourage stewardship or illegal logging.
salienc	+	Relative importance of annual income from timber harvesting as a proportion of the annual gross internal product of the <i>ejido</i> . Forest stewardship is relative to its importance to the <i>ejido</i> (Ostrom 1990).
sexratio	-	Proxy for emigration of <i>ejido</i> male members. Migration can divide communities, alter social networks, governance systems, and reduce community control over resources (Bray et al. 2005).

2.2. Data

The data were generated from a survey of 38 *ejidos* supplemented by interviews with key informant and stakeholder group representatives. Samples were selected randomly using an efficiency matrix with 3 variables that are known to affect CBF outcomes: user group size, cultural heterogeneity, and resource salience. This was done to make sure a sample with enough replicates for each variable category was obtained.

Environmental data were obtained from a variety of sources. Forest cover change rates were estimated from satellite imagery spanning from 1976 to 2001. Household socio-economic, demographic, and education data were obtained from the 2005 population census carried out by the National Institute of Statistics, Geography and Informatics. Appendix A shows scatter plots of response and predictor variables relationships.

2.3. Model

Data exploration revealed that the response variable for deforestation was not normally distributed (i.e., variance larger than the mean), and approximated a Poisson distribution with over dispersion (i.e., the mean-variance relationship was not met). In this case, a negative binomial generalized linear model (GLM) was deemed appropriate for analyzing this dataset (Vernables and Ripley 2002, Zuur et al. 2009, Kéry 2010). The GLM is a class of model that incorporates distribution functions from different exponential families, including the Poisson and negative binomial, giving it a framework that improves the parameterization of distributions, estimation efficiency and error accountability. The GLM function notation (Kéry 2010) is given by

$$\begin{aligned}
 y_i &= \alpha_{j(i)} + \beta_{j(i)} * x_i + \varepsilon_i & (1) \\
 \alpha_j &\sim Normal(\mu_\alpha, \sigma_\alpha^2) \\
 \beta_j &\sim Normal(\mu_\beta, \sigma_\beta^2) \\
 \varepsilon_i &\sim Normal(0, \sigma^2)
 \end{aligned}$$

where y contains deforestation rates for sample i , $i = 1, \dots, 38$, α is the intercept, β is the parameter coefficient or slope, x is an explanatory covariate for sample i , and ε is the residual random effect. I assumed that α and β came from independent normal distributions with means μ_α and μ_β and variances σ_α^2 and σ_β^2 , and that residuals ε for sample i came from another independent normal distribution with σ^2 variance.

2.4. Model selection

Logistical considerations on the ground somewhat constrained my sample size, which limited the number of predictors that I could model while retaining adequate statistical power. As such, my model selection procedure focused only on those models with at least 30 degrees of freedom. Model selection was based on Akaike's Information Criterion (AIC) (Burnham and Anderson 2002). Using the freely available software package R, I applied the `stepAIC` command to build the models, and the `anova` command (via an analysis of deviance) to compare the relative support for each (Vernables and Ripley 2002, Zuur et al. 2009). For the best fitting models I computed ΔAIC for the i -th model ($AIC_i - \min(AIC)$), and AIC weight (w) as a measure of relative support using the `AICtab` command.

3. Results

Forest cover analyses revealed that by 2001 12.54% of the STR was deforested, a 40% increase from 8% in 1976. Forest loss rates by *ejido* averaged 42.0 (2.26-180.3) ha/yr, while forest gains averaged 10.1 (0.58-23.3) ha/yr. Only 20% of *ejidos* presented forest gains equivalent to 0.14% of the study area (see Appendix B).

I selected the most parsimonious model based on AIC weights ($w = 0.719$, Table 2.2), and found linear relationships between forest change with distance to markets (`dist`, $w = 0.993$, $\beta = -0.082$, $SE = 0.003$), and average education (`avgschool`, $w = 0.8$, $\beta = -0.21$, $SE = 0.045$); and non-linear relationships with user group size (`ejsize3`), and proportion of indigenous population (`popind3`, see Table 2.3). The second best model had low bearing ($w = 0.084$), showed non-linear relationships between forest change, `popind3`, and `ejsize3`; and linear relationships with formal rules and sanctions (`rulesf`), and social models of forest extraction (`extmod2`), both indicators of effective local governance and social cohesiveness, respectively. While the covariate `dist` was

significant, estimates were considerably lower in this model. My hypothesis relating to general *ejido* assembly dynamics were not supported by the data. Only the covariate for number of meetings per year (*asemyr*) received support, although it was minimal at best ($w = 0.073$, $\beta = -0.268$, $SE = 0.045$, Table 2.4). Graphical validation tools for both models showing the superiority of model 1 are presented in Appendix C.

4. Discussion

This study sought to determine the long-term impact of different local governance structures on forest system state, and to predict its response to management actions and degradation. The top model demonstrated the statistical significance of well-known deforestation predictors such as the presence of roads and access to markets (Nelson and Hellerstein 1997, Perz and Skole 2003, Rodrigues et al. 2009). In addition, I was able to make connections between forest management practices and socio-cultural attributes of user groups for which few empirical analyses that allow for rigorous statistical inference exist. In the best model of forest change (i.e., the most parsimonious) I found that distance to markets (*dist*, AICc $w = 0.993$) was the most significant predictor. Forest change rates were significantly higher in areas closer to markets (simple linear regression between forest change rate and *dist*: $\beta = -6.375 \pm 3.161$, $F_{1,36} = 4.068$, $P = <.05$, $r^2 = 0.101$) and where market prices for timber are high (regression between forest change rate and *dfprice*: $\beta = -0.134 \pm 0.017$, $F_{1,36} = 60.98$, $P = <.001$, $r^2 = 0.628$). Increasing distance to markets alone can significantly reduce the profit margin for many *ejidos* because few of them own transportation and other harvesting equipment, and transporting logs to sawmills is by far the major operational cost in forestry operations (Perez-Cirera and Lovett 2006). However, proximity to markets in combination with high prices can be a main driver for legal harvesting, and a catalyst for illegal logging.

Table 2.2: Summary of model selection procedure for factors affecting deforestation in the Sierra Tarahumara region, México.

	Candidate models	AIC	<i>K</i>	Δ AIC	<i>w</i>
1	eysize3 + popind3 + dist + avgschool + sexratio	384.2	9	0.0	0.7195
2	eysize3 + popind3 + dist + rulesf + extmod2	388.5	9	4.3	0.0846
3	eysize3 + popind3 + dist + avgschool + assemyr	388.6	9	4.4	0.0808
4	eysize3 + popind3 + dist + rulesf	390.4	8	6.2	0.0329
5	eysize3 + popind3 + dist + rulesf + exttime	390.7	9	6.5	0.0284
6	eysize3 + salience + dist	391.9	6	7.7	0.0151
7	ressize3 + dist	393.1	4	8.9	0.0085
8	ressize3 + dist + exttime	393.2	5	9.0	0.0078
9	eysize3 + salience	393.5	5	9.3	0.0067
10	eysize3 + dist + salience + rulesf	393.7	7	9.5	0.0061
11	exttime + dist + ressize3 + rulesf	395.0	6	10.8	0.0031
12	eysize3 + dist	395.6	5	11.4	0.0024
13	eysize3 + dist + rulesi	396.1	6	11.9	0.0018
14	eysize3 + dist + rulesi + assemyr	396.4	7	12.2	0.0016

Table 2.3: Negative binomial GLMs to explain forest cover change in the Sierra Tarahumara Region, México. Sample size is 38 *ejidos*. Mean (SD) of the dependent variable is 91.9 (52.6).

Model 1: $\text{deforate3} \sim \text{popind3} + \text{eysize3} + \text{dist} + \text{avgschool} + \text{sexratio}$			
Coefficients	Estimate	SE	<i>P</i>
Intercept	7.70596	0.87548	<.001
Popind32	-0.05691	0.18676	<.1
Popind33	-1.12254	0.25147	<.001
Eysize32	-0.06357	0.16469	<.1
Eysize33	0.65278	0.15368	<.001
Dist	-0.10054	0.02418	<.001
Avgschool	-0.25609	0.08134	<.01
Sexratio	-1.49024	0.53983	<.01

Model 2: $\text{deforate3} \sim \text{rulesf} + \text{extmod2} + \text{popind3} + \text{dist} + \text{eysize3}$			
Coefficients	Estimate	SE	<i>P</i>
Intercept	5.277707	0.262343	<.001
Rulesf1	-0.263686	0.138462	<.1
Extmod21	-0.353470	0.165658	<.05
Popind32	-0.004121	0.201678	<1.0
Popind33	-0.523285	0.166685	<.01
Dist	-0.090331	0.025332	<.001
Eysize32	-0.132544	0.178748	<1.0
Eysize33	0.595298	0.161523	<.001

Table 2.4: Covariates influencing forest cover change rates using negative binomial GLMs ranked on the basis of summed model weights (w).

Covariate	Sum of AICc w	Mean β -coefficients	SE
Dist	0.9932	-0.0821	0.0039
Ejsize32	0.9803	-0.0345	0.0167
Ejsize33	na	0.5098	0.0313
Popind32	0.9463	0.0410	0.0441
Popind33	na	-0.6818	0.1275
Avgschool	0.8003	-0.2108	0.0453
Sexratio	0.7195	-1.4902	0
Rulesf	0.1553	-0.1591	0.0391
Extmod2	0.0846	-0.3535	0
Assemyr	0.0824	-0.2688	0.0455
Exttime	0.0394	-0.0089	0.0002
Salienc	0.0280	0.1368	0.0118
Ressize3	0.0196	0.1844	0.0068
Rulesi	0.0034	0.2402	0.0481

Although the data do not distinguish between forest change caused by legal or illegal logging, and no official statistics exist (National Forestry Commission—CONAFOR, www.conafor.gob.mx), it is estimated that between 30-70% of the forest products that enter the national market are of illicit origin (Gomez 2004, Navarro and Velazquez 2011). Statistics for the STR are even scarcer, but considering the limited amount of regulatory control over sawmill operations and the high degree of corruption in the regional forestry sector (Guerrero et al. 2000), proximity to markets most certainly increases the profitability of illegal logging. This is a serious concern because the analyses clearly show that the legal forestry sector in the STR is unsustainable. By law, the prescribed harvest quota is lower than the actual estimated timber volume to account for the uncertainty in stocking rate estimation (Perez-Cirera and Lovett 2006). I tested this regulation by regressing estimated timber volume (*ressize3*) by years of timber extraction (*exttime*), and found a significant negative relationship demonstrating

that harvest quotas diminish with time ($\beta = -0.195 \pm 0.092$, $F_{1,36} = 2.357$, $P = <.05$, $r^2 = 0.118$). Deriving inference from pattern is always a question of judgment (Gardner 2007), especially with a limited dataset such as this one. Nevertheless, I believe that the decreasing estimates of timber volumes and the discrepancy between estimated and actual timber harvest can only be explained by illegal extractions, and/or corruption in the process of estimation by state-supervised forestry technicians. In either case, this study has gone beyond previous analyses of forest change patterns, adding insight into the role and effectiveness of state agencies in regulating forest management practices.

Other factors that played important roles in forest management were related to *ejido* community structure and organization. Summed model weights show strong support for covariate *ejsize3* (AICc $w = 0.98$). Forest loss rates decreased in small (20-150 members) and medium-sized (150-280) *ejidos*, whereas rates increased in larger (≥ 280) *ejidos*. A closer inspection revealed that this relationship was not a restricted consequence of increased human pressure as measured by population density (simple linear regression between forest loss and population density: $\beta = -499.47 \pm 278.46$, $F_{1,36} = 3.217$, $P = <.1$, $r^2 = 0.082$). These findings are consistent with Nagendra (2007) and Poteete and Ostrom (2004). They report that small groups often cannot carry out forestry-related activities and other governance related tasks effectively, and as group size increases beyond a certain point, control of operations as well as group organization and coordination, becomes increasingly difficult. Chhatre and Agrawal (2009) differ, and argue that larger user groups are optimal for communal forest governance. However, their conclusions do not account for the variability caused by cultural and ethnic heterogeneity, which is known to significantly affect local governance outcomes (Poteete and Ostrom 2004, Perez-Cirera and Lovett 2006).

It is worth noting that the problem of efficiency and effectiveness of group size has also been examined by evolutionary anthropologists. Findings have established that

the number of people that can maintain a stable and cohesive social unit over time is limited by cognitive capacity (Dunbar 1992). Recent studies found that social unit optimization occurs in groups that average 150 (100-230) members, and that as groups increase in size, so does the need for more rules and enforced norms to maintain stability and cohesion (Hernando et al. 2010). The results of my study are consistent with these reported numbers, linking sustainable CBF practices with effective social group size.

In the analyses, ethnicity and culture played an important role in forest management. Popind3 had strong support (AICc $w = 0.9463$), and presented a non-linear relationship with forest change, which decreased significantly in *ejidos* with $\geq 50\%$ of indigenous members. This was true for *ejidos* near markets, as the presence of an indigenous majority resulted in lower rates of forest loss compared to *ejidos* without an indigenous majority (simple linear regression between dist and popind: $\beta = -0.493 \pm 1.696$, $F_{1,36} = 0.084$, $P = <1.0$, $r^2 = 0.002$). It has been argued that indigenous communities, most of which are economically disadvantaged, are less likely to possess the appropriate timber harvesting infrastructure that can result in forest cover changes. Alternatively, low rates of forest loss could be attributed to the sets of beliefs, perceptions, and attitudes toward material goods and the natural environment that characterize indigenous communities (Quezada 2007). I believe that the relationship of forest loss with more socially and culturally heterogeneous groups is likely the result of intracommunity divisions and conflicts. Poteete and Ostrom (2004) contend that group homogeneity is a result of shared social, cultural or economic values which provide a basis for trust, solidarity and common objectives that increase the likelihood of effective collective action. In turn, in communities with internal conflicts from cultural or ethnic divisions, solidarity and collective action are less likely to occur. That is, cohesive groups, based on a strong sense of cultural identity and dense social networks (i.e.,

relationships among its members), are more likely to effectively self-organize, coordinate collective actions, develop self-governance capacity, and maintain their natural resource base (Toledo 2000, Sarukhan and Larson 2001). In the study region, the differences between the Tarahumara, the main ethnic group in the region, and the *mestizo* (mixed European and indigenous population), are substantial. These ethnic groups have different languages, social forms of organization, and value systems that oftentimes clash and are a major source of tensions (Guerrero et al. 2000, Cordova 2001, Perez-Cirera and Lovett 2006), which can escalate into violence and even death (Simon 1997, Weinberg 2000). This is an issue of concern for forest management and conservation because tensions stemming from intra and intercommunity divisions and conflicts can disrupt traditional mechanisms of cooperation, and reduce the likelihood of participation in collective actions (Sanchez-Perez et al. 2007). In other parts of México, high rates of deforestation inside and outside of protected areas coincide with *ejidos* that are beset by intracommunity divisions and, as a result, have weak governing institutions (Klepeis 2003, Honey-Roses 2004)

The covariates for literacy (*noread*) and average education (*avgschool*) are relevant because they relate to capacity at the community level. In this study, average education levels were a significant predictor that had a negative relationship with forest change (AICc $w = 0.814$). Perhaps this is not surprising because capacity is considered to involve intellectual, educational, organizational, and cultural assets that lead to empowerment and community self-determination (Brown et al. 2007). In CBF settings, capacity translates into the ability of communities to hold authorities, forest technicians, and logging companies accountable for their involvement in their forests and affairs. Capacity is also necessary in all dealings with government agencies and the outside world. At the individual level, *ejido* members with more capacity can participate more actively in community affairs. At the community level, an imbalance of technical

capacity among its members can lead to a disproportional power distribution and marginalization of the most vulnerable groups, which often consist of women or indigenous people (Perez-Cirera and Lovett 2006). It is estimated that close to 80% of México's community forests are under-managed or mismanaged because of the lack of skills and capacity of local communities (Bray 2005, Larson et al. 2010).

Despite my expectations, the data did not reveal any statistically relevant relationships between forest change and the covariate measures I chose to represent *ejido* institutional dynamics and behavior. For example, covariate assembly ($\beta = -0.223 \pm 0.191$, $P = <1.0$) was included in one of the top ranked models, but overall support for it was low (AICc $w = 0.073$). My approach considered these covariates to be measures of the democratic participatory processes within the general *ejido* assembly that are generally considered an essential component of sustainable governance arrangements (Ostrom 1990). It should be noted that the general *ejido* assembly is important, but not the only socio-political structure responsible for social organization and regulation of social life in *ejidos*. Informal institutions are not easily quantifiable and vary greatly by *ejido*. These forms of organization can best be seen as a set of structural (e.g., rules, social networks and roles) and cognitive (e.g., norms, values, and attitudes) attributes that provide the basic foundation for trust, solidarity, and reciprocity in a community. Many communities, especially those that are far removed from public services, continue to develop endemic forms of social organization based on cultural affinities and their stake in the collectivity of the *ejido* (Toledo 2000, Sarukhan and Larson 2001).

5. Conclusions and management implications

Whereas some authors are of the opinion that biodiversity conservation is incompatible with rural development and poverty alleviation efforts in developing regions (Adams et al. 2004), others consider that with the proper conditions and

incentives CBF and agroforestry practices can be a viable means to achieve both (Steffan-Dewenter et al. 2007, Larson et al. 2010, Pokorny et al. 2010). Theory notwithstanding, in practice the successful implementation of such practices at the landscape-scale is no easy task. In this study of the STR, where CBF practices have been implemented for decades, I found successes and failures. I determined that forest change is significant and influenced by proximity to markets, timber prices, and local governance arrangements that are shaped by user group size, technical capacity, and ethnic composition. I also found that the tradeoffs between forest change and livelihoods benefits are mostly negative. To illustrate this, I used the most recent Social Marginalization Index measure (Mexican National Population Council–CONAPO, www.conapo.gob.mx) to assess the tradeoffs between the welfare of *ejidos* in the region in relation to the degree of forest use (Fig. 2.1). Ideally, a “win-win” situation would be one in which livelihoods are improved while the natural resource base is maintained (Geisler 2010). In contrast, a “lose-lose” situation would be one in which livelihoods are low and forest management is unsustainable (Steffan-Dewenter et al. 2007). In the STR, I found that most *ejidos* are marginalized and forests over used.

Although these tradeoffs are often inevitable and unpredictable, CBF is still one of the best ways of promoting social stability in rural areas by providing jobs and improving livelihoods while potentially sustaining forest resources and biodiversity. In order for CBF to be sustainable, effective local governance arrangements and the conditions that enable it need to be developed and sustained. Some of these conditions include land tenure security for user groups, technical capacity building to improve management practices, access to fair prices and markets, effective law enforcement to regulate illegal logging, and socio-political stability (Larson et al. 2010). Of these conditions, land tenure security is crucial. Livelihoods and local natural resource governance in México are protected by the structure of the communal land tenure

system. However, external influences, such as official programs that promote the parcelization of communal land into individual plots, as well as policies that undermine or ignore *ejido* institutions, can cause internal conflicts and create a self-feeding loop that can eventually fragment communities and territories (Wexler and Bray 1996, Klooster 2000, Klepeis 2003, Duran-Medina et al. 2005). This can potentially result in further habitat degradation and fragmentation with serious negative consequences for biodiversity and rural livelihoods.

While CBF may not make much sense from a profit-driven economic perspective given that few communities are able to compete successfully in a free market economy, CBF is a vital component of rural economies where income opportunities are limited. As such, the social, political, and environmental stability of vast forested regions of México depend on maintaining and enhancing effective governance arrangements, as well as the human and social capital that supports them.

The findings of my research can be particularly useful for such purposes. Inference derived from my results indicates how forest governance arrangements are shaped by the socio-cultural characteristics of *ejidos* and its geographic location with respect to markets. This means that to sustain effective governance arrangements, local socio-cultural structures need to be supported. Management and policy interventions, particularly in the form of external aid, need to be aware of these socio-cultural structures, and incorporate them into any required decision-making and implementation processes. Essentially, effective policy and management interventions that seek to improve governance and forest management in the region need to be ecologically and socio-politically based to fit the conditions of individual *ejidos* and their resources. Also, these results and analytical framework can be used to assess the potential of communities to become conservation partners in spatial reserve management based on their capacity to contribute effectively to natural resource co-governance arrangements.

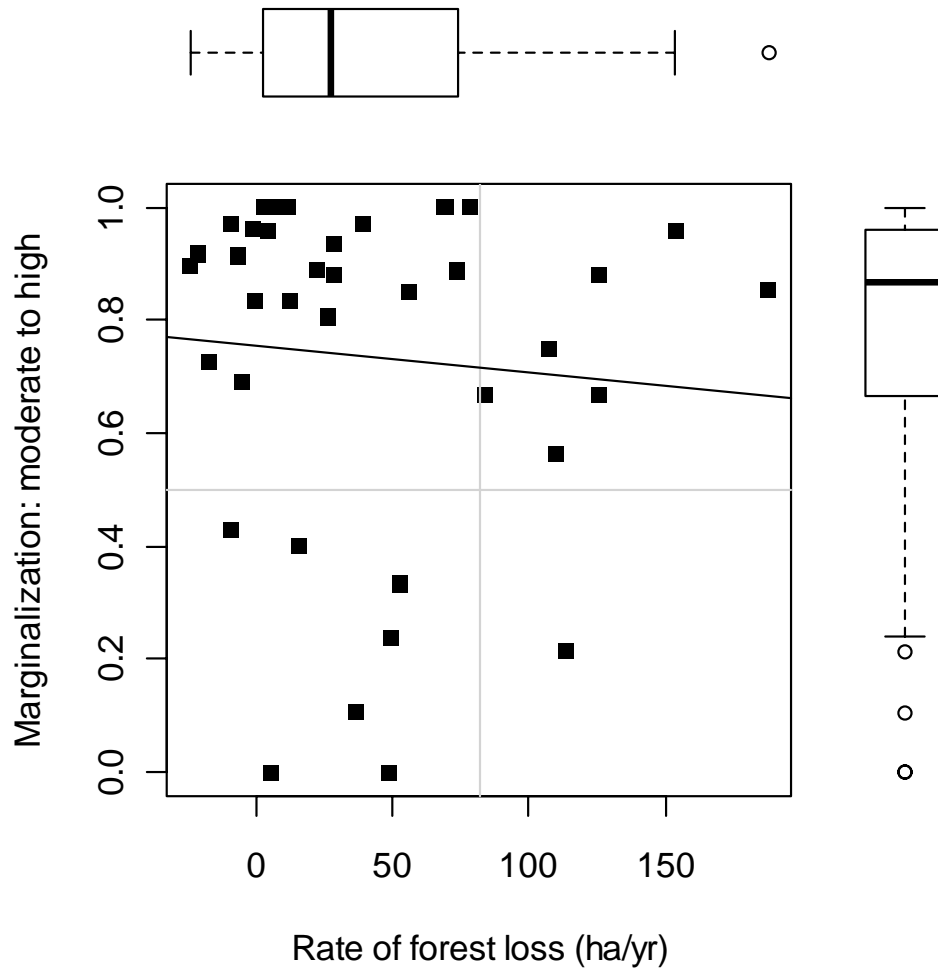


Figure 2.1: Two-dimensional plot and univariate frequency box plots (95% CI) of forest change and livelihoods tradeoffs as measured by the official Social Marginalization Index in the STR study area. The solid line indicates a linear relationship between forest change and livelihoods. Bottom left corner corresponds to those *ejidos* with higher livelihoods and lower forest change.

Improving the self-governance capacity of communities is perhaps the most important component of sustainable forest management. Better governance is linked to better stewardship, and can help communities gain access to market tools of certification and compensation, including payment for environmental services and Reduced Emissions from Deforestation (REDD) that acknowledge the importance of local institutions (Larson et al. 2010). Improved governance and access to these market tools add value to forests, and create additional incentives to protect them.

Further, I believe that ecological and economic forest sustainability is a matter of national security. Forest ecosystems provide invaluable goods and services that support millions of livelihoods directly and indirectly. Most water for agriculture and cities originates in forested regions. Forests are also essential for climate regulation, nutrient cycling, and biodiversity. In rural areas forests support millions of rural and indigenous people by providing food, fibers, fuel, and jobs in forestry-related activities. Legal forest production in Mexico has declined from of 12 million m³ of timber in the 1990's to roughly 6 million in 2010 as a result of free trade agreements that allow lower priced timber products to saturate the market. During the same time period, illegal logging and drug cultivation have increased to record levels, along with violence, public insecurity, and migration of people and communities out of these regions. These unfortunate consequences of poorly considered development and conservation planning underscore the importance of investing in socially and ecologically sustainable forestry in order to maintain political stability in the STR and other parts of the country.

Finally, despite the characteristics that make the CBF sector in the STR unique, I consider that my study approach, results, and conclusions present core elements that offer widely applicable lessons for other forested regions in México, and in other developing countries where forest governance has been transferred to local communities.

6. References

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Chapter 3

USE OF MULTI-SPECIES BAYESIAN OCCUPANCY MODELS TO EVALUATE THE IMPACT OF FOREST MANAGEMENT ON THE STRUCTURE AND DYNAMICS OF BIOLOGICAL COMMUNITIES

Abstract: Understanding how the distributions and occurrence of organisms respond to habitat disturbance is a recurring theme in ecological research and conservation planning, precisely because of its importance. Here I discuss the application of a multi-species hierarchical Bayesian model to estimate species richness and other community summaries as a function of species-specific probability of occupancy and habitat covariates. I use this model to make inference about the impact of timber harvesting on forest breeding birds, and underscore the utility of this technique to obtain important community summaries, and its applicability in management and conservation practices. For my analyses I used data from a breeding bird census of 32 study sites in managed (*ejido*, or communally-owned land parcels) and unmanaged (national parks) forests in the Sierra Tarahumara region, México, sampled 3-5 times/yr in 2008 and 2009. Site-specific and total species richness estimates were positively related to tree diameter size and negatively to tree density. These patterns support the original hypothesis that degradation caused by poorly considered forest management practices reduces occupancy, community size, and species composition. Contrary to *a priori* expectations, sites with higher richness had lower estimate uncertainty, and vice versa. Although these results can be readily incorporated into forest management plans to increase site-level avian occupancy and richness in the study region, this modeling framework also can be applied to other taxa and other areas to address questions of community ecology and resource management. Finally, I mention the importance of estimate uncertainty for sampling design and inference regarding community structure and dynamics.

1. Introduction

Widespread loss of species as a result of deforestation and degradation from human activities is a major conservation issue around the world (Tilman 2000, Rodrigues 2006). In developing regions biodiversity loss and deforestation are driven by intricate mechanisms. For the most part, comprehensive long-term solutions are lacking. For example, in México deforestation processes and other environmental issues are the result of a combination of factors including population growth, socioeconomic marginalization and government institutions that have other priorities, lack sufficient operational capacity and are in many cases corrupt (Howell and Webb 1995, Simon 1997, Guerrero et al. 2000, Cartron et al. 2005, Sefchovich 2008). Considering that environmental degradation is expected to worsen from increased human pressure and global climate change (Lyon et al. 2008, Rosenzweig et al. 2008), successful biodiversity conservation is now more than ever reliant on informed and effective planning and management actions (Wilson et al. 2007, Cook et al. 2010).

At the outset of designing a conservation or management plan for a resource or ecological system, developing accurate measures to assess and monitor its state is an essential first step. Vital system rates, or state variables, such as the size of a population of interest or species richness, are necessary for the effective monitoring of changes in space and time. They also are essential to make informed management decisions, design appropriate and timely management and conservation interventions, and make efficient use of limited funds (Yoccoz et al. 2001, Nichols and Williams 2006). In the case of forests and woodlands, remote sensing techniques are arguably the most common approach to monitor the impact of logging and other human activities on forest resources over large areas (Boyd and Danson 2005, Hansen et al. 2008). However, detailed inference about the ecological processes and functions of forested systems from remote sensors is limited when degradation processes in the subcanopy are not

addressed. For example, researchers recently found that common remote sensing methods fail to detect damages to soils and the forest subcanopy, underestimating overall degradation from logging activities by as much as 50% (Asner et al. 2005). Thus in order to better understand the structural processes and functional dynamics of a natural system, and how these processes might be affected by degradation or management interventions, alternative state variables that provide inference regarding the interactions between the environment, populations or communities are necessary (Nichols et al. 2005, Moniz et al. 2007).

Alternative state variables in wildlife studies, such as species richness (the number of species in an area) or occupancy (the proportion of sites occupied by a species) can be estimated using occupancy models, which are a recently-developed class of models useful for studying patterns of distribution and abundance of species. This approach uses detection/non-detection (i.e., presence/absence) data obtained from repeated observations at each site to model site occupancy dynamics (patch occupancy, colonization, and extinction) of single and multiple species while accounting for imperfect detection (MacKenzie et al. 2002, MacKenzie et al. 2003, MacKenzie et al. 2005, Royle and Dorazio 2008).

There are several advantages to using occupancy methods in ecological studies instead of counts or indices. Collecting detection/non-detection data can often take less time than a traditional abundance survey, making it less sampling intensive and often allowing for larger areas to be surveyed (MacKenzie et al. 2005). In addition to predicting occurrence rates for animals and estimating detection probabilities, these models can also be used to estimate population abundance, generate inference on population and meta-population dynamics (e.g., extinction and colonization rates), estimate species richness, and design spatial reserves (Royle and Nichols 2003, Bailey et al. 2004, Cabeza et al. 2004, Dorazio and Royle 2005, Royle and Dorazio 2008).

Recently developed multi-species occupancy models (hereafter, community models) can provide valuable inference regarding the impact of environmental gradients (Kéry and Royle 2009, Kéry et al. 2009), fragmentation and land cover changes (Zipkin et al. 2009a, Zipkin et al. 2009b), and silvicultural treatments (Russell et al. 2009) on biological communities. One of the main advantages of this technique over traditional estimation approaches is that species-specific detection probabilities are incorporated explicitly into the models, which greatly improves inference for rare and abundant species, and the precision of species richness estimates (Royle and Dorazio 2008). Species richness estimates that do not account for detection heterogeneity tend to be biased towards the more common and abundant taxa (Zipkin et al. 2009a), but inference about rare taxa is particularly useful for conservation purposes because rare and endangered species are usually the focus of spatial reserve design and habitat management interventions (Fleishman et al. 2000).

Community modeling can be a very powerful tool for managers and policy-makers to understand how biological communities respond to specific management activities –whether extractive or restorative. These flexible modeling tools can be highly effective at identifying areas of high diversity potential when the functional response to habitat covariates is known. As such, the objective of this study was to use a community model to estimate species richness in managed and unmanaged forests, and to explore the relationships between species richness and site-specific habitat covariates that reflect the changes caused by human activities. Specifically, this study focused on the community of diurnal forest breeding birds because their large number of species relative to other vertebrate groups makes them an attractive measure of biodiversity and environmental changes (Canterbury et al. 2000, Ceballos and Marquez 2000, Manley et al. 2006, Miller et al. 2009). The intended outcome was to inform management recommendations in order to enhance and improve local and regional biodiversity.

Although not a complete substitute for large spatial reserves, in areas where setting aside land is unfeasible, informed *ex situ* conservation can be an important strategy for large scale protection of biodiversity and ecological processes (Fischer et al. 2006, Morreale and Sullivan 2010).

2. Methods

2.1. Background

No obvious studies have examined the impact of forest use on biological communities and ecosystem state in the Sierra Tarahumara region (STR) of México. To better understand the relationships between human uses and ecological condition, it is necessary to acknowledge past and present land uses, geographical and environmental conditions, stakeholder characteristics, and the main drivers of resource degradation.

The STR is part of the Sierra Madre Occidental Ecoregion in northern México, and is one of the most biologically diverse and critically threatened ecoregions in North America (Brooks et al. 2006, WWF-Mexico 2007). Covering roughly 70,000 km² of forests and woodlands, the region holds 15% of México's forest biomass, and 10% of the forests currently under management in México (Perez-Cirera and Lovett 2006). The area is sparsely populated, with most people living in small settlements except for a few villages and towns of up to a few hundred inhabitants. The road network is unpaved and in poor condition most of the year, with many parts becoming inaccessible during the rainy season from June to September.

Interestingly, 90% of all land in the STR is owned and managed by common property forest user groups known as *ejidos*, a legal form of communal land tenure in which members collectively own a territory and have democratic institutions that regulate social life and natural resource use (Sarukhan and Larson 2001). Less than 0.1% is public as national parks, and the rest in private ownership.

The main sources of income in the STR include collective dividends from timber sales, subsistence agriculture, and small-scale animal husbandry (Guerrero et al. 2000). Widespread poverty, particularly in indigenous communities, is aggravated by diminishing forest growth and agricultural yields brought on by decades of poorly regulated timber harvesting and associated degradation of soils, forest, and range resources. The social and ecological stability of the region may be further threatened by the breakup of *ejidos* and subsequent fragmentation of communal lands into smaller, private landholdings. This is mostly caused by external factors, including neoliberal policies, fluctuating market prices for agricultural products, land speculation and corruption (Guerrero et al. 2000, Merino-Perez and Segura-Warnholtz 2005). Incidents regarding illegal crop cultivation and trafficking have increased along with federal military presence in the region since 2008 (Turati 2010). This is representative of steady landscape and social trends in the region.

2.2. Study area

The 1,228 km² study area is situated in the central portion of the STR and included parts of the Bocoyna, Carichi, and Chihuahua municipalities between -106.5 and -107.5°E and 27.8 and 28.8°N. Topography is characterized by undulating valleys and rugged slopes, with elevations ranging from 2,100 to 2,300 m. Several major rivers drain the region forming deep subtropical canyons. The STR is considered an area of high endemism, specially for amphibians, birds, and vascular plants (Felger and Wilson 1995). Vegetation is dominated by ponderosa pine (*Pinus ponderosa*) and oak (*Quercus spp.*) forests exposed to various degrees of human disturbance. Most *ejidos* in the area have experienced significant degradation from logging, livestock grazing, and fires. Some stands of mature forest are still found on inaccessible terrain and national parks.

2.3. Survey design and data collection

After field-testing, it was found that a random sampling design was not appropriate due to logistical limitations on the ground (i.e., manpower, rugged terrain, and poor condition of roads). I decided that a systematic sampling approach (Poon and Margules 2004) was more suitable for the number of spatial and temporal replicate samples needed to meet data collection and occupancy modeling assumptions. To begin with, topographic and vegetation maps were overlaid with a 5×5 km grid and used to identify suitable sampling points based on vegetation, land tenure, terrain, presence of secondary and tertiary roads, and the absence of human settlements within a 1 km radius. Subsequent ground verification and field protocol testing resulted in a total of 32 sampling sites distributed among 9 land parcels or management units. These included two located within national park lands and seven in *ejidos* of varying sizes and governance arrangements (see Appendix D). In all, there were 3-5 spatially independent replicates in each of the 9 management units that could be readily accessed within the short period of time which was required to meet the assumptions of closed populations.

Data of closed populations were collected during a 2 yr breeding bird survey conducted during the beginning of the local reproductive season (5 to 28 May 2008 and 15 May to 4 June 2009). Encounter histories for all species were constructed using 10 min point counts starting 30 min before sunrise and ending 5 hr later. All birds seen or heard within a 75 m radius were recorded as present (1) or absent (0) (Ralph et al. 1995a). All sites were sampled a minimum of three separate occasions in order to build the encounter histories needed to estimate detection and occurrence probabilities (MacKenzie and Royle 2005). Weather conditions were recorded every time a site was sampled. On separate visits canopy cover, basal area, height of all trees (>1.5 m), and cover of perennial shrubs (<1.5 m) were measured using 400 and 100 m² plots, respectively (Manley et al. 2006).

2.4. Model description

The community model framework was based on species-specific occupancy estimation (Kéry and Royle 2009) that incorporates a hierarchical Bayesian analysis and a data augmentation parameterization (Royle et al. 2007, Royle and Dorazio 2008). One of the main advantages of this modeling framework is that observations and the state processes are modeled separately. An observation model specifies a probabilistic approach to defining the mechanisms from which the data are derived from. In turn, the process model describes the process of interest (in this case, occupancy) and its inherent variation (Royle and Dorazio 2008). In this model, occurrence $z(i, j)$ is a binary process in which $z(i, j) = 1$ if species $i = 1, 2, \dots, N$ is detected at site $j = 1, 2, \dots, J$ during a 10 min point count, and 0 (zero) if not detected. The model for species occurrence is defined as

$$z(i, j) \sim \text{Bernoulli}(\psi_{i,j}) \quad (1)$$

where $\psi_{i,j}$ is the probability that species i occurs at site j . The probabilistic description of the mechanisms that produce the observed data is defined in the observation model as

$$x_k(i, j) \sim \text{Bernoulli}(z(i, j) * p_k(i, j)) \quad (2)$$

and is conditional on $z(i, j)$. Thus, if $z(i, j) = 0$, then all resulting observations are fixed zeros. I used logit transformations of occupancy and detection and assumed that these were the sum result of species- and site-specific effects. A simpler version of the model (Kéry and Royle 2008) without site-specific effects α_j and β_j assumes that μ_i and ν_i are normally distributed and that the only source of variation in detection and occupancy is specificity. In this case, occurrence is formulated by a logit transformation that sums species- and site-specific effects such that

$$\text{logit}(\psi(i,j)) = \mu_i + \alpha_j \quad (3)$$

and detection probability is

$$\text{logit}(p(i,j)) = v_i + \beta_j \quad (4)$$

Occupancy $\psi(i,j)$ is then defined as the probability that site j is occupied by species i , and $p(i,j)$ is the detection probability for species i at site j , with species-specific effects given by μ and v , and site-specific effects by α_j and β_j . In this particular situation, I was interested in describing the site-specific effects on occupancy for species i and site j as linear functions of quadratic mean diameter of trees at breast height (qdbh) and average tree density/ha (density), the two main variables used to estimate forest stocking rates and stand dynamics (Long 2005). The model was expanded to include an interaction term

$$\text{logit}(\psi(i,j)) = \mu_i + \alpha_{1i} * \text{qdbh}_j + \alpha_{2i} * \text{density}_j + \alpha_{3i} * \text{qdbh}_j * \text{density}_j \quad (5)$$

where μ_i is the species-specific effect and the intercept. Site-specific effect α is indexed i for each species, and j for site covariates. Considering that removal of trees in timber-harvesting operations directly affects the size and structural complexity of a stand, I assumed that species occupancy and richness depend on these covariates, and thus help describe variation across the landscape. Similarly, I was interested in describing the added effects of day of year when sites were sampled, and amount of canopy cover (linear and squared) on detection probability for species i at site j during survey k . In this formulation, species-specific effect on detection for species i was described by v_i , while β coefficients are site-specific to the date when sampling was conducted and for the canopy cover values at site j , such that

$$\text{logit}(p_k(i,j)) = v_i + \beta_{1i} * \text{date1}_{jk} + \beta_{2i} * \text{date2}_{jk} + \beta_{3i} * \text{canopy1}_j + \beta_{4i} * \text{canopy2}_j \quad (6)$$

2.5. Data augmentation and Bayesian analysis

The dataset consisting of 73 (n) species was augmented by adding 150 hypothetical species with all-zero encounter histories (Dorazio and Royle 2005, Royle et al. 2007). Having an unknown number of species creates some analytical issues that can be addressed by inflating the dataset, and thus fixing the total size of the dataset (i.e., the available number of species). Basically, this procedure uses an M number of available species instead of an unknown number of species ($M - n$). This can be seen as the equivalent of imposing a discrete uniform prior value on N , the total number of species from which species richness is estimated. Estimation of N is done by introducing a latent indicator variable w_i for $i = 1, 2, \dots, n, n + 1, n + 2, n + \dots, N, N + 1, N + 2, \dots, M$, in which M is the species universe from which the actual avian community is randomly sampled under the assumption that $z(i, j)$ is *Bernoulli* ($w_i * \psi(i, j)$) and $w_i \sim \text{Bernoulli}(\Omega)$.

All of these components were incorporated into a Bayesian modeling framework that uses Markov chain Monte Carlo (MCMC) methods and executed using the freely available software packages R and WinBUGS (Spiegelhalter et al. 2003). MCMC refers to the method of generating the random samples from which the posterior distribution is drawn. For detailed descriptions of MCMC and Bayesian inference, I refer readers to recent works that focus on ecological applications (McCarthy 2008, Kéry 2010). Guided by previous efforts (Kéry and Royle 2009) I applied vague prior distributions for all α and β parameters (see Appendix E, WinBUGS model script). Three Markov chains were run using random starting values and 30,000 iterations with a thinning rate of 10 and the first 5,000 discarded as burn-in. Chain convergence was facilitated by standardizing all covariate values to approximate them to zero, and was checked using the Brooks-Gelman-Rubin statistic (Kéry 2010).

Lastly, species richness was estimated using the subset of sampled estimates

generated from the MCMC procedure used to calculate ψ for all detected and hypothetical species as a function of simulated combinations of covariates qdbh and density. Let N_k be the sum of all occupancy probabilities for all potential species such as

$$N_k = \sum_{i=1}^M z_{ik} \quad (7)$$

3. Results

3.1. Multi-species occupancy and detection

In all, 73 different diurnal breeding bird species were observed during 2008 and 2009. The summaries estimated using encounter histories presented a varied range of species- and site-specific responses. For example, 55% of all species were detected 10 or fewer times, and only 27% were detected 21 or more times. The original model that included date and habitat covariate effects on detection probabilities provided evidence that detection remained constant throughout the survey periods, and that there was no significant habitat or seasonal effect on detection probability. This was expected given the short time period over which all surveys were conducted. Subsequently, detection was assumed constant over time for all species, and only covariate effects on occupancy were included. Detection estimates ranged from 0.002 to 0.96, with a mean of 0.26 (SD 0.06, 95% CI 0.15–0.4; Table 3.1, Fig. 3.1), whereas the mean probability of occupancy was 0.12 (SD 0.1, 95% CI 0.005–0.8). Detection and occupancy probabilities were not correlated, indicating that the majority of species detected were rare in terms of local abundance because both probability and occupancy estimates are low. Notably, the probability of occupancy and detection, and community size associated with variability of tree size and density, which is influenced by timber harvesting activities, was negative for density and positive for qdbh. Summary estimates for all response variables and covariate effects are shown in Table 3.1.

Table 3.1: Summaries of community-level posterior distributions for detection, occupancy, and species richness parameters.

Community-level parameters		Mean	SD	95% Credible Interval
$\mu\alpha_1$	Effect of tree density	-0.98	0.34	-1.55, -0.38
$\mu\alpha_2$	Effect of qdbh	3.44	1.52	0.97, 5.86
$\mu\alpha_3$	Effect of density-qdbh interaction	3.62	1.68	0.79, 6.45
$\sigma\alpha_1$	SD tree density effect	0.35	0.28	0.01, 0.89
$\sigma\alpha_2$	SD qdbh effect	3.38	1.05	1.28, 4.78
$\sigma\alpha_3$	SD density-qdbh interaction effect	2.27	1.18	0.38, 4.25
p	Detection probability	0.26	0.06	0.15, 0.4
ψ	Occurrence probability	0.12	0.10	0.005, 0.8
N_{total}	Metacommunity species richness (γ -diversity)	128.01	27.14	93.0, 182.0

3.2. Community structure and dynamics

The model estimated a metacommunity (N_{total} , γ -diversity) size of 128.01 species (SD 27.15; 95% CI = 93.0–182.0 with a maximum size of 223), which is almost twice the actual number of species detected. In fact, the posterior distribution (see Fig. 3.2) indicates that the probability of metacommunity size being equal to the observed number of 73 is virtually zero, and that the number of undetected potential species in the metacommunity is far greater. In addition, the posterior predictive distribution for the entire metacommunity is not piled up against the resulting upper limit, nor is it truncated on the lower limit of the distribution. Both of these are indications that the data augmentation formulation of 150 additional hypothetical species was reasonable.

Site-specific species richness (α -diversity) differences can be readily explained by accounting for covariate effects. Examination of these effects reveal how habitat heterogeneity associated with management practices influences community size and estimate uncertainty. In general, sites with high species richness and low uncertainty estimates were characterized by high qdbh and low tree density values. One site, located in Cumbres de Majalca National Park stands out as the one with the highest number of

species with a mean of 37.6, and lowest estimate uncertainty (SD 1.2, 95% CI 36–40). This site had high qdbh values (0.31 m), low tree density (500 trees/ha), and virtually no unobserved species (37.6 estimated vs. 36 detected). In comparison, a site located in *ejido* El Consuelo had one of the lowest estimates with a mean of 9.85 and the highest level of uncertainty for species richness (SD 2.03, CI 7–13). This site also exhibited low qdbh values (0.107 m), high tree density (650 trees/ha), and a large number of undetected species. The site-specific posterior estimates for species richness were used to make predictions of under different configurations of tree qdbh and tree density. The resulting levelplot (Fig. 3.3) reveals the resulting species richness pattern that increases with larger trees and decreases with higher densities of smaller trees.

4. Discussion

In this study, I used a hierarchical Bayesian multi-species occupancy model for detection/non-detection bird count data to evaluate the impact of forest management on biological communities. The positive response of community size to an increase of covariate qdbh and to a decrease in tree density illustrates how species richness can be maximized as a function of stand structural complexity. Stand characteristics with the highest estimates of species richness are consistent with the structure of moderately-disturbed uneven-aged stands (USFS 1997). Such stands are becoming uncommon in the STR as the current silvicultural model tends to favor even-aged harvesting and regeneration methods in order to simplify age structure and species composition (Guerrero et al. 2000).

Finding reliable quantitative measures of system state is not an easy task (Yoccoz et al. 2001). Adding to previous efforts (Russell et al. 2009, Zipkin et al. 2009a, Zipkin et al. 2009b), this study shows how community models can be used to estimate community summaries for biodiversity conservation and monitoring schemes.

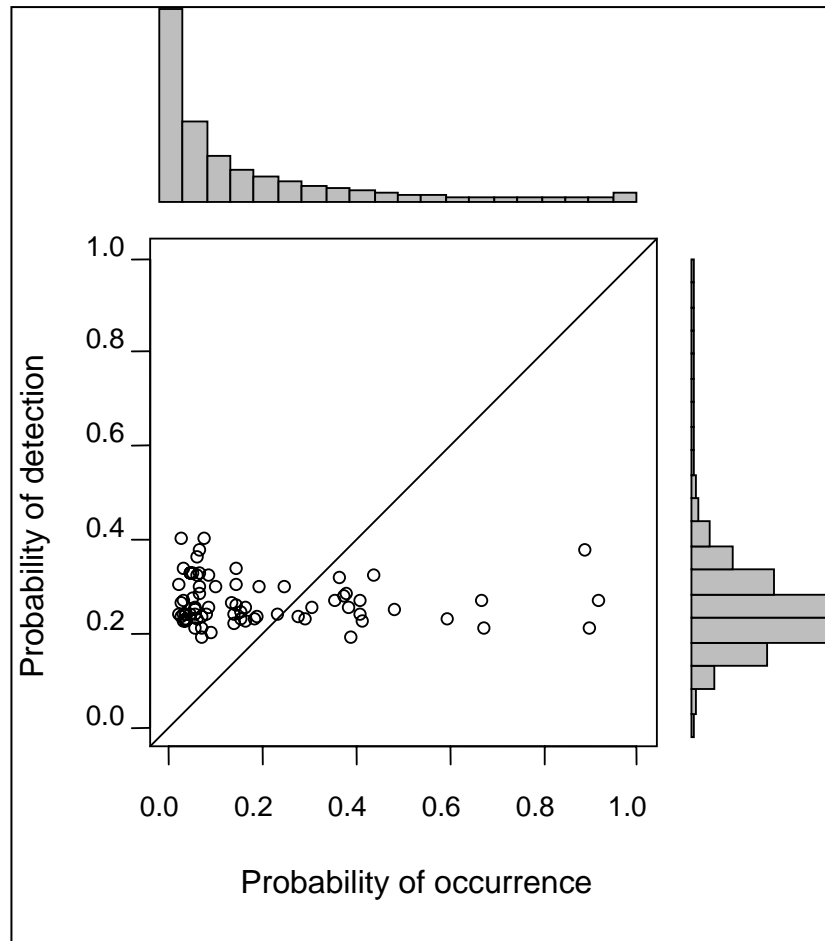


Figure 3.1: Two-dimensional scatterplot and univariate frequency histograms of estimated probabilities of occurrence and detection for the 73 diurnal breeding bird species observed during the 2008 and 2009 breeding seasons in the Sierra Tarahumara of Chihuahua, México. Individual species estimates for detection and occurrence probabilities are indicated by the black circles, and a one-to-one relationship between detection and occurrence probabilities is indicated by the solid line. The top histogram represents the frequency distribution for probability of species occurrence, while the histogram on the right corresponds to probability of detection.

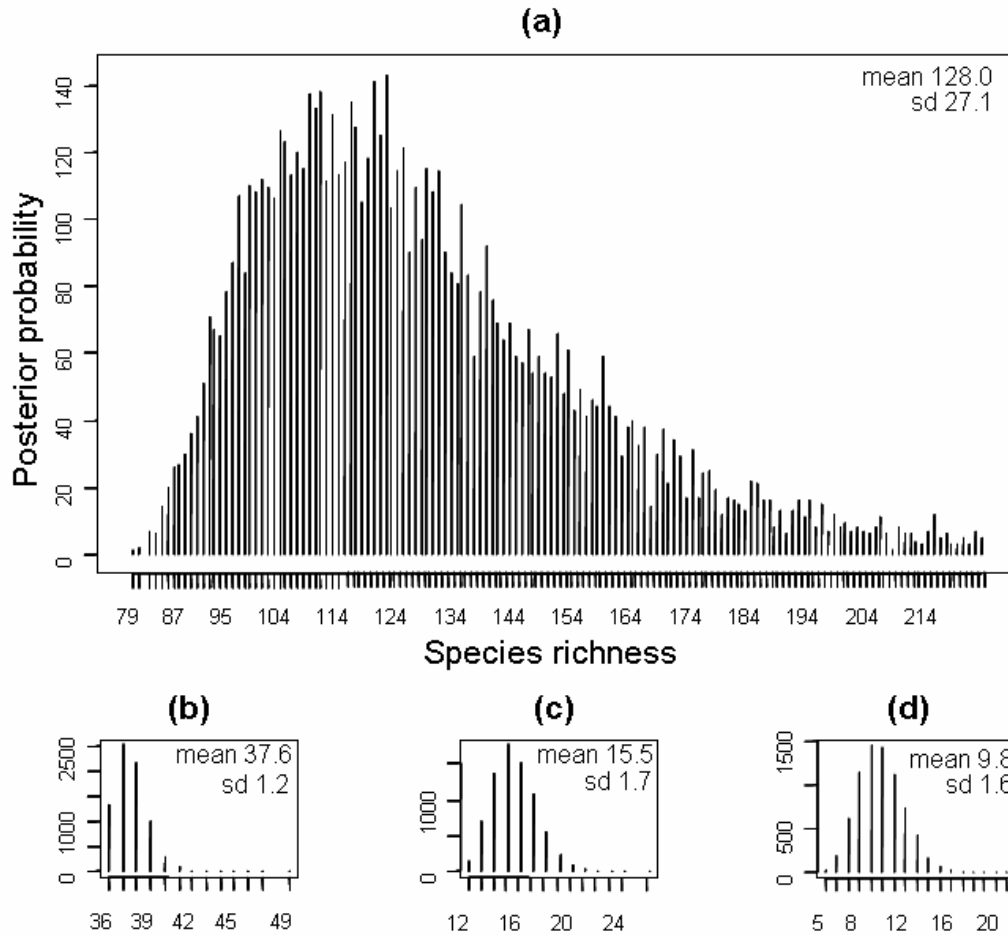


Figure 3.2: Posterior distributions of species richness under the Bayesian community model for (a) the entire metacommunity; (b) site 14 in Cumbres de Majalca National Park logged >50 years ago; (c) site 22 in *ejido* Magullachi logged 15 years ago; and (d) site 7 in *ejido* El Consuelo logged and subject to fire within the past 15 years. The posterior distribution is essentially the probability of the parameter species richness given the observed data from the breeding bird survey in which 73 species were detected. The posterior distribution for the metacommunity indicates that there are more species than 73, and that the data augmentation parameter was sufficiently large because the posterior does not pile against the resulting limit, or become truncated on the lower end. The posterior distributions for site-specific species richness indicate that there are virtually no unobserved species in Majalca, a moderate number of unobserved species in Magullachi, and a large number of unobserved species in El Consuelo.

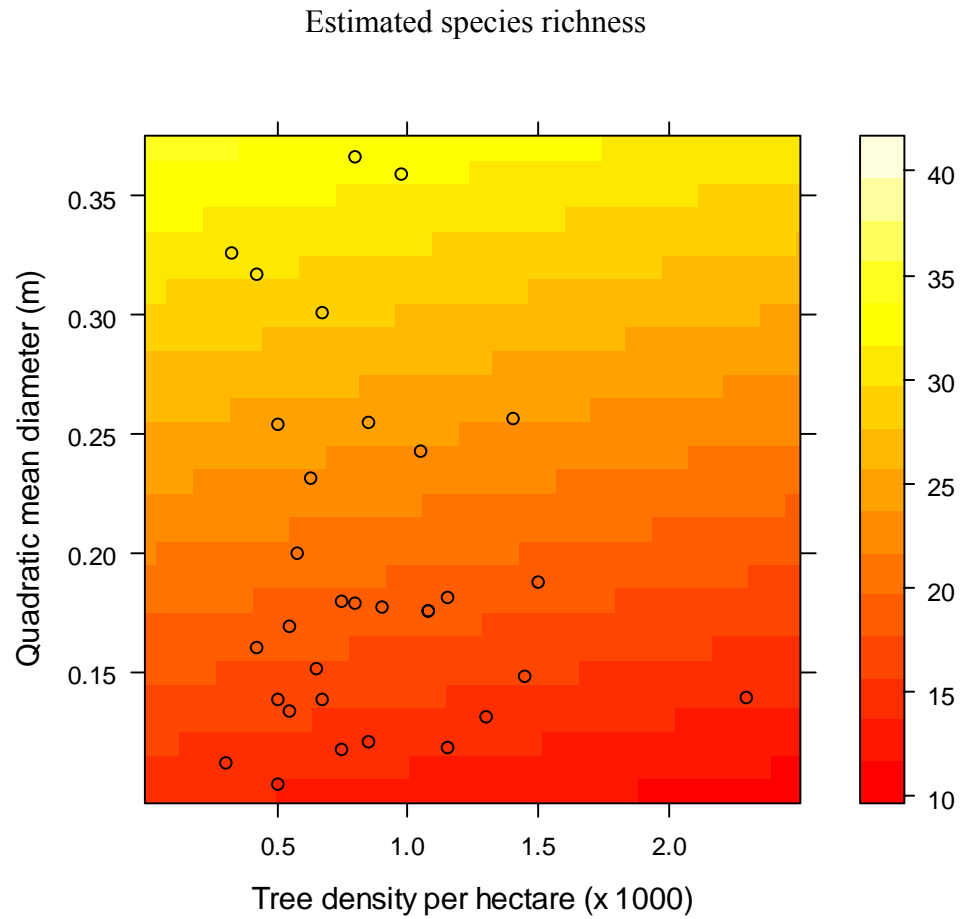


Figure 3.3: Density plot for total estimated species richness as a function of tree density/ha (x-axis) and quadratic mean diameter (y-axis) values for all potential habitat combinations in the Sierra Tarahumara Region of Chihuahua, México. Color scale from dark to light, indicates increasing number of species. Circles represent sampled sites along covariate value ranges.

The ability to incorporate a data augmentation procedure is an important feature of community models. In this case, analysis of the augmented dataset yielded a theoretical species-accumulation curve calculated from both detected and hypothetical species. Russell et al. (2009) argue against the use of data augmentation because they consider that inference derived from hypothetical species may not be applicable in real-life situations. However, the estimated species-accumulation curve has a number of practical applications in applied and theoretical fields of ecology. For example, the discrepancy between the actual number of observed species richness and potential species richness is a function of estimate uncertainty and spatial variability associated with the observed data. Because this uncertainty is statistically modeled in terms of probabilistic inference, it can be used to draw reliable conclusions and model the state, spatial stability, and turnover rate of communities and metacommunities. Associated uncertainty estimates also can be used to inform the allocation of future sampling efforts. For example, in the study area additional sampling will most likely not reduce uncertainty in sites with an already high number of estimated species, while additional sampling in sites with fewer species will likely be needed to reduce uncertainty.

The modeling framework used in this study assumes that all species are equally different and does not make any distinctions within and among ecologically functional groups of species, nor does it incorporate abundance data. Although the lack of specificity prevents us from commenting on the relative functional importance of species or groups of species in the community (e.g., evenness and heterogeneity), an advantage of these type of models is that they integrate all species regardless of their abundance (Zipkin et al. 2009a). In addition, integrated analysis of the community of species improves the precision of species richness summaries because the hierarchical model framework does not require *a priori* assumptions regarding community structure.

The assessment of community structure through inference from uncertainty

parameters SD and CI is a question of judgment in my view. I expected that sites with higher numbers of species would be more variable because of the expected temporal and spatial fluctuation of rare species that make up the bulk of the metacommunity. I also expected that degraded forest patches would have fewer species and less variability due to a dominant presence of generalist species. Estimated uncertainty parameters from the model, however, indicate otherwise. Uncertainty estimates were lower in sites with greater richness, and higher in sites with low richness. These parameters could be confounding and interpreted in various ways; thus it is important to understand how the species richness parameter is estimated. The species richness parameter summarizes all species, without distinction of guild or functional group, in a manner that can be compared to a random sample with replacement in which sample values are independent. In such a case, samples collected on survey $k, k + 1 \dots N$ are independent and the covariance between them would be close to zero. In biological terms –and in this particular situation- this means that uncertainty estimates reflect turnover in community size, rather than changes in taxa.

A valuable aspect of the summaries generated by the community model used in this study, is that they can be readily incorporated into forest management plans and to make predictions of species richness based on habitat covariates qdbh and tree density. One way of applying these results is to incorporate the predicted response of species richness into density management diagrams (DMDs). DMDs are one of the main tools used by foresters to estimate stand stocking densities and model stand dynamics using tree diameter and density data (Long 2005). DMDs could be used to simultaneously model stand development and species richness dynamics. By incorporating a biodiversity component to stand management practices, it would be possible to identify and predict site-specific distribution of species and manage stand rotation cycles more effectively to maximize biodiversity at the regional level. For conservation management

purposes, modeling forest dynamics and species richness patterns at a landscape scale can be used to better design areas and corridors with high conservation value (Zipkin et al. 2009a). It can also be used to support the idea of creating and maintaining protected areas of significant and quantifiable value for biodiversity, as is the case of Cumbres de Majalca National Park.

5. Conclusions

Species richness is part of a set of quantitative metrics that are considered to be vital rates of an ecological system, and is also one of the most important and frequently used measures of biodiversity. However, species richness is frequently estimated without accounting for imperfect detection and most likely biased towards the most common and abundant species. Using a hierarchical Bayesian modeling framework, it is possible to account for detection heterogeneity and model observation and occupancy processes separately. This modeling approach allows for more precise details regarding occurrence patterns, structural community properties, such as community size at local and regional scales, and the dynamic interactions of species with landscape features. Community metrics (e.g., species occurrence patterns, community structure and composition) are essential for understanding metapopulation dynamics and community structure (Holt 1997).

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Chapter 4

MULTI-SPECIES OCCUPANCY MODELS TO ASSESS FUNCTIONAL HOMOGENIZATION OF AVIAN COMMUNITIES IN MANAGED AND UNMANAGED FORESTS

Abstract: Functional homogenization of biological communities from habitat degradation is characterized by a disproportional decline of some species, and a shift towards domination by generalist taxa. This alters ecological functionality, productivity, and the supply of ecosystem goods and services. Consequently, understanding how biological communities respond to degradation is important. This study is one of the first to use multi-species occupancy modeling techniques to investigate the impact of forest degradation on species-habitat relationships and ecological functionality. For my analyses I used data from a breeding bird census of 32 sites in managed (communally-owned parcels) and unmanaged (national park) forests in the Sierra Tarahumara region, México, sampled 3-5 times/yr in 2008 and 2009. The results produced clear evidence of functional homogenization of bird communities as a result of forest degradation and even-aged forest management practices. Sites characterized with denser forest stands dominated by smaller diameter trees were species poor, and contained mostly generalist species. Further, results show that forest degradation reduces species occupancy and diversity, and thus ecological functionality. The use of occupancy modeling tools is a novel way of increasing our understanding and predictive capacity regarding the response of biological communities to system changes. My analyses used the same covariates used to design timber harvesting plans. As such, the results can be readily incorporated into these management plans to increase species diversity of birds and other groups of species at local and regional scales, and thus enhance the ecological sustainability of forest management practices.

1. Introduction

Forest degradation and deforestation as a result of human pressure is an issue of global concern that is expected to worsen in coming decades (Foley et al. 2005, Hansen et al. 2008). One of the most significant consequences of degradation is biodiversity loss (Stokstad 2010), because removal of species dilutes the relationships between organisms, food webs, and ecological processes that are the basis for stable, productive, and resilient ecological systems (McGrady-Steed et al. 1997, Tilman 1999, 2000, Fischer et al. 2006). Although the long term consequences of species loss are not always clear, studies have shown that removal of species is closely linked to decreased ecosystem functions, and subsequently, to ecosystem services. These links have far-reaching and long-lasting consequences for ecosystems and for human well-being (Diaz et al. 2006, Tilman et al. 2006), and motivates the implementation of forest management plans and actions that maximize the number of species in ecosystems. Hence, increasing our knowledge and predictive capacity regarding the response of biological communities to degradation or management actions can be extremely useful in a wide range of forest management and conservation settings.

It has long been established that habitat variability and the array of existing resources determines the number and specialization (i.e., biotic ability) of organisms that can be sustained in a given site or habitat patch (MacArthur and MacArthur 1961). In a niche-structured system, stable environments support a greater diversity of species and specialization (Tilman 1999, Tilman et al. 2006), and the abundance of any organism is directly affected by the abundance of other similar organisms (Kelly et al. 2008). Specialists and generalists can be distinguished by the range of resources (niche width) they need to satisfy all their habitat needs (MacArthur and MacArthur 1961, Begon et al. 1996). In contrast, in a dynamic system, species coexistence is driven by competition and colonization tradeoffs. A species survives by colonizing a new site or

by out-competing another species for an occupied site (Stevens 2010). These relationships are modified by system changes caused by disturbances, resulting in new competition-colonization equilibriums (Leibold and Miller 2004). In the face of disturbance, habitat generalists are superior competitors that can increase in abundance and range while specialists decrease (Holt 1997). It is through this process of habitat simplification and subsequent reduction of niches that habitat degradation results in species loss, a phenomenon known also as extinction debt (Stevens 2010).

In general, habitat degradation has an adverse effect on species composition and ecosystem functions as specialist species decrease and generalist increase. This process is called functional homogenization and occurs when a system is dominated by generalist species that can persist along a wider range of habitat conditions and variability (Clavel et al. 2011). Because of their tolerance to wider habitat gradients, generalists are considered functionally redundant. What this means is that the majority of a system's ecological functions are not linked to them when other functional groups are present (Devictor et al. 2010, Barnagaud et al. 2011a). By comparison, in a system with greater presence of species and diverse functional groups, functionality is complementary, and such systems are generally considered more productive and resilient (Clavel et al. 2011). Ecological functionality can best be seen as the additive impact of functional groups or species on the system. Thus, a system with few and mostly generalist species would offer fewer functions compared to a system with more specialist species (Finke and Snyder 2008). Reducing the unwanted loss of species from natural resource management activities would benefit from improving our understanding and predictive capacity of biological community response to degradation processes.

Some studies have used non-linear differential equations (e.g., Lotka-Volterra models), and generalized linear and additive models to answer questions about

colonization, competition and the relationships between specialization and habitat gradients (Stevens 2010, Clavel et al. 2011). The present study is one of the first to use occupancy modeling techniques (MacKenzie et al. 2002) to investigate the impact of resource degradation on species-habitat relationships, and ecological functionality (i.e., functional homogenization) of biological communities. Occupancy models use detection/non-detection (i.e., presence/absence) data from repeated observations and multiple sites to study occupancy dynamics and other vital rates of species while accounting for imperfect detection (MacKenzie et al. 2005, Royle and Dorazio 2008). Occupancy can also be used as a surrogate state variable to determine population status, a practical advantage that has proven to be extremely useful in a wide range of management and conservation applications (Ferraz et al. 2003, MacKenzie 2005, Krishna et al. 2008, Martin et al. 2009a, Martin et al. 2009b). Multi-species occupancy models, or community models, are an extension of the site occupancy model that, in addition to estimating species-specific estimates of occupancy and detection probability, can also estimate species richness and other important summaries of community structure (Dorazio et al. 2006, Kery and Royle 2008, Kéry et al. 2009, Zipkin et al. 2009a, Zipkin et al. 2009b). Metapopulation and metacommunity studies frequently use species occupancy as a state variable to assess population and species richness dynamics based on biotic ability (i.e., specialization) and coexistence patterns (Hanski and Gilpin 1997, Hanski and Gaggiotti 2004). With their multiple uses, occupancy models can be very effective in the study of communities and metacommunities. Moreover, occupancy models can incorporate variation in sampling effort and environmental heterogeneity explicitly into the modeling framework, resulting in more accurate and reliable parameter estimates. This modeling flexibility makes them an ideal means to study population dynamics, species co-occurrence, and turnover rates of species more efficiently than other conventional tools (Royle and Nichols 2003).

Although there can be inconsistency in the definition and measurement of ecological specialization (e.g., Grinnellian vs. Eltonian specialization, specialized vs. rare) (Devictor et al. 2010), occupancy-derived estimates are unambiguous and can address these issues explicitly in terms of probability distributions. This approach improves the inference about populations of abundant and rare species by incorporating species-specific detection probabilities explicitly into the models (MacKenzie et al. 2002), which can help distinguish those that are geographically restricted from those that have low abundance (Royle and Dorazio 2008). For example, a specialist may be consistently detected in specific locations that meet the species' habitat requirements; while a species that is considered rare as a result of sparse population numbers may have a lower probability of being detected over a wider geographical range. In terms of ecological specialization, occupancy and occupancy-based species richness estimates are more practical and reliable than other methods (e.g., habitat suitability models), because in addition to estimating detection probability, they can incorporate habitat covariates and other sources of sampling variability explicitly into the estimation procedure to produce quantifiable and comparable occupancy estimates (Bailey et al. 2004, Kéry and Royle 2009, Zipkin et al. 2009a). Thus, occupancy-based estimates can also provide valuable insights into species' interactions and niche overlap.

In this study I applied a hierarchical Bayesian community model (Kéry and Royle 2009) to a survey of diurnal breeding forest birds in the Sierra Tarahumara region (STR) of northern México. The objective was to assess the impact of timber harvesting activities on biological communities, on multi-species habitat relationships, and on ecological functionality. To do this, I estimated site-specific species richness (α -diversity) to compare the community size and turnover rates in managed and unmanaged forests. Then, I calculated the species-specific impact of forest degradation on occupancy probability for all species in order to make inferences about community

structure, functional homogenization, and species-habitat relationships.

2. Methods

2.1. Study area

The study area covered roughly 1,200 km² and is situated in the central portion of the STR, México between -106.5 and -107.5°E and 27.8 and 28.8°N. The STR is part of the greater Sierra Madre Ecoregion, one of the 200 threatened ecoregions of the world (Olson et al. 2001). Topography is characterized by undulating valleys and rugged slopes, with several major rivers draining the region and carving deep gorges. Vegetation is dominated by ponderosa pine (*Pinus ponderosa*) and oak (*Quercus spp.*) forests exposed to various degrees of human disturbance, including logging, livestock grazing, and firewood harvesting. Over 90% of the land is owned by rural and indigenous communities as *ejidos*, a communal form of legal land tenure in which user groups own and manage a territory (Sarukhan and Larson 2001). Less than 1% of the land is officially protected, and about 10% is privately held. Most *ejidos* in the area have experienced significant degradation. Nearly all of the remaining stands of mature forest are found on inaccessible terrain or in national park lands.

2.2. Survey design and data

The data used in this study were generated from a breeding bird survey conducted in managed (*ejido*) and unmanaged (national park) forests in the STR. The sites were established systematically using topographic and vegetation maps overlaid by a 5 × 5 km grid to assess accessibility and the absence of human settlements within a 1 km radius. Subsequent ground verification and field protocol testing yielded a total of 32 sampling sites distributed among 9 distinct land parcels, or forest study areas. These include two sites on national park lands and 7 in *ejidos* of varying sizes, forest

conditions, and governance arrangements. These included two located within national park lands and seven in *ejidos* of varying sizes and forest governance arrangements (for additional details, see Appendix D). In all, the 32 sites were sampled 3-5 times in 2008 and 2009 during the beginning of the local breeding season for diurnal forest birds (5 to 28 May 2008, and 15 May to 4 June 2009). Bird observations were recorded using 10 min point counts beginning 30 min prior to the local sunrise and ending 5 hr later. All species detected (seen or heard) within a 75 m radius were recorded as present (1) or absent (0) (Ralph et al. 1995b). Sites were visited on at least 3 separate occasions in order to build encounter histories for all species as required to estimate detection and occurrence probabilities (MacKenzie and Royle 2005). In addition, weather conditions were recorded during each sampling occasion. On separate visits, canopy cover, basal area, height of all trees (>1.5 m), and cover of perennial shrubs (<1.5 m) were measured using 400 and 100 m² plots, respectively (Manley et al. 2006).

2.3. Hierarchical model

The community model framework I used (Kéry and Royle 2009) is an extension of the single-species occupancy model that incorporates a hierarchical Bayesian and data augmentation parameterization (Royle et al. 2007, Royle and Dorazio 2008). This hierarchical structure allows observation and state processes to be modeled separately (see Table 4.1). In this case, the observation model specifies a probabilistic approach for the mechanisms from which the data are produced; whereas the process model describes the state variable of interest (occupancy). For this model, the occurrence of an organism $z(i, j)$ is a binary (Bernoulli) process in which $z(i, j) = 1$ if species $i = 1, 2, \dots, N$ is detected at site $j = 1, 2, \dots, J$ during the 10 min point count and 0 (zero) if it was not detected. As such, the model for species occurrence is defined as

$$z(i, j) \sim \text{Bernoulli}(\psi_{i,j}) \quad (1)$$

where $\psi_{i,j}$ is the occurrence probability for species i at site j . The mechanical process from which the observed data is produced is defined by the observation model

$$x_k(i, j) \sim \text{Bernoulli } z(i, j) * p_k(i, j) \quad (2)$$

which is governed by $z(i, j)$; thus if $z(i, j) = 0$ then all resulting observations are fixed zeros. I used logit transformations for occupancy and detection and assumed that these were the sum result of species (μ_i, ν_i) and site-specific effects (α_j, β_j). In this particular case, my main interest was to determine the impact of forest degradation caused by timber harvesting for i species at site j . This was done by incorporating linear functions of quadratic mean diameter at breast height (qdbh) and tree density (density), the two main variables used by managers to estimate tree stocking rates, stand dynamics and timber harvest rates (Long 2005). The occupancy model with qdbh, density and an interaction term among the two is written as

$$\text{logit}(\psi(i,j)) = \mu_i + \alpha_{1i} * \text{qdbh}_j + \alpha_{2i} * \text{density}_j + \alpha_{3i} * \text{qdbh}_j * \text{density}_j \quad (3)$$

in which μ_i is the species-specific effect and the intercept and site-specific effect α is indexed i for each i species and j site covariates.

Because timber harvesting is the most prevalent source of forest change in the region, I expected that occupancy and richness would respond to these covariates differently across the landscape as a result of long term management actions specific for each management unit. In a similar way, I expected that date would have an impact on detection probability as bird behavior changes during the breeding season. Thus I included the day of the year and canopy cover (linear and squared) in the formulation of detection probability for species i at site j during survey k . In this model the species-specific effect on detection for species i is expressed by ν_i , and the site-specific effect of date (when the sampling was conducted) and canopy cover values at site j given by β

coefficients. As such, species-specific detection probability is described by

$$\text{logit}(p_k(i,j)) = v_i + \beta_{1i} * \text{date}1_{jk} + \beta_{2i} * \text{date}2_{jk} + \beta_{3i} * \text{canopy}1_j + \beta_{4i} * \text{canopy}2_j \quad (4)$$

2.4. Data augmentation, Bayesian analysis and species richness

The dataset consisted of 73 (n) species, which was augmented by adding 150 undetected species with all-zero encounter histories (zero-inflation) to truncate the size of the dataset (Dorazio and Royle 2005, Royle et al. 2007). Having an unknown number of species creates analytical issues that can be solved by fixing the size of the dataset using data augmentation procedures. In other words, the model uses an M number of available species instead of an unknown number of species ($M - n$). This is the equivalent of using a discrete uniform prior on N , the pool of species from which species richness is estimated. N is estimated by introducing a latent indicator variable w_i for $i = 1, 2, \dots, n, n + 1, n + 2, n + \dots, N, N + 1, N + 2, \dots, M$, in which M is the available number of species from which the community is randomly sampled, assuming that

$$z(i, j) \sim \text{Bernoulli}(w_i * (\psi(i,j))) \quad (5)$$

and

$$w_i \sim \text{Bernoulli}(\Omega) \quad (6)$$

Species richness was estimated using the subset of sampled estimates generated by the model to calculate occupancy for all detected and hypothetical species as a function of simulated values for habitat covariates. As such, species richness (N_k) is the sum of all occupancy probabilities for all potential species given by the equation

$$N_k = \sum_{i=1}^M z_{ik} \quad (7)$$

Table 4.1: Hierarchical structure of the multi-species occupancy model used in this study. Numbers indicate the (1) observation model, (2) process model, and (3) species richness estimation procedure.

(1) Observation	$x_k(i, j) \sim \text{Bernoulli}(z(i, j) * p_k(i, j))$	(1)
	$\text{logit}(p_k(i, j)) = \nu_i + \beta_{1i} * d1_{jk} + \beta_{2i} * d2_{jk} + \beta_{3i} * c1_j + \beta_{4i} * c2_j$	(2)
(2) Process	$z(i, j) \sim \text{Bernoulli}(\psi_{ij})$	(3)
	$\text{logit}(\psi_{ij}) = \mu_i + \alpha_{1i} * qdbh_j + \alpha_{2i} * dens_j + \alpha_{3i} * qdbh_j * dens_j$	(4)
(3) Species richness	$z(i, j) \sim \text{Bernoulli}(w_i * (\psi_{ij}))$	(5)
	$w_i \sim \text{Bernoulli}(\Omega)$	(6)
	$N_k = \sum_{i=1}^M z_{ik}$	(7)

All of these components were incorporated into a Bayesian modeling framework using the freely available software packages R and WinBUGS (Spiegelhalter et al. 2003). This model uses Markov chain Monte Carlo (MCMC) methods, which refer to the specific approach used by the software to generate all the random samples from which the posterior distribution is drawn. Guided by previous efforts (Kéry and Royle 2009) vague prior distributions were used for all α and β parameters (see Appendix E, WinBUGS model script). Three Markov chains were run using random starting values and 30,000 iterations with a thinning rate of 10. The first 5,000 iterations were discarded as burn-in and covariate values were standardized to facilitate chain convergence. Convergence was checked using the Brooks-Gelman-Rubin (Rhat) statistic (Kéry 2010).

3. Results

A total of 73 diurnal forest bird species were detected in 2008 and 2009 (see Appendix F). However, the model estimated the number of species in the metacommunity (γ -diversity) to be 128.01 (SD 27.14; 95% CI = 93.0–182.0). A visual assessment of the posterior distribution output generated by WinBUGS indicated that the number of undetected species added was adequate. Site-specific species richness (α -diversity) varied greatly among sampling sites, with estimates ranging from 40.0 (SD 1.47; 95% CI 38–43) to 9.9 (SD 2.0; 95% CI 6–14) species. The difference between the total number of species detected per site and estimated species richness ranged from 2.0 to 7.0 species. Estimated species richness showed a positive response to increasing tree diameter and a negative response to higher tree density/ha (Table 4.2, Fig. 4.1). Sites with lower estimate variability (i.e., lower SD values) were located on national park lands, followed by sites with no recent logging activities. The sites with the greater estimate variability were those that had signs of greater and more recent disturbance. See Appendix G for estimates for all 32 forest study sites.

Mean estimated occupancy for all species was 0.199 (SD 0.218) and detection probability was 0.265 (SD 0.048). Contrary to what would be normally expected, occupancy and detection probabilities were not correlated (-0.054, SD 0.223). These results suggest that the majority of species detected in the STR are rare because both detection probability and occupancy estimates are low (Royle and Nichols 2003). Upon closer inspection, the results reveal some interesting details about the relationships between detection and occupancy (see Fig. 4.2a). Generalist species were more frequently detected and occupied a greater proportion of sites and habitat gradients (Fig. 4.2b). Generalists included the robin (*Turdus migratorius*), northern flicker (*Colaptes auratus*), yellow-eyed junco (*Junco phaeonotus*), and Steller's jay (*Cyanocitta stelleri*). Known specialists (e.g., raptors, cavity nesters, and canopy feeders) had high detection

probability but low occurrence (bottom of Fig. 4.2a). Only a small proportion of species (12/73) was found on 16 or more sites, with more than half of all species (34/73) found in three or fewer sites. Such disproportion was also found in occupancy estimates, which were found to significantly increase with larger tree sizes (qdbh) (see Fig. 4.2b). This clearly indicates that greater resource degradation results in a transition towards greater functional homogeneity characterized by an overall decrease in species richness and an increase in generalist species. Species-specific estimates of occupancy, detection probability and covariate effects for all 73 species recorded are included in Appendix F.

Table 4.2: Comparison of species richness and forest habitat characteristics for 5 sites each with the highest and the lowest estimated species richness in the Sierra Tarahumara region, México.

Sample sites	Species richness	SD	95% CI	qdbh (m)	Density (trees/ha)
<u>Unmanaged</u>					
Majalca, site 2	40.0**	1.5	38, 43	0.36**	0.296
Majalca, site 1	37.5**	1.2*	36, 40	0.25	-0.82
Majalca, site 5	30.2**	1.8	27, 34	0.32**	-0.99*
Majalca, site 4	30.0**	2.0**	27, 34	0.37**	-0.11
Majalca, site 3	28.3**	1.6	26, 32	0.31**	-0.41
<u>Managed</u>					
<i>Ejido</i> La Laguna, site 2	13.6*	1.8	11, 18	0.18	0.12
<i>Ejido</i> Sisoguichi, site 3	12.3*	1.7	9, 16	0.11*	-1.29
<i>Ejido</i> La Laguna, site 3	12.2*	1.7	9, 16	0.13	1.06**
<i>Ejido</i> El Consuelo, site 3	9.8*	2.0**	6, 11	0.15	-0.47
<i>Ejido</i> El Consuelo, site 2	9.7*	1.6	7, 11	0.12*	0.71

* One of five lowest estimates among the 32 sites.

** One of five highest estimates among the 32 sites.

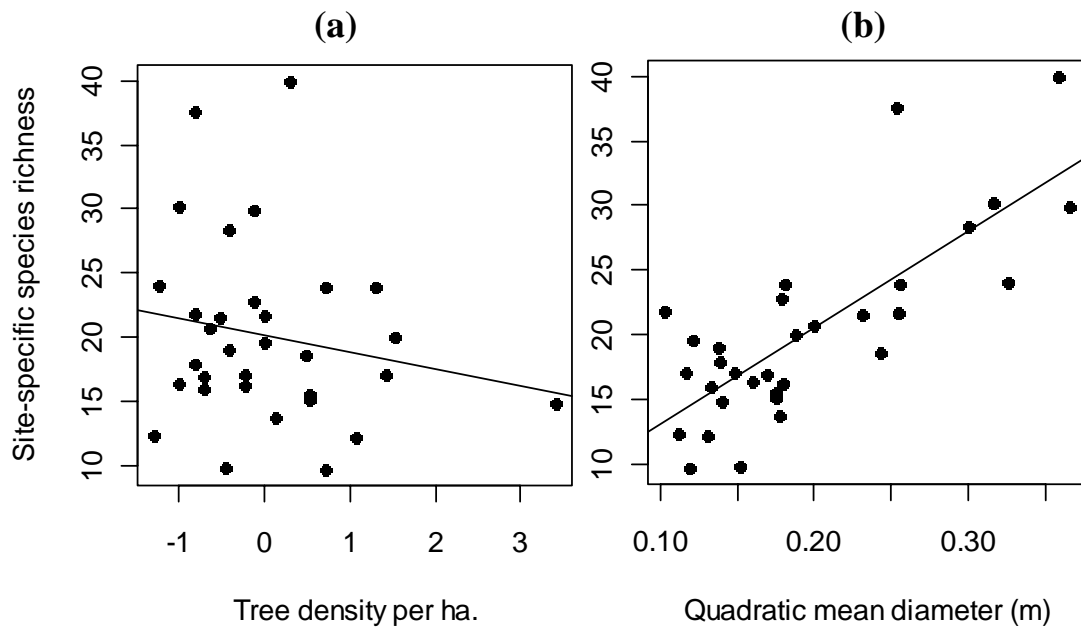


Figure 4.1: Estimated site-specific species richness as a function of (a) tree density/ha and (b) quadratic mean diameter values for all potential habitat combinations in the study area. Points represent sampling points and the lines the predicted linear relationship between species richness and covariates. Note the negative relationship with tree density, and positive relationship with quadratic mean diameter.

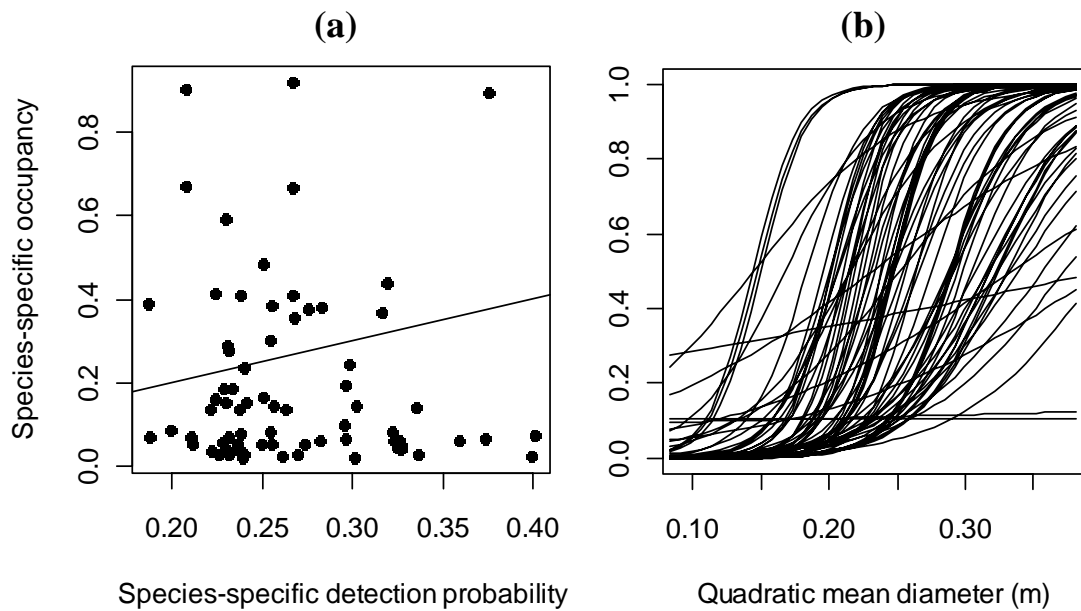


Figure 4.2: (a) Species-specific occupancy and detection probability relationships for all detected species ($n = 73$). Points indicate species and the line a 1:1 relationship between detection and occupancy probabilities; points above the line are generalists, and points below are specialists. (b) Species-specific occupancy probability and quadratic mean diameter relationships for all detected species. At tree diameters greater than 0.25 m, occupancy for all species increases substantially, indicating a clear relationship between resource degradation and a shift towards greater functional homogeneity.

4. Discussion

Occupancy-based parameters such as species richness derived from multi-species occupancy models have been shown to be an adequate measure of system state (Dorazio and Royle 2005, Dorazio et al. 2006, Kéry and Royle 2009, Zipkin et al. 2009a). By applying occupancy estimation methods to my breeding bird survey data, I show that community models can be used elegantly and efficiently to answer questions about the relationships between occupancy, species richness, ecological specialization, and resource degradation.

In this study, I applied a multi-species occupancy model to breeding bird survey data in managed and unmanaged forests. The model was used to estimate detection and occupancy probabilities, and species richness to derive inference regarding the impact of resource degradation on biological communities. Specifically, the goal was to determine if degradation was causing a disproportional decline of some species and causing a shift towards greater functional homogenization as a result of these changes. Indeed, I found that greater degradation reduces species richness and the probability of occurrence for multiple species. In fact, I did not find any species that responded positively to degradation. On the contrary, degradation caused a significant loss of species that are considered habitat specialists, which made up the bulk of the species richness estimates for the entire study region. Habitat generalists were found throughout the study area, including disturbed sites, but were not more abundant in degraded forests. In general, the occupancy probability for these species declined as well.

Recent studies have used different set of tools to define and measure ecological specialization, habitat segregation, and functional homogenization separately (Devictor et al. 2010, Barnagaud et al. 2011a, Clavel et al. 2011). The approach used in this study allowed me to generate inference regarding all of these issues efficiently and conveniently, offering other advantages in terms of practicality, inference, and

accuracy. In this process, individual species detections are separated into an imperfect occupancy state and an independent observation process. As a result, different factors (e.g., habitat heterogeneity, sampling effort, weather) affecting the observation and occupancy processes can be incorporated into the modeling procedure to derive more accurate and efficient estimates (Kéry and Royle 2009). The model also retains the identity of all species, providing inference not only about individual species, but about the community as well. This is a particularly useful advantage that allows for improved inference about communities, and in particular, about rare species. Inference about rare species is not easy to estimate because data is usually insufficient for such purposes. Multi-species occupancy models derive inference about the entire community by integrating data from all species (common and rare) (Zipkin et al. 2009a). That is, inference is derived for the entire community using the combined data for all species.

5. Conclusions

These methods can have a wide range of applications for biodiversity conservation and improving the sustainability of forest management practices. In this particular case, species richness and occupancy estimated as a function of habitat characteristics (qdbh, tree density) provided comprehensible estimates that reflect the impact of timber harvesting on biological communities and ecological function. These estimates are clear and easily interpreted, and can be readily incorporated into forest management plans. For example, the relationships between multiple species and habitat features (Fig. 4.2) can help identify how many species would be lost from altering the structure of a forest stand from timber extractions. It can also be used to identify local extinction thresholds and the species that are at greater risk from habitat changes. This will benefit decision makers assess the functional capacity and biological composition of forests, and define landscape-based management interventions to maximize species

richness. This can be particularly useful in situations where funding for conservation is limited, and pressure over resources is high.

Further modeling of communities within and outside protected areas to study metacommunity dynamics could help increase our understanding of source-sink dynamics in space and time. Incorporating species richness dynamics and occupancy predictions into land management strategies would greatly improve conservation planning for biodiversity by identifying and quantifying the most suitable source habitats, as well as the species spillover effect into adjacent/sink areas.

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Chapter 5

STATISTICAL MODELS FOR THE PEOPLE: QUANTITATIVE TOOLS FOR CONSERVATION PLANNING IN SOCIO-ECOLOGICAL SYSTEMS

Abstract: Community-based forestry (CBF) is a policy tool that is frequently used to address natural resource conservation and livelihood goals in developing regions. However, and despite a growing body of literature, important questions remain about the conditions affecting its successful implementation and the resulting conservation impacts of these practices. Improving our predictive ability of CBF outcomes and its pertinent causal correlates will be very useful for enhancing forest management and conservation strategies in regions where forest systems and local communities are closely interconnected. This chapter describes an empirical framework to estimate forest system state from field and remotely-based data, and examine the effects of any local and/or regional variables to assess and predict the outcomes of forest management practices. I demonstrate the usefulness of this framework with a case study of the CBF sector in the Sierra Tarahumara region (STR) of northern México. The results provide a comprehensive assessment of forest system changes in the STR, and reveal important mechanisms and relationships with human actions that can be used to inform policy and management interventions. I conclude by highlighting the importance of using quantitative tools for conservation planning and management, and the significance of enhancing local governance capacity for social, political, and ecological sustainability in the face of regional and national socio-political uncertainty.

1. Introduction

The issues facing forest managers in developing regions are very different from those found in developed countries. In the former, it is common to find rural and indigenous communities closely embedded and depending on forest systems and their resources as closely interconnected socio-ecological systems (Liu et al. 2007). It is also common to find high poverty rates leading to social and political tensions that give economic development and social stability goals priority over conservation goals (Cordova 2001). Furthermore, and in addition to high development pressure over natural resources, the implementation of conservation policies –including spatial reserves– is hampered by lack of official interest as well as limited regulatory and institutional capacity (Smith et al. 2003, Laurance 2004, Santana 2005).

Ex situ forest conservation practices that rely on local governance to improve management and livelihoods, are perhaps the most viable alternative in developing regions where people and natural resources are closely related (Navarrete et al. 2011, Persha et al. 2011). Effective local forest governance occurs when the major users of the resource are also the major actors in creating and adapting collective-choice appropriation strategies that result in better management practices and social equity. Community-based forestry (CBF) is one such approach that has become particularly widespread in recent decades as a result of state decentralization over natural resources in many parts of the world (Pokorny et al. 2010, FAO 2011).

CBF, defined as a composite of forest management actions that provide local economic opportunities (Pokorny et al. 2010), is considered by some authors to have the potential to become a model of rural sustainability in developing regions (Bray et al. 2003, Nagendra 2007). However, others find that when prescribed as a generic conservation policy tool, participatory *ex situ* conservation approaches are not very useful, and can result in further degradation (Brown et al. 2007, Ostrom et al. 2007).

Several CBF reviews have been published recently (Nagendra 2007, Ostrom and Nagendra 2007, Larson et al. 2010, Pokorny et al. 2010), but our current state of knowledge still lags behind in terms of (1) accurately assessing and predicting the ecological response of ecosystems or the components of ecological systems (e.g., biological communities and populations) to degradation and management interventions (Adams et al. 2004, Brockington et al. 2006); and (2) defining the precise social, economic, and political conditions that contribute to effective local governance and the success or failure of CBF practices (Perez-Cirera and Lovett 2006, Ostrom et al. 2007). This lag, especially with respect to ecosystem state, is largely due to the difficulties of quantifying the effects of management actions on ecological systems (Yoccoz et al. 2001, Mikkelsen et al. 2007). Also, because of the complexities of identifying, quantifying, and linking multidisciplinary concepts, conditions, and mechanisms that contribute to successful CBF outcomes, their study has been neglected (Perez-Cirera and Lovett 2006, Persha et al. 2011). The intent of this dissertation has been to develop an analytical framework to assess and predict the outcomes of CBF practices. Improving our predictive ability of CBF outcomes and its pertinent causal correlates will be very useful for enhancing forest management and conservation strategies.

2. An assessment framework

I present an empirical framework to estimate forest system state from field and remotely-based data, and to examine the effects of any local and/or regional covariates. Vital system rates, such as species richness (i.e., number of species in an area) and occupancy (i.e., the proportion of habitat patches occupied by a species) are effective measures useful for understanding system condition and trends (Yoccoz et al. 2001, MacKenzie et al. 2005). These system state variables can be estimated using occupancy models, a recently-developed class of models for studying the distribution and

abundance of species. Occupancy models use detection/non-detection (i.e., presence/absence) data obtained from repeated observations at different sites to model site occupancy dynamics (probability of occupancy, colonization, and extinction) of single and multiple species while accounting for imperfect detection (MacKenzie et al. 2002, MacKenzie et al. 2005, Royle and Dorazio 2008). Compared with traditional abundance surveys, collecting these data require less time, effort and financial resources, thus allowing larger areas to be surveyed. These system state variables can be used in paired analyses with environmental variables to establish functional relationships and increase our understanding of the system's structural dynamics (Nichols et al. 2005). Such analyses can help identify the organisms that account for the most variability in the system and determine spatio-temporal indicators of system state. They can also be used to inform management decisions, design timely management and conservation actions, and make better use of limited funds (Yoccoz et al. 2001, Nichols and Williams 2006).

Remotely-sensed data can provide important information about long-term, landscape-based changes in the system. Similarly, because socio-cultural structures and local governance institutions take time to form and develop, information about these elements would allow us to understand how local, long-term governance arrangements are formed and how they affect the landscape. These combinations can generate important information about the way that local institutions and user group characteristics influence forest resources (Ostrom and Nagendra 2007).

Combining system status measures from different spatial scales can link the larger patterns to local sources of variation, including human structures and resource use, and provide a comprehensive assessment of system changes and its causal correlates. My framework allows for the analysis of important mechanisms and relationships between vital rates of the system and its components and human actions.

3. Case study from Chihuahua, México

I demonstrate the usefulness of this framework with a case study of the CBF sector in the Sierra Tarahumara region (STR) of northern México. The STR covers 70,000-km² of temperate and semi-tropical forests and woodlands. Over 90% of the land is owned by rural and indigenous communities as *ejidos*, a communal form of legal land tenure in which user groups own and manage a territory (Sarukhan and Larson 2001). Less than 1% of the land is officially protected and about 10% is privately held. The region's major economic activities include timber harvesting, subsistence agriculture and small-scale animal husbandry. Poverty is widespread, particularly in communities with a predominant indigenous (Tarahumara) population. Recently, as a result of drought, failing prices for agricultural products, and public insecurity stemming from illegal drug trafficking, people have been increasingly migrating to cities in search of employment, and communal properties have been dismantled (Guerrero et al. 2000). These trends present a clear challenge to the social, political, and ecological stability in the region. At the same time, an increase in drug-related activities, violence, and federal forces in the region after 2006, has further deteriorated socio-political conditions (Turati 2011). This is representative of steady landscape and social trends in the region and other forested regions of México.

3.1. Methodology

I estimated forest change rates from 1976 to 2001 using satellite imagery in a sample of 38 *ejidos* with different forest management and governance arrangements. To describe long-term social, cultural and governance structures, as well as the socio-economic characteristics of *ejidos*, I used survey and official population census data for each *ejido*. I then applied negative binomial generalized linear models (GLMs) using forest change rates as the response variable. Akaike information criterion (AIC) based

model selection procedures, which measure the tradeoff between accuracy and complexity of the model (Burnham and Anderson 2002), were used to find the models and variables that best explained forest change.

To measure the impact of timber harvesting activities on biological communities and ecological functionality, I applied a hierarchical Bayesian multi-species occupancy model (hereafter, community model) that incorporated a data augmentation procedure (Kéry and Royle 2009) to data from a breeding bird census of 32 sites in managed (*ejido*) and unmanaged (national park) sites sampled 3-5 times/yr in 2008 and 2009. This model was extended to incorporate environmental covariates reflective of timber harvesting pressure, and describe species richness and occupancy as a function of tree density and average tree diameter at breast height. I focused on bird communities because the large number of species and wide range of habitat specialization makes them an attractive measure of biodiversity and environmental change (Canterbury et al. 2000, Ceballos and Marquez 2000, Manley et al. 2006).

3.2. Results

Deforestation in 2001 amounted to 12.54% of the study area, a 40% increase from 8% in 1976. Forest loss rates separated by *ejido* varied greatly, from 2.26 to 180.3 ha/yr with a mean of 42.0 ha/yr. Forest cover gains were found in 20% of the cases analyzed, but this only amounted to 0.14% of the total study area (compared to 12.54% that was lost), and ranged from 0.58 to 23.3 ha/yr with a mean of 10.1 ha/yr. Model results identified important linkages between the forest and the people who own and manage them. Forest change differences were explained by the location of the *ejido* in relation to markets, and the socio-cultural characteristics of its members. The most significant determinant of forest change was access to markets, with most deforestation occurring near them. The effect of ethnicity and size of *ejidos* on forest change was

non-linear, but in general *ejidos* with increasing numbers of indigenous members ($\geq 50\%$) suffered lower rates of forest loss. Similarly, fewer forest changes were associated with smaller *ejidos* (≤ 280 members). Enforcement of formal rules and sanctions, and social models of forest extraction, indicators of effective governance and social cohesiveness, respectively, were significantly related to lower deforestation rates. However, the model with the most weight (i.e., highest AIC score) only included distance, ethnicity, *ejido* size, and education. Results also indicated that stocking rates are decreasing in time, a clear indicator that forest loss exceeds regrowth and that the forestry sector in the region is unsustainable. Findings also indicate that corruption and illegal logging are significant factors affecting the loss of forest cover.

Although the effect of economic covariates was not significant, education and literacy were significant predictors, and are considered indicators of socio-economic inequality, specially in historically marginalized indigenous communities (Perez-Cirera and Lovett 2006). Inequality is a recurring theme in resource conservation, and research has shown that human-caused degradation and associated impacts on biodiversity and livelihoods are most severe where socio-economic inequality exists (Mikkelsen et al. 2007). Similar cases have been documented in other parts of México (Nadal 2003).

I had strong expectations regarding the influence of the independent variables chosen to reflect the performance of *ejido* institutions. For example, I expected that covariates which reflected democratic participatory process within the *ejido* general assembly, a legal entity created by México's agrarian law, would be highly significant. The results indicate that social organization, values, and regulation of social life in *ejidos* are strongly dependant on more traditional and informal socio-political structures. These informal social structures are not easily quantifiable and vary greatly by *ejido*, but are rooted in traditional forms of organization and culture. Such forms of organization are defined to be a set of structural (e.g., rules, social networks, and roles)

and cognitive (e.g., norms, values, and attitudes) attributes that provide the foundation for trust, solidarity and reciprocity in a community. These structures are more influential in *ejidos* that are more cohesive (i.e., there is a greater social affinity between its members), and weaker in those that are plagued by intracommunity divisions. In the CBF literature, social cohesiveness has been closely linked to a shared sense of cultural identity and land tenure security, which are essential components of long-term effective local governance arrangements (Bray 2005). Cohesive communities are more likely to develop effective socio-cultural structures, organizational arrangements, and mechanisms of cooperation than communities that are divided by internal and external influences (Sanchez-Perez et al. 2007). Intracommunity divisions are often caused by socio-economic inequality, which allows some members to accumulate more power than others to benefit themselves at the expense of the community (Perez-Cirera and Lovett 2006). In this case study, *ejidos* with higher average levels of education and higher cultural homogeneity regained forest cover or had low deforestation rates.

The community model yielded sensible estimates of site-specific and total species richness that were positively related to tree diameter size and negatively to tree density. These patterns support my hypothesis that degradation caused by timber extraction reduces occupancy, size, and species composition of bird communities. Community turnover, given by the standard errors generated by the model, show that sites with higher species richness also had lower estimate uncertainty, and vice versa. This indicates that sites with greater diversity are also more stable in time, whereas sites with lower diversity had higher turnover of species and community size. Species-specific occupancy estimates indicate an overall functional homogenization of bird communities as a result of forest degradation and even-aged forest management practices. Habitats characterized by denser forest stands dominated by small diameter trees were species-poor and contained mostly generalist species. However, functional

homogenization varied significantly among managed and unmanaged forests. Areas with the highest species richness values and lower turnover rates were found on national park lands. Occupancy and detection probabilities were not correlated, indicating that the majority of species detected are rare because both probability and occupancy estimates are low. It is worth noting that recent studies have used different set of tools to define and measure ecological specialization, habitat segregation, and functional homogenization separately (Devictor et al. 2010, Barnagaud et al. 2011b, Clavel et al. 2011). Multi-species occupancy models allowed me to generate inference regarding all of these issues efficiently and conveniently, thus highlighting the utility of occupancy models to increase our understanding and predictive capacity regarding the response of biological communities to degradation and management activities.

4. Contributions to the field

The goal of this research was to develop an empirical framework with honest metrics that could provide simple, informative, and practical information for managers and policy makers regarding two implementation problems: enhancing forest governance, and quantifying the impact of forest management activities on forest system state. I demonstrated this framework with a case study in which inference was drawn about the functional relationships between deforestation rates and local governance, and the impact of forest degradation on vital system rates. The result is an assessment of CBF practices that describes the state of the forest system and its components, and the attributes of the *ejidos* that define the outcome of long-term forest management practices. These metrics can be applied to other situations involving conservation and/or rural development practices. They can also be used to test the impact of different variables reflecting policy and management interventions, and to answer questions about population and community ecology for a wide range of taxa.

4.1. Methodology

With regards to estimation efficiency, the community model –which incorporated a hierarchical Bayesian analysis and a data augmentation procedure, offers several important advantages compared to more traditional estimates of occupancy and species richness. Modeling observation and occupancy processes while accounting for detection heterogeneity significantly improves estimate accuracy and inference for both rare and abundant species (Royle and Dorazio 2008, Russell et al. 2009, Zipkin et al. 2009a). Species richness, occupancy and abundance estimates that do not account for imperfect detection are biased towards the more common and abundant species, but inference about rare species is particularly useful for conservation as these are the focus of spatial reserve design and policy interventions (Fleishman et al. 2000).

The ability to incorporate a data augmentation procedure is another advantage of hierarchical community models. Data augmentation is used to solve estimation and model implementation issues when the size of the community (n) is unknown (i.e., not all the species are detected). This is accomplished by inflating the dataset with zeroes (i.e., all-zero encounter histories for undetected species) to fix the total size of the dataset. In other words, the model with data inflation is applied to a dataset representing a fixed number of available species (M) that can be determined *a priori* instead of an unknown number ($M - n$). This is done with the intention of estimating the number of species that were not detected in the field, and can be seen as the equivalent of imposing a discrete uniform prior on N , the total number of species from which species richness is estimated (Royle et al. 2007). In this case, the total number of species detected ($n = 73$) was augmented by adding 150 hypothetical species. The model estimated a mean of 128 species, a reasonable estimate for the STR considering biodiversity inventories for similar ecosystems. This estimate is consistent with the heterogeneous levels of occurrence for species in general in the STR. As noted by Royle et al. (2007),

occurrence heterogeneity suggests that low detection probabilities of many species are caused by low rates of occurrence, and not by low detection probability. As such, I infer that the avian community is made up of a substantial portion of rare species, a fact that explains why the estimated number of species is much larger than the number of species that was actually detected. This indicates that the results are accurate and reliable.

Some authors (e.g., Russell et al. 2009) oppose data augmentation on the basis that inference from undetected species may not have practical applications. I disagree and find the arguments by Royle et al. (2007) highly persuasive, and the potential applications of data augmentation methods extremely useful. The result from a data augmented dataset is the equivalent of a species-accumulation curve, which has numerous applications in applied and theoretical fields of ecology (Gotelli 2001, Stevens 2010). Moreover, the discrepancy between the actual number of observed species and potential species richness is a function of estimate uncertainty and spatial variability associated with the observed data. Because this uncertainty is statistically modeled in terms of probabilistic inference, it can be used to draw reliable conclusions and model the state, spatial stability, and size turnover of communities and metacommunities. Associated uncertainty estimates can also be used to inform the allocation of future sampling efforts, and to establish explicit biodiversity conservation and restoration goals in forest management settings.

With regard to forest change and governance, AIC-based model selection and multi-model inference allowed me to test a wide array of hypotheses regarding the long-term impact of social, political, and environmental variables on forest system status. The results provided statistical evidence of the impact of well-known deforestation predictors (i.e., roads and access to markets) (Nelson and Hellerstein 1997, Perz and Skole 2003, Rodrigues et al. 2009), and of socio-cultural attributes of user groups for which few empirical analyses that allow for rigorous statistical inference exist. AIC

weights for individual models and predictor variables are considered solid measures of data-based evidence about parameter values, and have other important uses and interpretations (Burnham and Anderson 2002). In this case, the relative AIC weight for predictor variables indicates that forest cover change rates vary greatly based on the characteristics of each *ejido*. Arguably, policy and management interventions to curb deforestation in *ejidos* have to be distinct due to the different conditions found in each. If this is the case, forest management in the region needs to be ecologically and socio-politically based to fit the conditions of individual *ejidos*.

4.2. Management

I believe my framework can be very useful for forest management and biodiversity conservation planning. Species richness and occupancy estimates calculated as a function of habitat characteristics (average stand diameter, tree density) provide comprehensible estimates of the impacts of timber harvesting on biological communities and ecological function that can be readily incorporated into forest management plans. Greater understanding of how management interventions and degradation shape forest systems and its components can help managers and policy makers identify thresholds and the species that are at greater risk from these changes. In turn, this can help managers assess the functional capacity and biological composition of forests, and define landscape-based management interventions to maximize species richness at the local and regional scales.

Despite the potential of CBF practices to achieve long-term, large-scale forest conservation, the comparison between managed and unmanaged forests highlights the importance of spatial reserves for biodiversity conservation. Certain forest habitat structures (e.g., old-growth stands) are unattainable without exclusion from all human uses and provide invaluable benefits for biodiversity, ecosystem services, and functions

that other approaches cannot (Phalan et al. 2011). Recent studies into the spillover conservation effects of marine reserves has resulted in strong support for the establishment of more no-use zones to enhance biodiversity and population stocks of these reserves and adjacent areas (Claudet et al. 2008). Further use of occupancy modeling techniques within and outside spatial reserves to study metacommunity dynamics will improve our understanding of source-sink dynamics. This knowledge can further inform management actions to enhance species diversity at the local and regional scales where reserves are found, or aid in the identification and establishment of no-use zones where unique resources are located.

4.3. Implementation challenges

In many stances CBF is not considered a viable strategy from an economic point of view because few communities are able to compete successfully in a free market economy. However, CBF is an essential component of many local economies where income opportunities are limited. In other words, CBF is one of the best ways of providing jobs, improving livelihoods, and maintaining social stability in rural areas while potentially sustaining forest resources (Larson et al. 2010). Establishing the appropriate market infrastructure to promote sustainable management practices and improve livelihoods could significantly reduce pressure over natural resources, enhance stewardship, and provide direct and indirect conservation benefits (Lewis et al. 2011).

In order for CBF to be sustainable, effective local governance arrangements and the conditions that enable it need to be developed and sustained. Some of these conditions include land tenure security for user groups, technical capacity building to improve management practices, access to fair prices and markets, effective law enforcement to regulate illegal logging, and socio-political stability (Larson et al. 2010). By enhancing local governance, along with the use of market tools of certification and

compensation for the implementation of best management practices, value can be added to CBF products, and the economic, social and environmental sustainability of CBF practices enhanced (Larson et al. 2010).

4.4. External uncertainty

It is worth mentioning that this research was conducted before political instability in the STR increased as a result of federal policies for combating organized crime. As a consequence, new and different challenges stemming from the lack of public security and the loss of state control over a growing number of territories, particularly in rural areas, can be expected to arise in the near future with unforeseeable and unpredictable social and environmental consequences.

There are several direct and indirect impacts of violence that bear on my study which need to be addressed. Public insecurity has a direct impact on poverty and rural development, and in turn on CBF and conservation of natural resources. Violence and public insecurity disrupt the social processes and conditions that are necessary for the supply of public services, the development of economic activities, and most aspects of human social life. In the STR, it has displaced people and communities, disrupted transportation and a number of public services including rural education, poverty alleviation programs, fire suppression, and protected area management (Enciso 2011, Turati 2011). For example, forest fires during 2011 could not be properly suppressed in the STR and other parts of the country because the presence of illegal activities and armed gangs threatened the integrity of fire brigades (Anonymous 2011). The Protected Areas Commission (Comisión Nacional de Áreas Protegidas-CONANP) faces similar challenges, and in many cases, staff has been evacuated for security reasons (Enciso 2010).

Indirectly, the Mexican state's inability to address public insecurity and the loss

of territorial control reflect a grave crisis of governance indicative of a failing state and of failed economic, political, and social policies. This systematic weakening of the Mexican state began in the 1980's when México, in exchange for loans from international financial institutions, began to enact a series of neoliberal policies (including governance decentralization of natural resources, free-trade agreements) that to this date continue to dismantle the state's capacity to regulate markets and other public spheres (McMichael 2004). Since then, and particularly after the year 2000, labor, agricultural, and environmental conditions have significantly deteriorated, along with national indicators of public security, corruption and governance capacity, productivity and competitiveness, democratic efficiency, human rights, freedom of press, public safety and justice, and poverty (Wise et al. 2003, Sefchovich 2008). Moreover, México's troubled democratic and political institutions are experiencing an unprecedented crisis of domestic and international credibility, along with increasing levels of attention after the 2006 presidential election. Numerous cases of illegal interference by federal agencies and officials were documented during this process, which produced a fraudulent, unpopular, and illegitimate outcome that experts from many fields described as statistically atypical and highly improbable (Miramontes 2006).

Reducing rural poverty and environmental degradation will require following alternative paths that are not entirely dependent upon a centralized bureaucracy that has demonstrated to be more motivated by political interests than by an interest in implementing policies that effectively address economic stagnation, corruption, and unchecked bureaucratic growth (Paz 1998, Wise et al. 2003). CBF, and other participatory approaches to natural resource management that focus on local/community self-governance capacity, equity, and democratic decision-making, are perhaps the most viable alternative for conservation and poverty alleviation in rural areas of developing

regions. Considering the limitations and meager outcomes of state and market-centered strategies in general, and the numerous successful CBF experiences of Mexican *ejidos*, it is hard not to think of CBF as a panacea that can solve all rural development problems (Ostrom et al. 2007).

It is worth mentioning that despite the growing number of cases in which communities have been more efficient at managing forests and other natural resources than state and market institutions, there have also been numerous failures. Indeed, the existence of democratic local institutions in natural resource management schemes, as is the case of all Mexican *ejidos*, does not necessarily solve all problems, nor automatically guarantee social justice and equity. Nevertheless, it is one way of ensuring that progress is not realized at the expense of the majority (Paz 1998).

Ejidors are not homogeneous, and some can be deeply divided by ethnicity, culture, or socio-economic inequality. In such cases, community-based conservation without careful consideration or implementation can create a new class of conservation and social problems (Bray 2005). Effective implementation of CBF approaches presents managers with numerous challenges, but also with many opportunities for further research and action. Numerous communities in the STR and other parts of México have developed effective governance institutions, as well as the necessary social and human capital needed to protect and manage natural resources sustainably, improve their livelihoods, and safeguard the integrity of their territories and members more effectively than the state. There is still much to be learned about the relationships between social and ecological systems, and how to best maintain and develop the attributes of user groups that make effective local governance possible.

5. References

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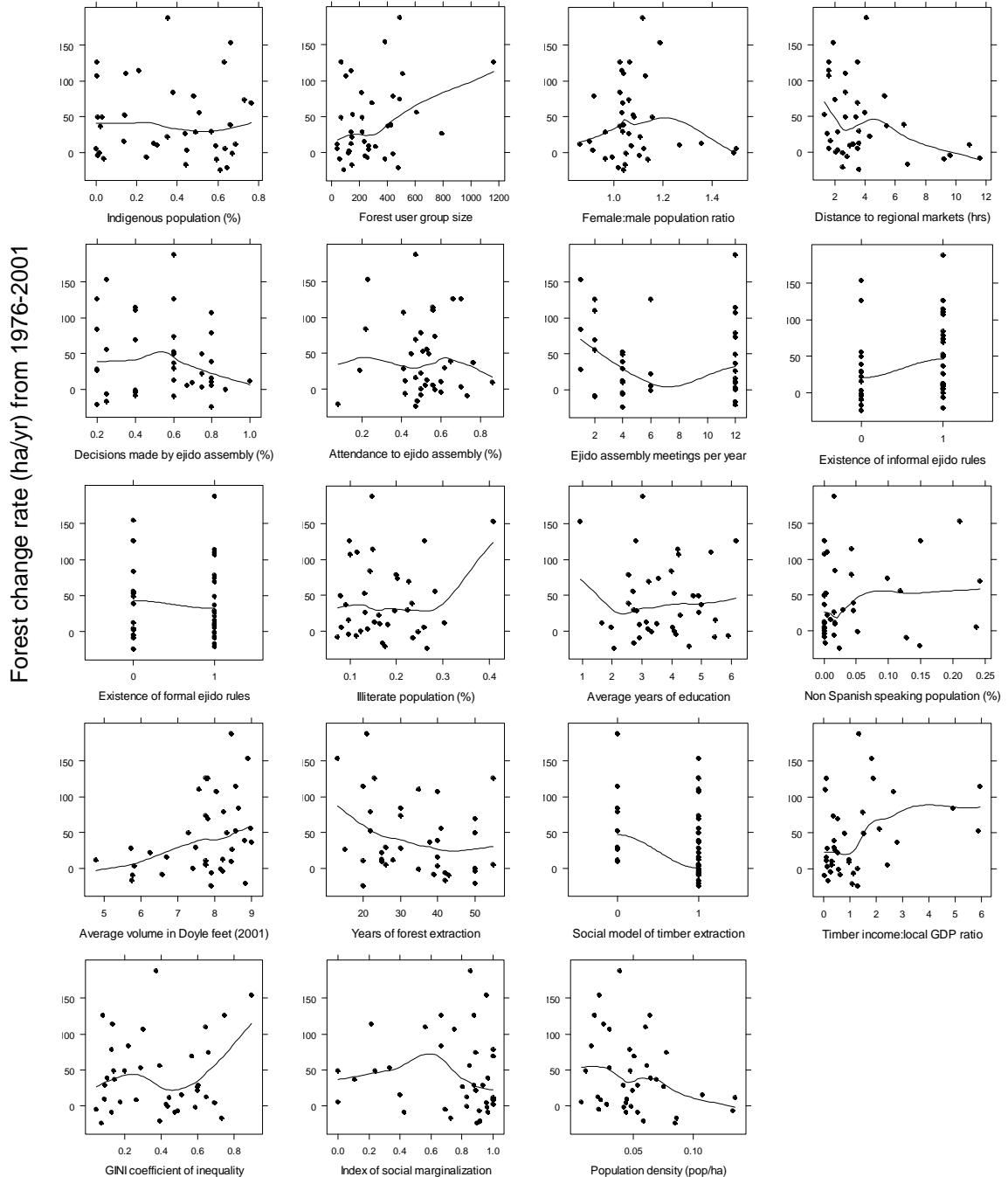
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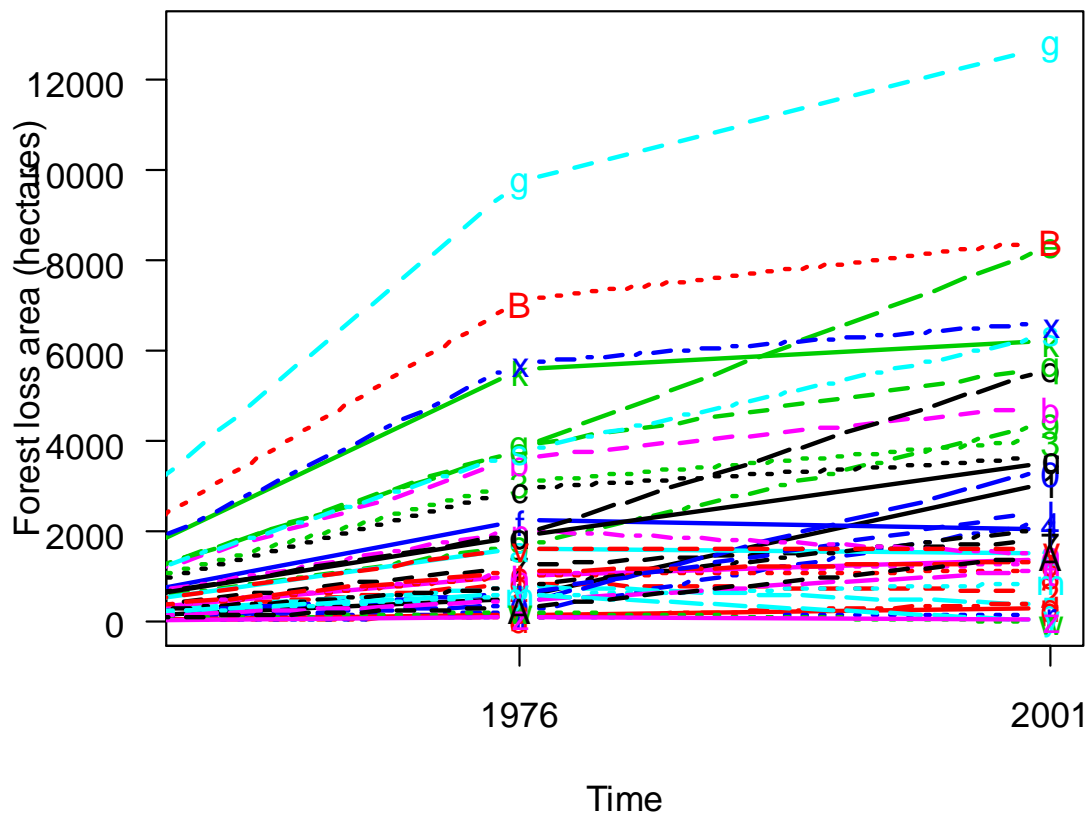
Appendix A

Scatter plots for the dependent variable forest change rate and all covariates used in the analyses with an added LOESS smoother to aid visual interpretation. Most covariates exhibit a non-linear relationship with the dependent variable. Dots indicate individual *ejidos*. Dependent variable on the y-axis, covariates on the x-axis.



Appendix B

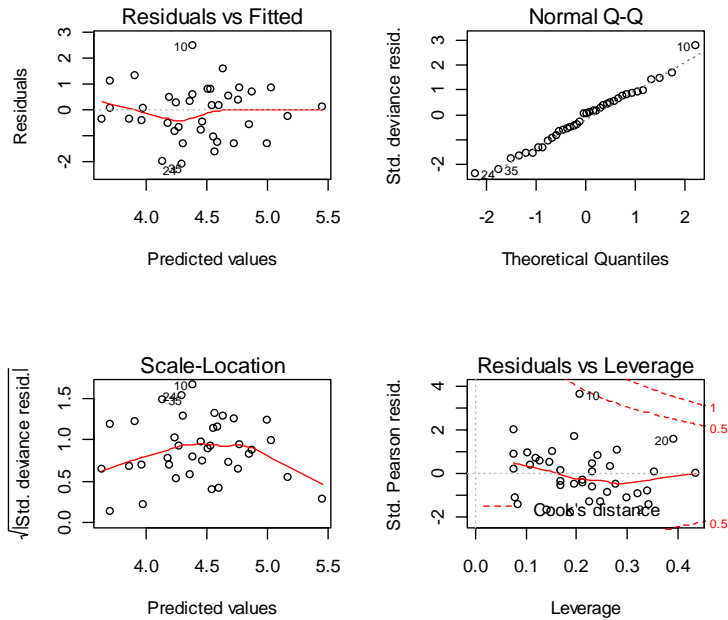
Forest conversion to agriculture (ha) from 1976 to 2001 in 38 *ejidos* of the Sierra Tarahumara region, México plotted using the `matplot` function in R. Deforestation in 2001 amounted to 12.54% of the study area, a 40% increase from 8% in 1976. Forest loss rates separated by *ejido* varied greatly, from 2.26 to 180.3 ha/yr with a mean of 42.0 ha/yr. Forest cover gains were found in 20% of the cases analyzed, but this only amounted to 0.14% of the total study area (compared to 12.54% that was lost). Forest cover gains ranged from 0.58 to 23.3 ha/yr with a mean of 10.1 ha/yr. Each line corresponds to an individual *ejido*.



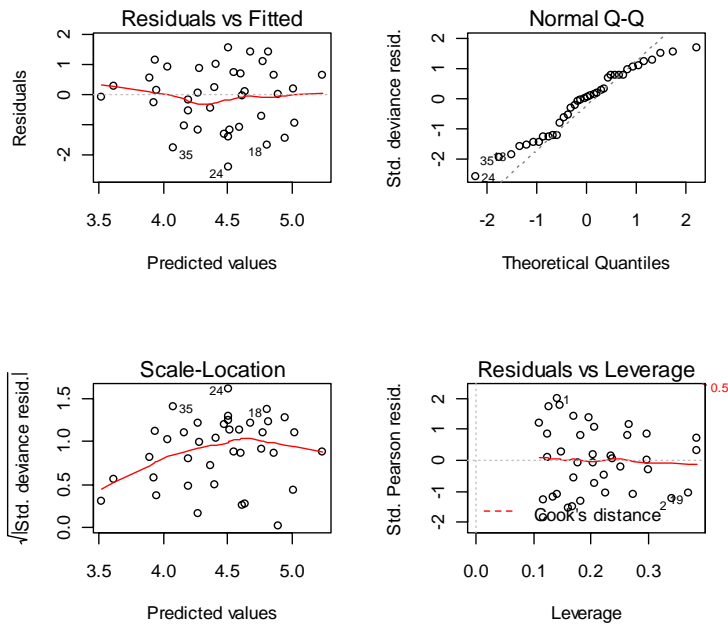
Appendix C

Graphical validation for the top two models selected based on AIC scores using the `par(mfrow=c(2, 2))` and `plot` commands in R. Neither graph shows any clear pattern in the residuals, but model 1 is preferred because it has a significantly better AIC score (384.2) and weight (0.7195) than model 2 (388.5 and 0.0846, respectively).

(1)



(2)



Appendix D

Characteristics of study sites

The following table describes the national park and *ejidos*, or communal land parcels, where I conducted my fieldwork in the Sierra Tarahumara region, México during 2008 and 2009. The sites column indicates the number of spatial replicates in each forest study site (parcel column) where breeding bird census and habitat sampling were conducted. Detailed logging and fire information was unavailable, but I was able to determine if a site had been logged and/or burned (*) during the 15 years prior to the beginning of my field work from visual inspections and interviews with local people (recent timber harvest and recent fire columns).

Parcel	Land tenure	Sites	Area (ha)	User group size	Recent timber harvest	Recent fire
El Alamo	National park	4	4,772	30	-	*
El Consuelo	<i>Ejido</i> El Consuelo	3	1,836	47	*	*
Egochi	<i>Ejido</i> Panalachi	3	56,552	430	*	-
La Laguna	<i>Ejido</i> La Laguna	3	8,431	164	*	*
Magullachi	<i>Ejido</i> Magullachi	4	8,435	74	-	-
Molinares	<i>Ejido</i> Molinares	4	5,468	48	-	-
Panalachi	<i>Ejido</i> Panalachi	3	56,552	430	-	-
Sisoguichi	<i>Ejido</i> Sisoguichi	3	38,028	512	*	*
Majalca	National park	5	4,772	30	-	-
Total study area		32	184,846			

Appendix E

WinBUGS code for the hierarchical Bayesian community model

I used a community model written by Kery and Royle (2009). This model estimates species richness based on species-specific occupancy using a hierarchical Bayesian framework and a data augmentation procedure (Royle et al. 2007). I made some slight modifications to the original model and did several test runs using different priors, data augmentation parameters, number of iterations, number of burn-ins, and habitat covariates.

```
model {  
  
  omega ~ dunif(0,1)          # Prior distributions and parameter transformations  
  p0 ~ dunif(0,1)  
  psi0 ~ dunif(0,1)  
  sigmap ~ dunif(0,10)  
  sigmapsi ~ dunif(0,10)  
  rho ~ dunif(-1,1)  
  
  taup <- (1/(sigmap*sigmap))  
  taupsi <- (1/(sigmapsi*sigmapsi))  
  mup <- log(p0/(1-p0))  
  mupsi <- log(psi0/(1-psi0))  
  var.eta <- taup/(1.-pow(rho,2))  
  
  for(i in 1:M){  
    alpha1[i] ~ dnorm(mu.alpha1, tau.alpha1)I(-16,16)  
    alpha2[i] ~ dnorm(mu.alpha2, tau.alpha2)I(-16,16)  
    alpha3[i] ~ dnorm(mu.alpha3, tau.alpha3)I(-16,16) # Interaction term  
  }  
  mu.alpha1 ~ dnorm(0, 0.1)  
  tau.alpha1 <- 1 / (sd.alpha1 * sd.alpha1)  
  sd.alpha1 ~ dunif(0, 5)  
  mu.alpha2 ~ dnorm(0, 0.1)  
  tau.alpha2 <- 1 / (sd.alpha2 * sd.alpha2)  
  sd.alpha2 ~ dunif(0, 5)  
  
  mu.alpha3 ~ dnorm(0, 0.1) # Interaction Parameters  
  tau.alpha3 <- 1 / (sd.alpha3 * sd.alpha3)  
  sd.alpha3 ~ dunif(0, 5)  
  for(i in 1:M){ # Process model  
    w[i] ~ dbin(omega,1)
```

Appendix E

(continued).

```
lpsi[i] ~ dnorm(mupsi,taupsi) I(-16,16)
mu.lp[i] <- mup +(rho*sigmap/sigmapsi)*(lpsi[i]-mupsi)
lp[i] ~ dnorm(mu.lp[i], var.eta) I(-16,16)
for(j in 1:nsites){ # sites
  z[i,j] ~ dbern(mu.psi[i,j])
  mu.psi[i,j] <- psi[i,j]*w[i]
  logit(psi[i,j]) <- lpsi[i] + alpha1[i] * treedensity[j] + alpha2[i] * dbhq[j] + alpha3[i]
* treedensity[j] * dbhq[j] # Added interaction parameters
}
}

for(i in 1:M){ # Observation model
  for(j in 1:nsites) {
    for(k in 1:K){
      # The observed, augmented data array
      y[i,j,k] ~ dbern(mu.p[i,j,k])
      mu.p[i,j,k] <- z[i,j]*p[i,j,k]
      logit(p[i,j,k]) <- lp[i]
    }
  }
}

for(j in 1:nsites){ # Species-richness N as a derived parameter
  Nsite[j] <- sum(z[1:M,j])
}
n0<-sum(w[(nspecies+1):M])
Ntotal<-nspecies+n0
}
```

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Appendix F

Species-specific estimates of occupancy, detection probability, and covariate effects for 73 species detected in the STR. Mean, standard deviation, and 95% posterior intervals for probabilities of occupancy, detection, and habitat covariate values (tree density and diameter) on the logit scale. Number of sites in which the species was detected is included. Numbers in bold indicate highest estimates among the 73 species.

Species	Total sites	Ψ mean	Ψ SD	P mean	P SD	Density mean	Density SD	qdbh mean	qdbh SD
<i>Colaptes auratus</i>	32	0.919	0.094	0.267	0.030	-0.801	0.586	5.351	3.617
<i>Turdus migratorius</i>	31	0.893	0.114	0.375	0.035	-0.790	0.587	5.321	3.597
<i>Junco phaeonotus</i>	29	0.900	0.108	0.207	0.024	-0.803	0.571	5.235	3.592
<i>Poecile sclateri</i>	21	0.594	0.228	0.230	0.037	-0.654	0.643	4.265	3.587
<i>Aphelocoma ultramarina</i>	19	0.485	0.209	0.250	0.037	-0.771	0.544	5.043	3.432
<i>Contopus pertinax</i>	19	0.376	0.179	0.275	0.043	-0.943	0.515	5.743	3.333
<i>Pheucticus melanocephalus</i>	19	0.668	0.176	0.267	0.036	-1.118	0.549	3.382	3.501
<i>Cyanocitta stelleri</i>	18	0.673	0.196	0.208	0.041	-0.770	0.556	2.147	4.105
<i>Empidonax occidentalis</i>	18	0.410	0.198	0.238	0.034	-0.824	0.545	5.789	3.368
<i>Sitta carolinensis</i>	18	0.411	0.194	0.267	0.041	-0.795	0.528	5.444	3.261
<i>Contopus sordidulus</i>	17	0.438	0.177	0.319	0.045	-0.965	0.500	4.766	3.155
<i>Tyrannus vociferans</i>	16	0.380	0.178	0.282	0.045	-0.904	0.505	4.640	3.246
<i>Melanerpes formicivorus</i>	14	0.277	0.164	0.231	0.038	-0.906	0.526	6.303	3.273
<i>Corvus corax</i>	13	0.391	0.209	0.187	0.045	-0.752	0.554	4.033	3.411
<i>Empidonax fulvifrons</i>	13	0.246	0.143	0.298	0.040	-0.986	0.506	5.924	3.183
<i>Sialia mexicana</i>	13	0.305	0.165	0.254	0.043	-0.864	0.518	4.559	3.252
<i>Vireo plumbeus</i>	13	0.386	0.180	0.255	0.048	-0.882	0.511	2.820	3.393
<i>Pipilo maculatus</i>	12	0.357	0.174	0.267	0.048	-0.951	0.501	3.449	3.229
<i>Thryomanes bewickii</i>	12	0.196	0.127	0.296	0.050	-0.922	0.502	6.585	3.224
<i>Zenaida macroura</i>	11	0.368	0.177	0.316	0.053	-0.853	0.511	1.076	3.503
<i>Catherpes mexicanus</i>	10	0.186	0.130	0.229	0.045	-0.997	0.514	6.435	3.238
<i>Pipilo fuscus</i>	10	0.416	0.193	0.224	0.051	-1.013	0.524	1.812	3.535
<i>Myioborus pictus</i>	9	0.291	0.167	0.231	0.044	-0.879	0.516	2.235	3.415
<i>Peucedramus taeniatus</i>	9	0.156	0.116	0.230	0.042	-0.741	0.564	4.565	3.259
<i>Trogon elegans</i>	9	0.154	0.115	0.241	0.051	-0.938	0.511	6.324	3.218
<i>Piranga flava</i>	8	0.139	0.108	0.237	0.051	-0.956	0.515	6.216	3.234
<i>Psaltiriparus minimus</i>	8	0.188	0.131	0.234	0.053	-0.940	0.512	4.547	3.145
<i>Cathartes aura</i>	6	0.139	0.113	0.220	0.052	-1.122	0.563	5.868	3.215
<i>Dendroica coronata</i>	6	0.137	0.105	0.263	0.051	-0.975	0.515	4.572	3.228
<i>Dendroica graciae</i>	6	0.163	0.123	0.224	0.049	-0.928	0.518	3.790	3.291
<i>Polioptila caerulea</i>	6	0.235	0.155	0.240	0.059	-0.974	0.527	1.717	3.534
<i>Certhia americana</i>	5	0.063	0.060	0.359	0.068	-0.847	0.539	5.566	3.207
<i>Picoides villosus</i>	5	0.103	0.089	0.295	0.058	-0.924	0.524	4.071	3.293
<i>Zenaida asiatica</i>	5	0.145	0.114	0.256	0.061	-1.036	0.538	3.938	3.293
<i>Buteogallus anthracinus</i>	4	0.072	0.078	0.187	0.058	-1.011	0.548	6.222	3.333
<i>Carduelis psaltria</i>	4	0.090	0.088	0.199	0.058	-0.981	0.539	5.235	3.290

Appendix F

(continued).

Species	T. sites	Ψ mean	Ψ SD	P mean	P SD	Dens mean	Dens SD	qdbh mean	qdbh SD
<i>Emberizidae spp</i>	4	0.143	0.121	0.335	0.061	-0.775	0.551	0.769	3.793
<i>Spizella passerina</i>	4	0.165	0.132	0.251	0.061	-0.985	0.526	1.678	3.628
<i>Tachycineta bicolor</i>	4	0.067	0.065	0.296	0.068	-1.018	0.539	5.491	3.246
<i>Accipiter cooperi</i>	3	0.056	0.061	0.236	0.062	-1.028	0.548	5.672	3.315
<i>Carpodacus mexicanus</i>	3	0.086	0.087	0.254	0.064	-1.048	0.554	3.993	3.416
<i>Coragyps atratus</i>	3	0.057	0.063	0.249	0.066	-1.065	0.566	5.824	3.330
<i>Hirundo rustica</i>	3	0.057	0.063	0.211	0.056	-1.018	0.548	5.813	3.335
<i>Meleagris gallopavo</i>	3	0.078	0.079	0.401	0.080	-1.114	0.584	4.287	3.336
<i>Myiarchus cinerascens</i>	3	0.146	0.125	0.302	0.065	-1.084	0.570	1.157	3.821
<i>Sitta pygmaea</i>	3	0.085	0.080	0.322	0.076	-0.940	0.530	3.106	3.479
<i>Trochilidae spp</i>	3	0.054	0.059	0.273	0.068	-0.960	0.538	5.045	3.408
<i>Wilsonia pusilla</i>	3	0.060	0.066	0.228	0.063	-1.063	0.560	5.701	3.360
<i>Baeolophus wollweberi</i>	2	0.072	0.085	0.210	0.068	-1.059	0.585	3.577	3.470
<i>Buteo albonotatus</i>	2	0.033	0.041	0.336	0.083	-0.986	0.532	5.277	3.383
<i>Buteo jamaicensis</i>	2	0.070	0.079	0.232	0.067	-0.984	0.539	2.790	3.575
<i>Cardellina rubrifrons</i>	2	0.065	0.073	0.282	0.072	-0.968	0.539	2.696	3.539
<i>Coccothraustes vespertinus</i>	2	0.057	0.068	0.255	0.069	-0.752	0.590	2.165	3.593
<i>Columba fasciata</i>	2	0.052	0.060	0.326	0.087	-0.998	0.551	3.765	3.472
<i>Eugenes fulgens</i>	2	0.046	0.056	0.236	0.064	-0.928	0.540	4.298	3.467
<i>Euptilotis neoxenus</i>	2	0.068	0.076	0.373	0.085	-1.055	0.557	2.678	3.623
<i>Molothrus aeneus</i>	2	0.065	0.071	0.325	0.076	-1.088	0.574	3.183	3.494
<i>Passer domesticus</i>	2	0.064	0.069	0.323	0.074	-0.956	0.545	2.438	3.571
<i>Sayornis saya</i>	2	0.048	0.057	0.324	0.082	-1.007	0.552	3.764	3.488
<i>Selasphorus platycercus</i>	2	0.079	0.087	0.238	0.066	-1.075	0.580	2.890	3.551
<i>Troglodytes aedon</i>	2	0.045	0.053	0.326	0.084	-0.821	0.552	3.047	3.525
<i>Accipiter gentilis</i>	1	0.025	0.040	0.261	0.076	-1.005	0.562	4.569	3.486
<i>Accipiter striatus</i>	1	0.029	0.043	0.231	0.073	-0.888	0.548	3.369	3.564
<i>Ardea herodias</i>	1	0.038	0.055	0.230	0.072	-1.035	0.567	3.235	3.596
<i>Dendroica townsendii</i>	1	0.039	0.055	0.222	0.073	-1.058	0.571	3.471	3.599
<i>Picoides arizonae</i>	1	0.033	0.049	0.226	0.071	-1.066	0.581	4.207	3.527
<i>Piranga ludoviciana</i>	1	0.031	0.046	0.269	0.079	-0.993	0.554	3.446	3.503
<i>Progne subis</i>	1	0.027	0.038	0.399	0.115	-1.072	0.582	4.229	3.471
<i>Regulus calendula</i>	1	0.023	0.035	0.301	0.086	-1.005	0.556	4.554	3.447
<i>Sayornis nigricans</i>	1	0.038	0.057	0.237	0.078	-1.053	0.569	3.489	3.567
<i>Vermivora celata</i>	1	0.037	0.052	0.239	0.074	-0.876	0.548	2.341	3.665
<i>Vermivora graciae</i>	1	0.024	0.035	0.239	0.074	-0.978	0.550	4.519	3.516
<i>Vireo huttoni</i>	1	0.032	0.051	0.240	0.077	-1.027	0.569	3.870	3.529

Appendix G

Comparison of species richness and forest habitat characteristics for all sites (n = 32) in the Sierra Tarahumara region, México.

Sampling sites	Species richness	SD	95% CI	Tree size qdbh (m)	Tree density/ha
<u>Unmanaged</u>					
El Alamo, site 1	19.06	1.4*	17, 22	0.138	-0.41
El Alamo, site 2	21.77	1.3*	20, 25	0.103*	-0.82*
El Alamo, site 3	21.7	1.8	19, 26	0.255	0.001
El Alamo, site 4	16.3	1.73	13, 20	0.16	-1.01*
Majalca, site 1	37.5**	1.2*	36, 40	0.25	-0.82*
Majalca, site 2	40.0**	1.5	38, 43	0.36**	0.29
Majalca, site 3	28.3**	1.6	26, 32	0.31**	-0.41
Majalca, site 4	30.0**	2.0**	27, 34	0.37**	-0.11
Majalca, site 5	30.2**	1.8	27, 34	0.32**	-1.01*
<u>Managed</u>					
<i>Ejido</i> El Consuelo, site 1	16.95	1.9**	14, 21	0.169	-0.704
<i>Ejido</i> El Consuelo, site 2	9.68*	1.6	7, 13	0.12*	0.71**
<i>Ejido</i> El Consuelo, site 3	9.81*	2.0**	6, 11	0.15*	-0.468
<i>Ejido</i> Panalachi, Egochi 1	15.1*	1.7	12, 19	0.175	0.53
<i>Ejido</i> Panalachi, Egochi 2	16.21	1.71	13, 20	0.18	-0.23
<i>Ejido</i> Panalachi, Egochi 3	20.68	1.77	18, 24	0.2	-0.64
<i>Ejido</i> La Laguna, site 1	14.83	1.38*	13, 18	0.14	3.41**
<i>Ejido</i> La Laguna, site 2	13.61*	1.8	11, 18	0.18	0.12
<i>Ejido</i> La Laguna, site 3	12.21*	1.7	9, 16	0.13	1.06**
<i>Ejido</i> Magullachi, site 1	22.81	1.35*	21, 16	0.179	-0.12
<i>Ejido</i> Magullachi, site 2	23.91	1.44	22, 27	0.181	0.71**
<i>Ejido</i> Magullachi, site 3	19.62	1.27*	18, 23	0.121	0.001
<i>Ejido</i> Magullachi, site 4	15.52	1.76	13, 19	0.175	0.53
<i>Ejido</i> Molinares, site 1	23.94	1.72	21, 28	0.256**	1.31**
<i>Ejido</i> Molinares, site 2	18.54	2.19**	15, 23	0.243	0.47
<i>Ejido</i> Molinares, site 3	20.05	1.67	17, 24	0.188	1.53**
<i>Ejido</i> Molinares, site 4	21.53	1.95**	18, 26	0.231	-0.53
<i>Ejido</i> Panalachi, site 1	24.02**	2.34**	20, 29	0.326**	-1.23*
<i>Ejido</i> Panalachi, site 2	17.13	1.42	15, 20	0.148	1.41**
<i>Ejido</i> Panalachi, site 3	17.03	1.52	15, 20	0.117*	-0.23
<i>Ejido</i> Sisoguichi, site 1	17.94	1.65	15, 21	0.138	-0.82
<i>Ejido</i> Sisoguichi, site 3	12.31*	1.7	9, 16	0.11*	-1.3*
<i>Ejido</i> Sisoguichi, site 2	15.91	1.64	13, 19	0.133	-0.7
Total	128.01	27.141	93, 182		

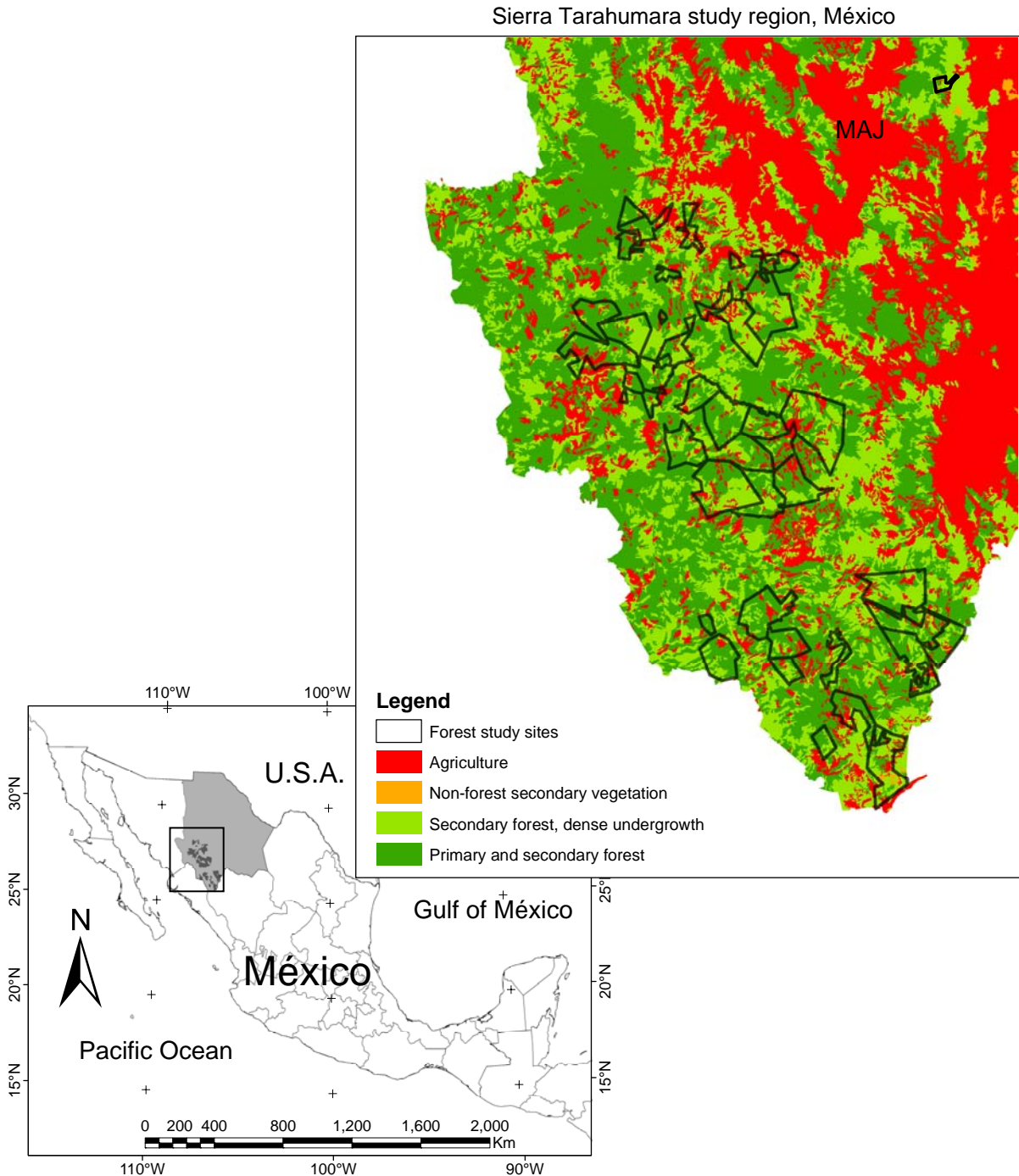
* One of six lowest estimates among the 32 sites.

** One of six highest estimates among the 32 sites.

Appendix H

Map of the study region

Geographic location of the Sierra Tarahumara, México. The lower map shows the general location of the study region, and the blown-up map shows land cover data for 2001 and the forest study sites. Majalca National Park (MAJ) is on top right corner.



*Majalca NP-Sierra Tarahumara-Chihuahua MX,
2008-2009 / Greenbelt MD, Summer 2008 / Fernow
Hall-Ithaca NY, Fall 2009, 2010, Spring 2011 /
Sempach CH, February 2010 / Chihuahua, January
2011 / Rice Hall-Ithaca NY, Summer-Fall 2011.*