BALANCING BIODIVERSITY AND HUMAN LAND USE:

EFFECTS OF FIRE, GRAZING AND HARVEST ON PLANT INDIVIDUALS, POPULATIONS AND COMMUNITIES IN THE WESTERN GHATS, INDIA

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF
THE UNIVERSITY OF HAWAIʻI AT MĀNOA IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

IN

BOTANY

(ECOLOGY, EVOLUTION AND CONSERVATION BIOLOGY)

MAY 2012

By
Lisa Mandle

Dissertation Committee:
Tamara Ticktin, Chairperson
Curtis C. Daehler
David C. Duffy
Rebecca Ostertag
Andrew D. Taylor

Keywords: ecosystem services, functional diversity, integral projection model, non-timber forest product, *Phoenix loureiri*, savanna woodland

ACKNOWLEDGEMENTS

I am grateful for the many people who helped in the development and completion of this work and who made my time as a graduate student a wonderful adventure. I am especially indebted to my adviser Tamara Ticktin for her endless encouragement, advice and enthusiasm. I don't think there could ever be a more supportive and caring adviser! Thank you to my committee – Andy Taylor, Becky Ostertag, Curt Daehler and Dave Duffy – for valuable feedback and ideas from beginning to end.

This work would not have been possible without the knowledge, skills and dedication of my collaborators at Keystone Foundation and the Ashoka Trust for Ecology and the Environment (ATREE). I am particularly grateful for the assistance I received from Anita Varghese, Snehlata Nath, Pratim Roy, Sumin George Thomas, Siddappa Setty, R. Ganesan and Ankila Hiremath. Thank you to everyone who helped with data collection, especially B. Mahadesh, Basavanna, Mahadevan, K. Sudhakar, T. Aradukuttan, Kumbegowda, Kettegowda and Javanna, and to local community members who shared their knowledge and many cups of tea with me. Thank you also to the Karnataka and Tamil Nadu Forest Departments and the Palaniappa Estate for permission to conduct fieldwork.

I feel incredibly fortunate to have been part of such an inspiring and talented lab group at University of Hawai‘i and am grateful for the support of Ticktin lab members past and present, especially Isabel Schmidt, Orou Gaoue, Anita Varghese, Vandana Krishnamurthy, Georgia Hart, Tamara Wong, Shimona Quazi, Katie Kamelamela, Heather McMillen, Leyla Cabugos and Clay Trauernicht.

Plant identification by R. Ganesan, Shiny Rehel and L. Rasingam was critical to completing this work. Brian Chrysler processed camera trap photos with astonishing, and appreciated, speed. My dissertation was much improved by guidance and feedback on analyses and interpretation from Andy Taylor and the mixed-effects modeling group, as well as Orou Gaoue and the IPM group. I thank Eileen Herring for assistance researching the history of mountain date palm harvest. For invaluable help with paperwork and logistics, I owe many, many thank yous to Patty Bedoya, Kori-Ann Phillips, Lucy Kida, Rena Duhl and Gerry Nakamoto, as well as Graduate Division Deans Patricia Cooper and Peter Garrod. Thank you to Gretchen Daily and her lab group for providing a stimulating place from which to work in California.

Thank you to the many people whose generosity and hospitality (and delicious food!) have made me feel at home around the world, including Isabel Schmidt and Alexandre Sampaio, Henrietta and Dave Whitcomb, Cliff and Sharon Hu, Anita and Merab Varghese, Vandana Krishnamurthy, Vishnu Ramaprasad and the Krishnamurthy family, Leyla Cabugos, Helen Felsing and Wayne Watkins, SamitaVasudevan and Kunal Sharma, Renuka, Samira Agnihotri, K. Sudhakar and Mageshwari, Dave Elliott and Daniela Dutra Elliott, Nat Bletter and Abby Cuttriss, Courtney Angelo, Jennifer Bufford, Marian Chau and Matt Lurie.

I am grateful to my family for their unwavering support for what I do, even when I don't always succeed in making it clear what exactly that is. And to Chris for sticking with me and being a source of sanity throughout.

This work was supported by funding from the National Science Foundation in the form of a Graduate Research Fellowship (grant no. 0822443) and an International Dissertation Enhancement Award (grant no. OISE-1104989); the Society for Economic Botany; the W.T. Yoshimoto Foundation; Maybelle Roth and Sarah Ann Martin scholarships from ARCS Foundation; as well as several sources within the University of Hawai‘i including Beatrice Krauss and Charles H. Lamoureux awards from the Botany Department; the Ecology, Evolution and Conservation Biology Program (National Science Foundation grant DGE05-38550 to K.Y. Kaneshiro); the Arts and Sciences Advisory Council; and the Graduate Student Organization.

ABSTRACT

Effective conservation of the world's remaining diversity requires determining to what degree preservation of biodiversity is compatible with meeting human needs. However, there is still a limited scientific understanding of the compatibility and trade-offs between biodiversity conservation and human land use. I used the case study of wild mountain date palm (*Phoenix loureiri* Kunth) in savanna woodland ecosystems of India's Western Ghats biodiversity hotspot to investigate the ecological effects and conservation implications of fire, grazing and palm leaf harvest – three widespread and commonly co-occurring forms of land management activities in the tropics. I integrated results from a manipulative experiment, a regional observational study and mathematical models to determine how the effects of and interactions among these activities scale from palm individuals to populations to plant communities. I found that mountain date palm populations exhibited resilience to fire and low intensities of harvest and grazing, indicating a high potential for sustainable harvest. Individual-level compensatory growth, vegetative reproduction and density-dependent survival contributed to palm population resilience to disturbance. At the community level, areas managed for palm leaf harvest and livestock grazing retained similar levels of plant species and functional diversity to areas protected from these activities. However, the combined effects of fire, wild plant harvest and livestock grazing were associated with reduced tree cover and diversity and increased understory diversity. I also found evidence for a trade-off between maximizing the growth of mountain date palm populations and maximizing tree species diversity, mediated by the relationship between fire and canopy openness. Overall, my results suggest that human-managed savanna woodlands can both support mountain date palm leaf harvest and contribute to conservation objectives. Promoting a mosaic of land management practices would be an effective way to balance the need to preserve plant diversity with the potential for these ecosystems to contribute to the livelihoods of local people. Protected areas with reduced human land use may more effectively conserve tree cover and tree diversity, while areas managed for plant harvest and livestock grazing could still maintain substantial overall plant diversity and provide connectivity between protected areas, while additionally providing benefits to local people.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1. INTRODUCTION

Human activities today have an unprecedented effect on ecosystem processes and biodiversity around the world (Sanderson *et al.* 2002; Ellis & Ramankutty 2008). Along with our intensifying impact on ecosystems, there is a growing awareness than our well-being is critically linked to biodiversity and ecosystem processes (Millennium Ecosystem Assessment 2005). Protected areas are inadequate for conserving much of the world's remaining biodiversity, which predominantly exists in human-managed systems (Chape *et al.* 2005; Gardner *et al.* 2009; Mora & Sale 2011). Effective conservation of this remaining diversity requires determining to what degree preservation of biodiversity is compatible with meeting human needs.

Conservation decisions have thus become increasingly motivated by the aim to both preserve native biodiversity and enhance the provision of ecosystem services. These management goals are often assumed to be compatible or even complementary (Mace *et al.* 2011). A number of recent studies have suggested that increased species richness enhances the rates of ecosystem processes that underlie ecosystem services (Balvanera *et al.* 2006; Hector & Bagchi 2007; Isbell *et al.* 2011). At least over the short term, however, many individual ecosystem processes and services depend on the abundance of particular species or groups of species rather than the richness or diversity of species in the ecosystem (Garnier *et al.* 2004; Leisher *et al.* 2010; Laughlin 2011). Changes to plant communities resulting from land management for a select set of ecosystem services from a particular set of species, such as agricultural production, may reduce biodiversity as well as compromise future ecosystem resilience and provision of ecosystem services over the long term (Foley *et al.* 2005). Managing a single ecosystem to maximize both native biodiversity and desired ecosystem services may rarely be possible (Polasky *et al.* 2011). At the same time, we have only a shallow understanding of the relationships among biodiversity, ecosystem processes and ecosystem services (Mace *et al.* 2011). Quantifying trade-offs among ecosystem services and biodiversity conservation, as well as determining the mechanisms underlying these trade-offs, will be critical to managing ecosystems for the benefits of both people and biodiversity.

In my dissertation, I use the case study of mountain date palm (*Phoenix loureiri* Kunth) in savanna woodland ecosystems of the Western Ghats, India to investigate the ecological effects and conservation implications of three common land management activities. Specifically, I investigate the effects of and interactions among fire, grazing and palm leaf harvest, scaling from palm individuals to populations to plant communities. I then assess potential trade-offs between managing for a species-based ecosystem service (palm leaves harvested to make brooms) and conservation of native plant diversity.

Biodiversity and human land use in the Western Ghats, India

The Western Ghats region of India is well-suited for investigating trade-offs between human land use aimed at acquiring benefits from a limited set of species and conservation of overall biodiversity. The Western Ghats makes up the majority of the Western Ghats and Sri Lanka biodiversity hotspot, an area of high conservation priority (Mittermeier *et al.* 2005). Covering less than 6% of India's land area, the Western Ghats contains over 30% of the country's plant and animal species (Bawa *et al.* 2007). It includes critical habitat for endangered megafauna such as the Asian elephant (*Elephas maximus*) and tiger (*Panthera tigris*).

The region has a long history of human land use – people have been present in the area for over 12,000 years (Chandran 1997). Current human population densities are high, greater than any other biodiversity hotspot (Cincotta *et al.* 2000). There is also a history of traditional conservation practices such as the recognition of sacred groves (Gadgil & Vartak 1976). With many human communities living within and near forests, management aims to balance conservation of the region's unique flora and fauna with the livelihood needs of local people.

In an attempt to meet these multiple goals, many of the region's forests have been designated as protected areas. Other areas are managed as reserve forests. Communities living near and within reserve forests are frequently permitted to graze livestock and harvest select wild species for commercial purposes in these areas. In contrast, human activities within protected areas are more restricted and commercial harvest of wild plants is generally been banned, though harvest for household use is common (Bawa *et al.* 2007).

The recent passage and implementation of India's Forest Rights Act is likely to lead to changes in human land use across much of India's remaining forests. This law recognizes local communities' rights to manage natural resources and biodiversity and provides for joint management of these resources with the state (Bawa *et al.* 2011). It represents a substantial change in government policy, which historically sought to exclude local communities from forest areas while managing forests for commercial products such as timber (Saxena 1999). The Forest Rights Act provides an opportunity for the explicit consideration of trade-offs between biodiversity conservation and human benefits in management decisions.

Land use and conservation in seasonally dry tropical ecosystems

Previous research on the relationship between biodiversity and human land use has demonstrated that human-managed areas can contribute to the conservation of at least some degree of native plant, bird, insect and mammal diversity (e.g., Estrada & Coates-Estrada 1997; Gascon *et al.* 1999; Mayfield *et al.* 2005), including in the Western Ghats (Ranganathan *et al.* 2008; Anand *et al.* 2010). However, these studies have focused primarily on tropical moist forests. Less is known about the compatibility of human land use and conservation in seasonally dry tropical ecosystems. Although tropical dry forests, woodlands and savannas harbor lower levels of plant diversity than moist forests, these ecosystems are centers of land conversion and fragmentation, provide important provisioning and regulating ecosystem services, and are less protected than moist forests (Murphy & Lugo 1986; Chape *et al.* 2005; Balvanera *et al.* 2010). As a result their conservation in human-managed landscapes is especially critical.

My dissertation research was located in tropical savanna woodlands of the southern Western Ghats within the states of Tamil Nadu and Karnakata. These plant communities have traditionally been classified as tropical dry deciduous forests. However, there is a current preference for classification of such communities with C_4 grasses in the understory and a largely fire-resistant tree community as mesic savannas or savanna woodlands (Ratnam *et al.* 2011). Given the range of canopy openness I observed

(20-70%) I refer to these communities as savanna woodlands. The Western Ghats has a tropical monsoonal climate, receiving precipitation from both the southwest and northeast monsoons between June and November. The dry season extends from February to April. Rainfall ranges from 900 to 1500 mm, and varies with elevation (Bawa *et al.* 2007). In the Western Ghats, these seasonally dry tropical ecosystems are important sources of fuelwood, livestock fodder and non-timber forest products (NTFPs) for local communities (Davidar *et al.* 2010) as well as critical habitat for endangered megafauna (Das *et al.* 2006).

Fire, grazing and non-timber forest product harvest are widespread, often co-occurring, land management activities

Fire as a natural and anthropogenic disturbance

Fire is a globally common and widespread disturbance and a natural occurrence in many ecosystems (Bond *et al.* 2005). Fire regime – including the frequency, intensity, timing and extent of fire – is an important determinant of plant community structure and composition (Whelan 1995; Bond & Keeley 2005; Bond *et al.* 2005). Since prehistoric times, humans have altered fire regimes in multiple ways to benefit land-use activities (Willis & Birks 2006). In some areas, people have suppressed fire to prevent property damage (Kareiva *et al.* 2007). In many other places, people set fire deliberately for numerous reasons, including to increase fodder for livestock, to improve visibility of and fodder for game animals, to manage agricultural lands and to promote NTFPs (e.g., Yibarbuk *et al.* 2001; Saha & Howe 2003; Schmidt *et al.* 2007; Fulé *et al.* 2011).

In the savanna woodlands and dry deciduous forests of the Western Ghats, fires tend to be low-intensity surface fires, consuming grasses and leaf litter in the understory (Kodandapani *et al.* 2009). These ecosystems have an average of a 3 year fire-return interval, representing an apparent threefold increase in fire frequency over the 20th century (Kodandapani *et al.* 2004; Sinha & Brault 2005). These fires are primarily anthropogenic in origin and are currently set primarily for promoting livestock fodder and NTFP harvest (Hiremath & Sundaram 2005; Schmerbeck & Seeland 2007; Roveta 2008).

Grazing is the most extensive land use globally

Over 25% of the Earth's land surface is managed for livestock grazing (Asner *et al.* 2004). Grazing lands are the most extensive land use type across the globe, having increased in area six-fold over the past three centuries. The intensity and ecological effects of grazing are known to interact with fire regime, vegetation and climate (e.g., Wilsey 1996; Díaz *et al.* 2007; Fuhlendorf *et al.* 2009; Midgley *et al.* 2010; Kirkpatrick *et al.* 2011). Given the vast extent of grazing lands, understanding the effects of grazing and interactions with other forms of disturbance on vegetation is important to effectively managing these systems for their benefits to humans and for the conservation of the high levels of diversity they can maintain.

In the Western Ghats, cattle and goats are frequently grazed within and bordering reserve forests and protected areas (Bawa *et al.* 2007). Cattle are valued primarily for the dung they produce, which is used for fertilizer, and as draft animals (Madhusudan 2005). In the Western Ghats, as throughout India and in many areas managed for livestock around the word, livestock and wild ungulates occupy the same land and may rely on the same resources (Madhusudan 2004; Dave & Jhala 2011; Odadi *et al.* 2011).

Non-timber forest product harvest in multi-use landscapes

Despite the millions of people who rely on NTFPs for subsistence or income and the thousands of commercially traded, wild-harvested NTFP species, we still know relatively little about the consequences of harvest for plant populations or the ecosystems in which they occur (Ticktin 2004; Schmidt *et al.* 2011). On the one hand, harvest of wild plants – logging excluded – ranks as one of the greatest threats to plant diversity (Brummit & Bachman 2010). On the other hand, managing ecosystems for the harvest of NTFPs has been considered to be more compatible with biodiversity conservation than other competing land uses like timber extraction or conversion to agricultural land (Myers 1988). Understanding the ecological effects of harvest is further complicated by the fact that NTFP harvest often occurs within landscapes managed for multiple uses, such as fuelwood collection, timber harvest and livestock grazing (Endress *et al.* 2004; Gaoue & Ticktin 2007; Schmidt *et al.* 2007). Distinguishing the effects of harvest from other co-occurring land uses has been challenging. Only a few studies have investigated interactions between harvest and other disturbances (Farrington *et al.* 2009; Martínez-Ramos *et al.* 2009; Schmidt 2011).

In the Western Ghats, NTFP harvest represents a substantial source of income to many communities living within or near forest areas (Hegde *et al.* 1996; Biswal 2009; Girish & Girish 2009). Poorer households are especially reliant on NTFP harvest (Shaanker *et al.* 2004a). Though there are many commercially important NTFPs that are harvested at high intensities in the Western Ghats (e.g., Shankar *et al.* 1998b; Nath 2000; Shaanker *et al.* 2004b), ecological information about the effects of harvest is available only for a limited number of species (Murali *et al.* 1996; Shankar *et al.* 1998b; Shaanker *et al.* 2004b; Varghese & Ticktin 2008; Varghese *et al.* in press). Detailed studies of the effects of harvest on population dynamics are even rarer (but see Sinha & Brault 2005). In the Western Ghats, as elsewhere in the tropics, there is a need for a better understanding of the conditions under which sustainable NTFP harvest can occur, providing benefits to local people without compromising the existence of harvested populations or the functioning of the ecosystems in which they occur.

Palms in multi-use landscapes

Palms (Arecaceae) are a particularly useful system in which to study the effects of multiple forms of disturbance on plant demography because palm populations commonly experience multiple natural and anthropogenic disturbances including fire, harvest of leaves, fruit and stems, and grazing by livestock and wild animals (Endress *et al.* 2004; Souza & Martins 2004; Pulido *et al.* 2007; Lopez-Toledo *et al.* 2011). Palms are an important part of ecosystems around the globe and one of the most-used plant groups in the tropics, providing valuable resources for large numbers of people (Balick & Beck 1990). Because of the prevalence of palms' occurrence and use, knowledge of palms' responses to multiple forms of disturbance can have widespread management implications. Compared to other kinds of plants and other plant parts harvested, the effects of leaf harvest on palm population dynamics have been relatively well studied (Zuidema *et al.* 2007; Schmidt *et al.* 2011). However, studies of the effect of mammalian herbivory and fire on palm population dynamics are much less common, despite the prevalence of these forms of disturbance for palms growing in human-managed areas

(Montúfar *et al.* 2011). More importantly, as studies on interactions among disturbances are rare across all plant species, little is known about interactions among these forms of disturbance on palms.

In my dissertation, I focus on mountain date palm (*Phoenix loureiri* Kunth). Mountain date palm is widely distributed across sub-Himalayan Asia, from India through southern China into Taiwan and the Philippines, occurring from sea level to 1700 m in open grasslands and scrublands or forest understory (Barrow 1998). The species is dioecious and can reproduce clonally by basal suckers. In South India, mountain date palm has been commercially harvested for the manufacture of brooms since at least the mid-20th century (Sundararaj & Balasubramanyam 1986). It continues to be harvested in large quantities, and where it occurs, it can be one of the most harvested NTFP in terms of biomass (Nath 2000; Shaanker *et al.* 2004a).

Importance of understanding interactions among disturbances for plant demography

In the savanna woodlands of the Western Ghats, as in many other tropical human-modified ecosystems, fire, grazing and wild plant harvest commonly co-occur within the same area. Each factor individually has the potential to significantly impact plant populations and communities. Despite this, studies of plant demography rarely test for the impact of these disturbances on population dynamics (Buckley *et al.* 2010). When such disturbances are included, their effects are nearly always determined independently and only integrated through simulation (Sinha & Brault 2005; Farrington *et al.* 2009). Given the tendency for non-additive interactions among ecological processes (Agrawal *et al.* 2007), predicting the outcome of these multiple forms of disturbance from studies of their independent effects is unlikely to produce accurate results. Studies testing interactions among drivers of plant demography are needed to make appropriate management recommendations that can effectively conserve plant populations in the face of changing disturbance regimes and environmental conditions.

Importance of understanding effects of human land use at multiple ecological levels

To date, ecological studies of the effects of grazing, fire and their interaction with each other and with environmental conditions have primarily focused at the plant community level (e.g., Saha & Howe 2003; Archibald *et al.* 2005; Díaz *et al.* 2007; Collins & Calabrese 2011). In the tropics especially, there are a limited number of studies of the population-level effects of fire or grazing (Sinha & Brault 2005; Staver *et al.* 2009; Schmidt 2011). Knowledge of the individual and interactive effects of grazing and fire at the plant population level is important to understanding the mechanisms underlying plant populations' resilience to these forms of disturbance.

In contrast, despite a number of studies of the population-level effects of NTFP harvest effects, few studies have considered the effects on surrounding communities (see review by Ticktin 2004). It is frequently assumed that plant harvest is ecologically sustainable as long as the population of the plant being harvested does not decline. However, this assumption fails to consider that a specific population may be stable or even growing under harvest conditions that coincide with declining plant biodiversity, an increasing presence of non-native species or other conditions that from a community- or ecosystem-level perspective are not considered sustainable. An integrated understanding of the consequences of fire, grazing and harvest at multiple ecological levels is necessary in order to manage both for the benefits these activities provide to people, often based on the biomass of a select set of harvested or grazed plant species, and for conservation of diversity at the plant community level.

Research questions and dissertation outline

In order to investigate the interactive ecological effects of human land management activities and potential trade-offs between ecosystem services and biodiversity, I present results from a manipulative experiment, a regional observational study and mathematical models. I use these approaches to ask:

1. What are the impacts of and interactions among fire, grazing and leaf harvest on mountain date palm individuals?
2. How do the effects of fire, grazing and leaf harvest on mountain date palm individuals translate into effects at the population level?
3. How do differences in land management history in terms of fire history, livestock grazing and non-timber forest product (NTFP) harvest affect the structure, composition and diversity of plant communities?

4. What do these results suggest about the capacity to manage the savanna woodland ecosystems in which mountain date palm occurs both for mountain date palm leaf harvest and conservation of native plant diversity?

Chapter 2 of this dissertation describes the ecological context in which mountain date palm leaf harvest occurs in South India. Along with co-authors from two collaborating Indian non-governmental environmental organizations (Keystone Foundation and the Ashoka Trust for Research in Ecology and the Environment), I bring together data on the intensity of harvest in the region, palm harvest and land management practices, and the ecological context of harvest.

In Chapter 3, I present the results of a two-year manipulative field experiment in which I test for the effects of and interactions among fire, grazing, palm leaf harvest as well as abiotic environmental conditions on palm individuals.

Chapter 4 moves from the individual to the population level. In this chapter, I use integral projection models (IPMs) based on two years of data from 14 palm populations and over 2,300 palms to explore how the individual-level effects of and interactions among fire history, grazing and leaf harvest scale-up to influence mountain date palm population dynamics.

Together Chapters 5 and 6 investigate the consequences of land management for the diversity and composition of plant communities using results from an observational study. I assess differences in species richness and diversity among areas with different histories of fire, livestock grazing and NTFP harvest in Chapter 5. Here I also test for differences in the geographic range of species (as a proxy for rarity and species-based conservation value) with variation in land management history. To better understand the consequences of differences in species composition and diversity for ecosystem processes and response to disturbance, I assess differences in the functional composition and functional trait diversity with land management across the same plant communities in Chapter 6.

I conclude with Chapter 7, in which I synthesize my findings from the preceding chapters and discuss their implications for managing the woodland-savanna ecosystems for the dual goals of providing benefits from mountain date palm leaf harvest to local people and conserving the native plant diversity within a biodiversity hotspot. In addition, I summarize the contributions of my research to the fields of ecology and conservation biology, discuss the limitations of this study and suggest future lines of research for understanding trade-offs between ecosystem services and biodiversity conservation.

CHAPTER 2. THE IMPORTANCE OF CONSIDERING THE BROAD ECOLOGICAL CONTEXT OF HARVEST FOR COMMON PLANT SPECIES: MOUNTAIN DATE PALM (*PHOENIX LOUREIRI*) LEAF HARVEST IN SOUTH INDIA

Lisa Mandle, Tamara Ticktin, Snehlata Nath, Siddappa Setty and Anita Varghese

Abstract

Many economically important non-timber forest products (NTFPs) come from widespread and common plant species. Harvest of these species is often assumed to be sustainable due to their commonness. However, because of the ecological roles of common species, harvest may impact and be impacted by ecological interactions at broader scales, which are rarely considered when evaluating the sustainability of harvest. We use a case study of the mountain date palm (*Phoenix loureiri*), harvested in South India to produce brooms, to illustrate how intensive harvest of a common species interacts with other anthropogenic management practices, plant-animal interactions and surrounding environmental conditions. Fire return interval, herbivory by wild animals and livestock, as well as the light environment in which harvest occurs must be considered when assessing the sustainability of mountain date palm harvest. Ecosystem- and community-level properties and processes should to be incorporated into assessments of the sustainability of NTFP harvest more frequently – especially for widespread and common species – in order to ensure that their important economic and ecological roles are maintained.

Introduction

Widespread and abundant non-timber forest product (NTFP) species have a high potential to be harvested sustainably (Cunningham 2001). Because of their high levels of biomass, however, these same species are likely to influence ecosystem processes and have significant interactions with other components of the ecological community, interactions which may be altered by harvest (Gaston & Fuller 2008; Gaston 2010). If promoting NTFP harvest is meant to contribute both to local livelihoods and to the conservation of ecosystems, as is often the case (Leisher *et al.* 2010), it is critical to assess the sustainability of harvest from an ecosystem perspective, especially for common species.

Many heavily harvested NTFP species are locally abundant and/or widely distributed. For example, several species of shrubs, grasses and reeds that are harvested to make hand brooms in South Africa are locally dominant, respond positively to disturbances such as grazing or fire, or are otherwise considered “weedy” (Shackleton 2005). Similarly, the multi-use palm *Phoenix reclinata* is widely distributed across temperate and tropical Africa (Barrow 1998) and can be one of the most abundant species where it occurs (Kinnaird 1992). Studies of the ecological impacts of harvest of these kinds of common species are limited compared to studies that focus on species perceived to be rare or in decline, often under the expectation that abundant and disturbance-tolerant species have a high potential for sustainable harvest (Reid 2005; Shackleton 2005; Shackleton *et al.* 2009).

While there may be a high potential for sustainable harvest of common species from a population perspective, high levels of harvest are particularly likely to alter species interactions and ecosystem processes. High levels of fruit or seed harvest can have negligible impacts on populations of long-lived and clonally reproducing plant species (Ticktin 2004), but may affect frugivores, including birds (Mogenburg & Levey 2003) and primates (Kinnaird 1992). When harvest involves removing large amounts of biomass from an ecosystem, this may also impact nutrient cycles (O’Hara 1999). Despite growing recognition that NTFP harvest affects and is affected by management practices and ecological interactions at multiple levels, these interactions are rarely studied above the population level (Ticktin 2004). Understanding the larger ecological context in which harvest of common NTFP species occurs is necessary to devise appropriate management plans to maintain both the economic and ecological roles of such species.

We use a case study of mountain date palm (*Phoenix loureiri* Kunth, formerly *P. humilis)* to illustrate the importance of considering the broad ecological consequences of harvesting common NTFP species. Mountain date palm is a widespread and common species, heavily harvested for its leaves in India’s southern Western Ghats. Information about the ecology, current harvesting intensities and management practices of mountain date palm is not available. We integrate available data on: 1) the extent and levels of commercial harvest, 2) local management practices, and 3) the ecological context in which harvest occurs to demonstrate how a framework that considers harvest in the context of ecological communities and ecosystems is important for assessing the impacts of harvest of common NTFP species.

Methods

Study species

Mountain date palm often inhabits disturbed environments and is widely distributed across sub-Himalayan Asia from India through southern China into Taiwan and the Philippines, occurring from sea level to 1700 m in open grasslands and scrublands or forest understory (Barrow 1998). Although it can reach heights of up to 5 m, in dry habitats it often remains short-stemmed and shrubby, reproducing vegetatively.

Known locally in Tamil as *seemar* or *eecham* and in Kannada as *porake* or *echalu*, leaves of the mountain date palm have been commercially harvested for the manufacture of brooms in South India since at least the mid-20th century (Sundararaj & Balasubramanyam 1986). High levels of harvest have led to concerns that this species could become rare (Padmanabhan & Sudhersan 1988). Mountain date palm continues to be harvested in large quantities; where it occurs, it can be one of the most harvested NTFP in terms of biomass (Nath 2000; Shaanker *et al.* 2004a). Mountain date palm leaves, along with other NTFP, provide an important source of income to local communities in the southern Western Ghats, especially those living in and near government-owned forests (e.g., Nath 2000; Biswal 2009).

Study area

Our study focuses on the southern part of the Western Ghats biodiversity hotspot (Myers *et al.* 2000), including Tamil Nadu and Karnataka (Figure 2.1). Here, mountain date palm occurs primarily in grasslands, savannas and dry deciduous forests on rocky hill slopes. Commercial harvest of mountain palm leaves by local indigenous (*adivasi*) communities takes place in Reserve Forests managed by the Forest Department. Mountain date palm is also found in protected areas where commercial harvest is commonly prohibited.

In Tamil Nadu, harvest is managed through Village Forest Committees (VFCs) formed through the Joint Forest Management Process in the 1980s. Each VFC has an area demarcated from where commercial harvest is allowed during a particular season. If the VFC has adequate funds, it pays harvesters to collect leaves and then auctions the leaves to the highest bidder among registered forest contractors. If the VFC lacks funds to pay harvesters up front, it will auction the right to the leaves to be collected to a contractor, and then use an advance from the contractor to pay wages to harvesters. In Karnataka, harvest is run by co-operative societies called LAMPS (Large Scale Adivasi Multi Purpose Societies), which organize the collection and sale of NTFP in a similar manner. The Indian government initiated the organization of LAMPS in 1971 to promote development of local indigenous groups through marketing of NTFPs, provision of credit, agricultural inputs and rationed goods.

Data collection

In an attempt to obtain a holistic view of mountain date palm leaf harvest in the region, we bring together data from multiple sources. These sources include: 1) Records from five VFCs (Tamil Nadu) and three LAMPS (Karnataka) on the amount of mountain date palm leaves purchased and price paid to harvesters. These records include harvest in and around the Sathyamangalam Reserve Forest in Tamil Nadu, and the Biligri Rangaswamy Temple Wildlife Sanctuary (BRT) and the Male Mahadeshwara Hills Reserve Forest in Karnataka (Figure 2.1). 2) Semi-structured interviews conducted with 13 individual harvesters in 2009 and discussions with two harvester groups in 2011 about harvesting practices and the land-management context in which harvesting occurs. These interviews were conducted in local languages with the help of an interpreter. We obtained informed consent from interviewees and Human Subjects Review Board exemption (Appendix K). 3) Observations of harvesting and marketing practices based on our (S.N., A.V. and S.S.) combined decades of work on conservation and livelihoods in the Western Ghats. 4) Published documents, as well as gray literature on the subject of NTFP harvest in the Western Ghats. 5) Experimental and observational ecological studies of mountain date palm demography (Appendix A, Chapters 3 and 4).

Calculating the extent of harvest

Levels of harvest were recorded in terms of number of broom bundles in Karnataka and metric tonnes of leaves harvested in Tamil Nadu. We converted broom bundles to metric tonnes using measures of palm leaves per kilogram (Keystone Foundation unpublished data). We also estimated harvest impacts in terms of number of leaves harvested, number of plants harvested and area under harvest using 95% confidence intervals for mean leaves harvested per palm and per hectare from eight palm populations in areas with commercial harvest across the study area from 2009-2011.

Results and discussion

Extent of and trends in mountain date palm harvest levels

Our results show mountain date palm is both widely and heavily harvested across the southern Western Ghats. Mountain date palm leaves are currently harvested commercially from numerous reserve forests in the southern Western Ghats. During the 2009-2010 harvest year, for the eight locations for which we have data, a total of 328 metric tonnes were harvested through the five VFCs in Tamil Nadu and an additional 29 metric tonnes harvested from one LAMP in Karnataka. The documented harvest comprises an estimated 23 million leaves (95% confidence interval: 21-25 million), from 7.5 million plants (95% confidence interval: 6.5-8.6 million). These leaves come from hundreds of hectares of palm habitat (95% confidence interval: 300-1,500).

The quantities of harvest have declined in recent years in all areas (Figure 2.2a), while the price per kilogram has increased (Figure 2.2b). In the Tamil Nadu sites, levels of harvest have declined since 2007 in four out of five areas. During this time, the mass of harvested leaves declined 18.8% in the region as a whole, while the price paid per kilogram increased 16.7%, leading to an overall decline of 5.3% in the total value of leaves harvested (Figure 2.2c). The same pattern of decreasing harvest with increasing prices appears in the Hasanur Range over the past five years, while harvest has ceased in two of three Karnataka areas. Commercial harvest occurred previously in BRT but was banned by the Forest Department after 2004. With the passage of the Forest Rights Act (FRA), communities in BRT are in the process of obtaining the right to resume harvest. As of October 2011, 25 of approximately 62 *gram sabhas* (village assemblies) have obtained NTFP harvest rights under community forest rights provision of the FRA. It is the first case in the country that NTFP collection and conservation rights have been awarded in a protected area.

The harvesters interviewed generally did not perceive a change in availability of palm leaves, or believed that there are more available for harvest now than in the past. However, three of 13 harvesters interviewed individually reported that there was decreased leaf availability due to the invasive plant *Lantana camara* shading out palms (in the Sathyamangalam region of Tamil Nadu) and from increased elephant herbivory (in the Sigur region of Tamil Nadu).

Recent declining levels of palm leaf harvest coupled with rising prices may be due to a number of factors, not necessarily including over-exploitation. Reduced leaf harvest could occur if harvesters are choosing to pursue other economic opportunities, such as wage labor. Opportunities for wage labor have been increasing. For example, with the passage of the Mahatma Gandhi National Rural Employment Guarantee Act (NREGA), which was implemented starting in 2006, rural households are assured 100 days of wage labor per year (NREGA 2005). Mountain date palm leaf harvest occurs primarily in the first half of the year, during the agricultural off-season, which is when people are likely to be taking advantage of NREGA. Levels of harvest may also be declining due to the lack of organization for collection and trade of NTFPs through VFCs, which vary in levels of competency (Keystone Foundation 2009). Harvesters are less likely to collect leaves if it is uncertain they will be paid for their efforts.

A decline in the demand for mountain date palm leaves due to the availability of more modern styles of brooms which are lighter and considered more efficient could also contribute to reduced harvest levels. However, a decline in demand would not explain the increasing value of leaves over time. Finally, reduced availability of leaves due to increased abundance of the invasive *Lantana camara* or other environmental changes could explain the declining levels of harvest in some areas.

Mountain date palm harvesting practices and management

Commercial palm leaf harvest generally occurs during the dry season and agricultural off-season during the first half of the year, though harvesters say they collect leaves for personal use as needed throughout the year. Leaves are only cut if they are at least an arm's length; shorter leaves cannot be used for brooms. Generally, all leaves meeting the size requirement that are not damaged or senescing are harvested from an individual plant. This sometimes includes all fully emerged leaves.

Results integrated from multiple sources show that multiple ecological pathways have the potential to affect the sustainability of mountain date palm leaf harvest. We illustrate some of these possible pathways – which are likely to be relevant to other common NTFP species – in a conceptual diagram (Figure 2.3). Fire is the primary tool used to manage mountain date palm populations for harvest. Harvesters in some areas report setting ground fires to remove palm leaves are that too old and damaged to be harvested, while promoting the growth of new leaves. Harvesters also benefit from low-intensity ground fires set by livestock herders to promote fodder, or from accidental fires that spread. Harvesters report that the quality of palm leaves is higher after ground fires.

Fire is a common management tool for many NTFPs, including palms (Blancas *et al.* 2010). Despite this, studies of NTFP harvest that explicitly consider the relationships among fire, harvest and sustainability are rare (but see Varghese & Ticktin 2008; Schmidt 2011). In the case of the mountain date palm, individual mortality increases following fire (Chapters 3 and 4). Although surviving palm individuals grow more after fire (Chapters 3 and 4), the intensity of leaf harvest as well as the intensity of grazing by both domestic livestock and wild animals may increase following fire (Chapter 4). This could decrease projected population growth rates (Appendix A). Because people prefer to harvest in areas with recent fire, and because grazing on palms increases after fire, the sustainability of harvest of this species cannot be assessed without understanding the role of fire (Figure 2.3a). Increased grazing following fire has also been documented in many grassland and savanna ecosystems (Fuhlendorf *et al.* 2009). The impacts of fire and the fire-grazing interaction on the potential for sustainable harvest should be considered for any NTFP species occurring in areas with frequent fire.

Apart from the use of fire, harvesters did not report any other management activities deliberately used to increase leaf production or enhance palm populations. Competing vegetation is not removed (except to create access paths) and no efforts are made to propagate palms through seeds. Because of the palm's natural abundance, other management efforts were viewed by harvesters as unnecessary.

Leaf harvest and ecological interactions

Results from multiple sources show that mountain date palm is a resource shared by people and wildlife. Interactions between a harvested plant species and its herbivores, pollinators and dispersers must be kept in mind when considering sustainability of harvest (Figure 2.3b). In the case of the mountain date palm, based on interviews with harvesters, this includes endangered species such as the Asian elephant (*Elephas maximus*), as well other animals of conservation concern such as sambar deer (*Rusa unicolor*, vulnerable), gaur (*Bos gaurus*, vulnerable) and sloth bear (*Ursus ursinus*, vulnerable). Elephants eat the fruit, as well as uproot whole plants (Sukumar 1990). While likely not a preferred food source, harvesters report that palm leaves are sometimes grazed by wild ungulates as well as cattle. Porcupines dig up and consume underground parts. Birds and bear eat – and disperse – fruit. Seeds are consumed by rodents. People also eat the apical shoots when plants resprout after fire. On the one hand, harvesting levels that can be sustained over time from a human-plant perspective could have impacts on wildlife if that plant is a shared resource. On the other hand, harvest levels that have negligible effects in one context may be unsustainable under a different set of conditions.

Harvest in a multi-use landscape

Our interviews and observations reveal that mountain date palm leaf harvest is carried out in areas that are managed by local communities for multiple purposes. Palm leaf harvest frequently occurs along with the harvest of other NTFPs, fuel wood collection and livestock grazing. The land management context in which NTFP harvest occurs has the potential to impact palm populations indirectly by altering light availability, soil properties and competitive relationships (Figure 2.3c and d). The impacts of these factors have been assessed in relatively few instances (e.g., Endress *et al.* 2004; Ticktin & Nantel 2004). In the case of mountain date palm, more open canopies are associated with higher levels of flowering and fruiting (Chapter 3). This matches trends found for other understory species (Cunningham 1997; Anten *et al.* 2003; Ticktin

& Nantel 2004), suggesting that the potential for sustainable harvest may be greater in areas with more understory light availability. In addition, activities that create more open canopies – such as fuel wood collection – might increase the potential for sustainable harvest of understory species, but have negative effects on other species (Shankar *et al.* 1998a; Davidar *et al.* 2010). Understanding the impacts of anthropogenic activities that co-occur with NTFP harvest is critical to sustainable management of harvested species and the ecosystems in which they occur.

Conclusions

Like many economically important NTFPs, mountain date palm is a widespread and common species. Palm leaf harvest generally has a high potential for sustainability from a population-level perspective (Zuidema *et al.* 2007; Schmidt *et al.* 2011). While these characteristics would suggest that leaf harvest is unlikely to threaten mountain date palm as a species, its prevalence and the extent of harvest means that it is probable that harvest both impacts and is impacted by larger community- and ecosystem-level processes. Common species have rarely been a priority for conservation efforts (Gaston & Fuller 2008; Gaston 2010). Similarly, harvest of many NTFPs is presumed to be sustainable on the basis of their abundance, without any ecological assessment. In the case of mountain date palm and other common, harvested species, there is a need to establish monitoring before they decline, for the sake of maintaining both their larger ecological role and their economic value to harvesters.

Ultimately, our findings point to two aspects of palm leaf harvest that must be incorporated into assessments of sustainability: 1) Palm harvest occurs in a landscape that is managed for multiple purposes in addition to leaf harvest, and 2) Mountain date palm is involved in other plant-animal interactions that have the potential to both influence and be influenced by leaf harvest. These factors are likely applicable to many other NTFP species harvested from human-managed landscapes, and must be considered when assessing the sustainability of NTFP harvest and developing management plans.

Figure 2.1. Map of areas of commercial harvest for which mountain date palm harvesting practices and/or harvesting levels are documented in this study are shown in dark gray. Harvest occurs in and around the reserve forests (RF) and formerly occurred in the wildlife sanctuary (WLS).The Western Ghats biodiversity hotspot is shown in light gray.

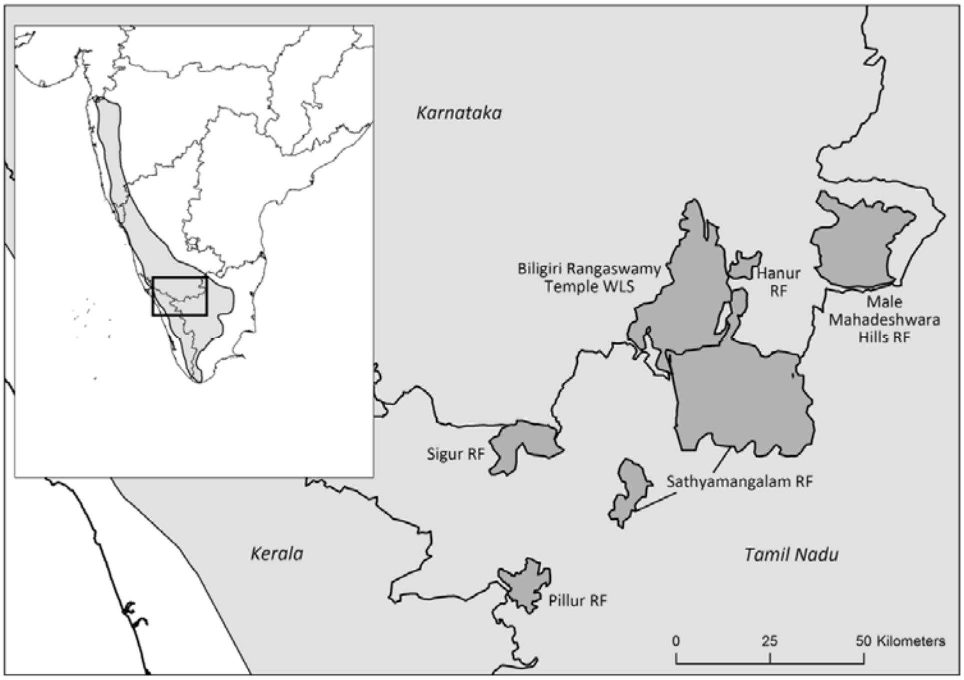


Figure 2.2. Mass (a), unit price (b) and total value (c) of mountain date palm leaves harvested from eight areas in Tamil Nadu and Karnataka from 1990-2010. No points are printed for years without data. Unit prices for all Tamil Nadu sites are the same and so overlap in panel b.

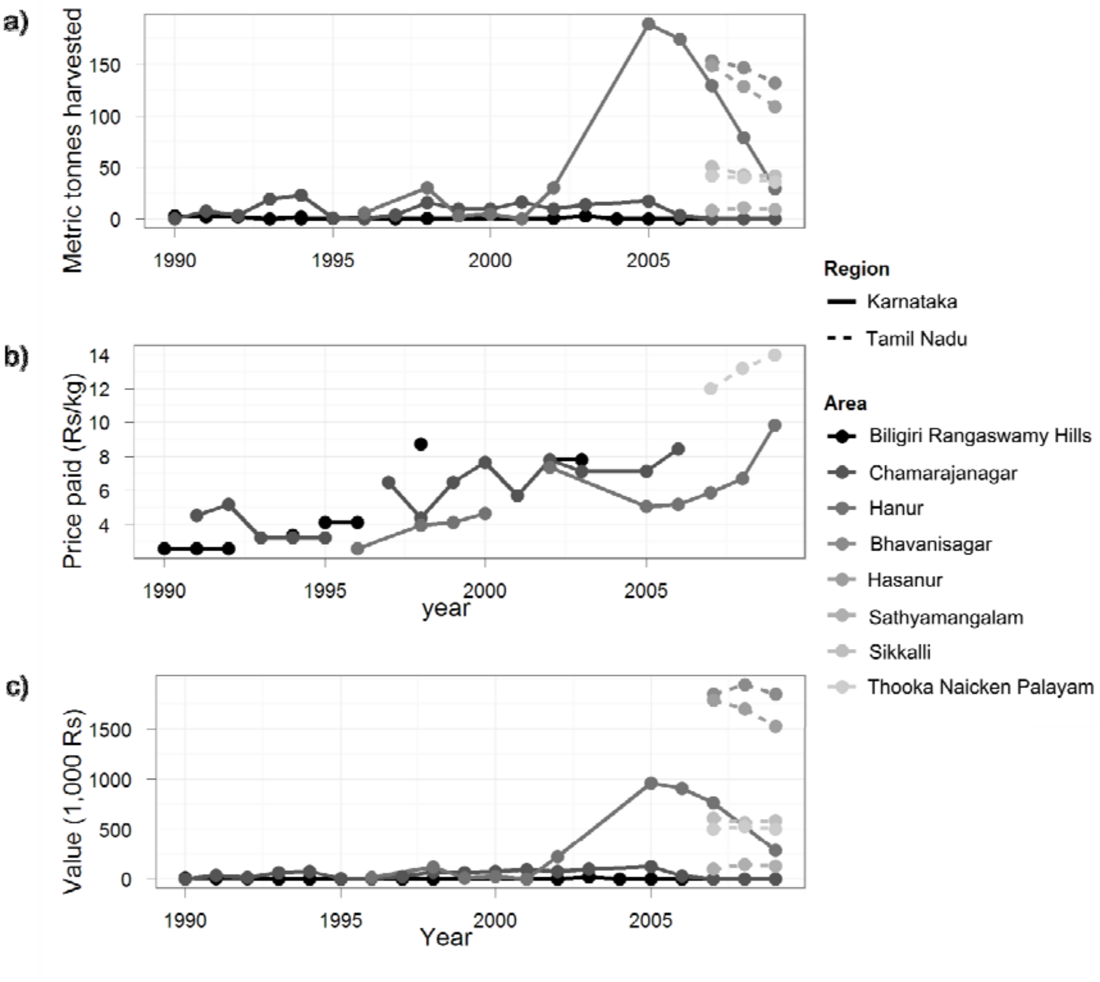
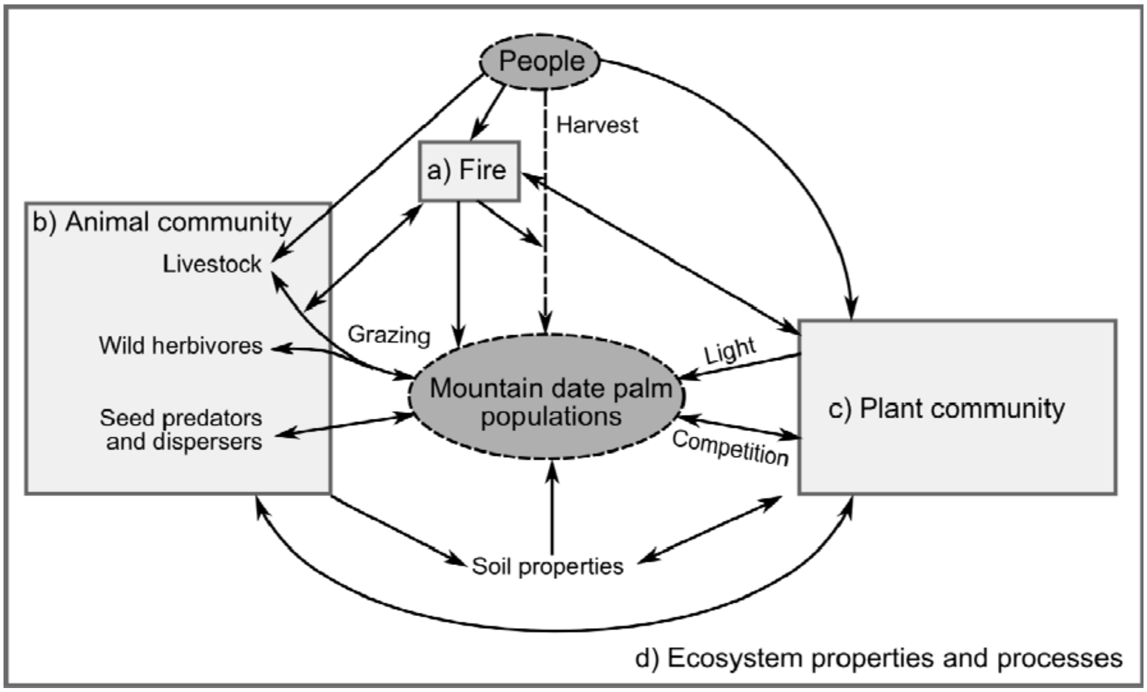


Figure 2.3. Conceptual diagram for assessing the sustainability of mountain date palm harvest. Assessing the sustainability of mountain date palm harvest requires going beyond the direct relationship between people and harvested palm populations (dashed lines). Sustainability of harvest is mediated by the use of fire through multiple pathways (a). Furthermore, harvest both affects and is affected by the surrounding animal (b) and plant (c) communities, as well as the ecosystem-level context in which harvest occurs (d). The management activities of people additionally depend on socio-economic context.



CHAPTER 3. INTERACTIONS AMONG FIRE, GRAZING, HARVEST AND ABIOTIC CONDITIONS SHAPE PALM DEMOGRAPHIC RESPONSES TO DISTURBANCE

Lisa Mandle and Tamara Ticktin

Summary

1. Determining the drivers of plant demography is integral to understanding the processes that shape plant species abundances and distributions. Despite recognition that interactions among drivers have important effects on demographic processes, few demographic studies test for interactions among multiple drivers in plants.

2. We used a factorial-design experiment to study the interactive effects among three common forms of disturbance in the tropics (fire history, grazing and leaf harvest by humans) on the vital rates of *Phoenix loureiri* (mountain date palm) in South India. In addition, we tested for interactive effects among these disturbances, abiotic conditions and plant size. We also tested for non-consumptive effects of grazing and harvest, such as trampling, by measuring the intensities of grazing and harvest in plots open to these disturbances.

3. Intensities of leaf harvest and grazing varied with abiotic conditions and disturbance. Leaf harvest decreased with increasing grazing intensity, suggesting that the net effect of harvest on palm populations is less where it co-occurs with grazing. In areas without fire, plots with lower soil moisture had higher grazing intensities.

4. We found multiple significant main and interactive effects of disturbance on palm vital rates. Palm mortality increased with fire and grazing. Grazing and harvest reduced growth, but growth increased following fire. The negative impact of harvest on palm individuals was reduced when harvest occurred in plots with fire.

5. We found evidence of non-consumptive effects of grazing and harvest on palm growth, likely from trampling. Studies inferring the effects of grazing by comparing grazed and ungrazed individuals within an area where grazing occurs will likely underestimate grazing effects.

6. ***Synthesis.*** Our findings reveal that *Phoenix loureiri* demographic rates are driven by interactive effects among multiple forms of disturbance and abiotic factors, and that the intensities of disturbance are themselves driven by interactions between other forms of disturbance and abiotic factors. These results illustrate that understanding

the effects of, and interactions among, multiple drivers will be key in attempts to mitigate the effects of environmental change on plant species declines.

Introduction

Understanding the processes that shape patterns of species abundances and distributions is a fundamental goal of ecology. Determining the drivers of population dynamics is a critical step towards achieving this goal. Several recent studies have demonstrated that plant populations of the same species exhibit substantial spatial and temporal demographic variation (Buckley *et al.* 2010; Jongejans *et al.* 2010), but we still lack an understanding of the factors responsible for this observed variation.

Moreover, despite a recognized need to understand interactions among drivers in order to determine the mechanisms underlying ecological processes (Agrawal *et al.* 2007; Didham *et al.* 2007), a limited number of studies have examined the interactive effects of drivers on plant demography. The few studies that have explicitly tested for interactions suggest that they are likely to be common and that overlooking them impairs our ability to understand population dynamics (Elderd & Doak 2006; Schleuning *et al.* 2008; Farrington *et al.* 2009; Martínez-Ramos *et al.* 2009). Interactive effects may be sub-additive, with less of an impact in combination than would be predicted from each alone. For example, root harvest of *Panax quinquefolius* (American ginseng) reduced long-term population growth rates less when harvest co-occurred with deer browsing because browsed *Panax* individuals were less visible to harvesters and therefore had higher rates of survival (Farrington *et al.* 2009). Interactive effects may also be synergistic, having a greater impact in combination. For example, population growth rates of the boreal shrub *Vaccinium myrtillus* declined with both increasing herbivory and increasing resources, but herbivory had a stronger negative effect in high resource conditions (Hegland *et al.* 2010).

With this complexity, experimental tests of the effects of drivers on plant demography are especially needed but limited in number (Crone *et al.* 2011). Furthermore, if this ecological understanding is to be used to mitigate the effects of disturbance and climate change, it is necessary to differentiate among interaction chain and interaction modification effects (Didham *et al.* 2007). An interaction chain is a series of directly linked drivers, whereas an interaction modification effect occurs when the per-unit effect of one driver depends on the environmental context of other drivers. With interaction chains, manipulation of a single driver might effectively produce the desired outcome. With interaction modification effects, managing the multiple interacting drivers simultaneously is likely necessary (Didham *et al.* 2007). Determining the relative importance of demographic drivers and the nature of their interactions is critical to understanding and managing for the effects of global environmental change.

Disturbance is recognized as an important driver of the demography of many plant populations (Sousa 1984). Disturbances can have both consumptive effects (due to the removal of biomass) and non-consumptive effects on plant demography. In the case of grazing, for example, non-consumptive effects may include direct effects such as trampling, as well as indirect effects such as changes in soil fertility or reduced competition (e.g., Hobbs 1996; Rooney & Waller 2003; Heckel *et al.* 2010). Separating consumptive from non-consumptive effects in demographic studies has proved difficult (Maron & Crone 2006), and most studies have not done so. However, ignoring non-consumptive effects can lead to under- or over-estimation of the effects of disturbance.

We used an experimental study, integrated with observational data for important covariates, to test for interactions among drivers of plant demography of wild *Phoenix loureiri* Kunth (mountain date palm) in a savanna woodland in South India. *Phoenix loureiri* populations are subject to multiple forms of disturbance, including frequent anthropogenic ground fires, herbivory by ungulate grazers (both domesticated and wild) and leaf harvest by local human communities. These three forms of disturbance – fire, grazing and plant harvest – are common and frequent sources of disturbance in tropical forests and savannas (FAO 2010). Furthermore, these disturbances are similar to naturally occurring disturbances with which the palm has evolved (i.e., wildfires, grazing by wild ungulates and leaf loss to falling overstory branches). However, due to increasing anthropogenic activities, these disturbances occur today with greater frequency and intensity than they have in the past, as is the case in many other tropical systems (Oesterheld *et al.* 1992; Olff & Ritchie 1998; Bond *et al.* 2005). With these increases, understanding the effects of fire history, leaf harvest and grazing is especially important to understanding how environmental change is likely to influence plant demography and, therefore, species distributions and abundances.

Vegetation, disturbance regime and abiotic conditions are known to have reciprocal and interactive effects on each other (e.g., Bezemer *et al.* 2006; Kirkpatrick *et al.* 2011). However, the implications of these interactions for plant demography have not been well studied (Hawkes & Sullivan 2001; Maron & Crone 2006; Wisdom *et al.* 2006). Fire and grazing may have synergistic effects, as grazers have been shown to prefer burned areas (Sensenig *et al.* 2010). There are also likely to be synergistic interactions among fire, grazing and leaf harvest based on evidence that resilience to disturbance in palms decreases with multiple concurrent forms of disturbance (Chazdon 1991). The negative effects of harvest and grazing may be lower in high light conditions – a sub-additive interaction – as understory palms are often light limited and better able to compensate for disturbance in high-light conditions (Anten *et al.* 2003). Previous studies of palm demography have demonstrated that loss of palm leaves can reduce palm survival, growth and reproduction, and that these vital rates are additionally affected by abiotic conditions (e.g., Ratsirarson *et al.* 1996; Endress *et al.* 2006; Martínez-Ramos *et al.* 2009). The effect of grazing on palm demography has also been found to vary with substrate type (Berry *et al.* 2011). However, experimental tests of the interactive effects among multiple forms of disturbance have not been carried out in wild palm populations. As individual vital rates and fitness are often correlated with plant size, determining how the effects of disturbance and abiotic conditions vary with plant size is also important to understanding demographic responses to these drivers.

To test the effects of and interactions among these three forms of disturbance on palm demographic rates and their relationship with abiotic environmental factors, as well as the non-consumptive effects of grazing and harvest, we established a split-plot fully crossed three-way factorial experiment. The actual intensities of grazing and harvest on plants exposed to these disturbances were allowed to vary. We used this study design to ask:

1) Do the intensities of grazing and leaf harvest differ across abiotic conditions?

2) What are the effects of fire history, grazing and leaf harvest on rates of palm mortality, growth and reproduction? Are there interactive effects between fire history, grazing and leaf harvest?
3) Do the effects of and interactions between fire history, grazing and leaf harvest depend on plant size?
4) Do the effects of and interactions between fire history, grazing and leaf harvest differ with abiotic conditions (soil moisture and light availability)?
5) Are there non-consumptive effects of grazing and leaf harvest on palm vital rates?

We expected to find higher intensities of grazing in plots with recent fire. Given palm harvesters' reported preference for leaves from plants recovering from fire, we also expected to find higher intensities of harvest in areas with recent fire. In addition, we expected synergistic interactions among harvest, grazing and fire, as well as sub-additive interactions between light levels and harvest and grazing. We expected to find evidence of non-consumptive effects of grazing and leaf harvest such that palm growth rates would be lower in plots open to harvest and grazing, even on individual plants that escaped harvest and grazing.

Materials and methods

Study species and site

Phoenix loureiri is widely distributed across sub-Himalayan Asia, from India through southern China into Taiwan and the Philippines, where it occurs from sea level to 1700 m in open grasslands and scrublands or forest understory (Barrow 1998). The species is dioecious and can reproduce clonally by basal suckers. Within our study site, nearly all genets had multiple genetically identical stems (ramets). Individual palms can grow up to 5 m tall, but in our study site they remain shrubby with stems less than 30 cm tall, as is common in dry and disturbed areas (Barrow 1998). In South India, leaves of ~60 cm in length or longer are harvested for hand brooms.

Our study took place in the Sathyamangalam Reserve Forest, Tamil Nadu state, India, part of the Western Ghats biodiversity hotspot (Mittermeier *et al.* 2005). Our study site was located in a savanna woodland with ~900 mm of annual rainfall, on mountain slopes at 1400 m. Here, *P. loureiri* occurs abundantly in the understory, and its leaves are harvested by local people during the dry season, generally from February through May. Commercial palm leaf harvest has occurred in the study area since 1975. Livestock from local villages graze in the study site and may browse on palm leaves, though the palm is not preferred fodder. Wild ungulates, including gaur (*Bos gaurus*) and sambar deer (*Rusa unicolor*), are also present at the site and browse on palm leaves. In addition the Asian elephant (*Elephas maximus*) consumes palm leaves and the stems of young plants and may uproot palms (Sukumar 1990). No elephant herbivory occurred within our study plots. From the perspective of the palm, ungulate grazing and harvest are similar in that both reduce the photosynthetic area of the palm. However, ungulate grazing removes only the upper part of the palm leaf, whereas harvest removes the full leaf and part of the petiole. Ungulates preferentially graze from leaves that have not fully expanded, while harvesters collect larger, fully developed leaves (L. M. personal observation). Ground fires, often set by local people to manage for fodder and harvested plant species, are a frequent occurrence. It is rare to find areas that have not burned within the past three years. The frequency of fire has likely increased over the past century, based on trends in similar vegetation in a neighboring area (Kodandapani *et al.* 2004).

Experimental design and treatments

We established five replicate blocks of eight plots each, for a total of 40 plots. Blocks were located in areas that had partially burned in February-March during the dry season just prior to the establishment of the study in August 2009. We used a split-plot design, with four fire plots per block located within a burned patch and four corresponding no-fire plots located outside and adjacent to the burned patch. The burned split plots in the five blocks were produced by two separate fires that burned a larger area. We established blocks to control for potential spatial variation in environmental conditions including soil and fire properties. Within each fire and no-fire area of each block, we randomly selected four palm genets of 5-21 ramets (mean = 10) located a minimum of 5 m apart (see Figure B.1). These four genets were randomly assigned to the four harvest-grazing treatment combinations (harvest and grazing, harvest and no grazing, no harvest and grazing, no harvest and no grazing), yielding a 3 x 3 fully crossed factorial design. A 2 x 2 m plot was demarcated around each focal genet, and all ramets belonging to that genet were tagged. In nearly all cases, palms were sparse enough that each plot contained a single genet and it was clear which ramets made up that genet. Otherwise, ramets separated by more than 25 cm without a visible connection were considered separate genets.

Plots assigned to the no-grazing treatment were enclosed by 2.5 x 2.5 x 1.5 m tall wooden fences to exclude ungulate grazers. Fences were checked monthly for damage, and repairs were made if needed.

All focal genets were flagged, and local harvesters were asked not to harvest from flagged plants. Field assistants from a nearby village harvested palm leaves from plots assigned to the harvest treatment just prior to re-monitoring in 2010 and 2011, which was during the normal harvest season. Consistent with local harvesting practices, field assistants harvested all the leaves from a plant that would have been taken if they were harvesting for commercial broom making. Useable leaves (> ~60 cm) were cut at the base of the petiole with a machete; leaves that were too small were left intact on the plant.

This study design allowed us to establish a gradient of harvest and grazing intensities, and also to determine how these intensities varied within the environment with abiotic conditions and plant size, as well as covaried with each other and with fire. This provided us with detailed information on the relationships among environmental drivers of demographic variation in a wild palm population.

Data collection

Palms were monitored at the time of the establishment of the experiment in August 2009 (after fire occurred, but before the harvest and grazing treatments were implemented) and again in May 2010 and May 2011. For every ramet, at the start of the study we measured the stem height, and at each census we measured the width of the petiole of longest leaf, the number of grazed leaves, the number of harvested leaves and the total number of leaves (including harvested or grazed leaves that still had green petioles). We used the petiole width of the longest leaf as an indicator of plant size because most palms did not have above-ground stems and because petiole width correlates with survival, growth and reproduction in this (L.M. & T.T. unpublished data) and other palm species (e.g., Joyal 1996). For reproductive ramets, we recorded the number of flowering or fruiting stalks produced. During re-monitoring in 2010 and 2011, new vegetative sprouts were tagged and measured, and plots were examined for seedlings. We monitored over 400 palm ramets.

Due to similarities in dentition between domestic and wild ungulates present at the study site, we were unable to differentiate herbivory on palms by livestock from herbivory by wild grazers. Based on a year of camera trapping in the area, 85% of ungulates sighted were livestock, compared to 15% wild (L.M. & T.T. unpublished data), suggesting observed grazing is primarily from livestock.

To account for possible environmental differences among plots that could explain differences in palm demographic rates, we measured canopy openness at the start of the study using hemispherical photos taken 1 m off the ground, analyzed with Gap Light Analyzer version 2 (Frazer *et al.* 1999). Soil moisture (m^3 water/m^3 soil) was measured on each monitoring date using a Dynamax TH_2O Theta soil moisture meter with a ML2 Theta probe by averaging over five points within each plot.

Data analysis

To incorporate both fixed and random effects, as well as the hierarchical nature of the data with covariates measured at different levels, we used linear and generalized linear mixed-effects models (LMM and GLMM). We modeled the variation in harvest and grazing intensities across study plots, as well as variation in palm vital rates (mortality, growth, flowering and vegetative reproduction; Table B.1).

Random effects included ramets nested within genets (plots) within split plots (fire treatment) within blocks. Because random effects were based on the spatial configuration of the experimental design, all random effects were retained in all models (Littell *et al.* 2006). Fixed explanatory variables included the main effects of fire, harvest, grazing and year, as well as covariates – measures of abiotic conditions and of ramet and genet size. For the model of plant growth, a quadratic term for ramet size (petiole width) was added based on checks of model residuals. When harvest and grazing were used as explanatory variables, we used the proportion of leaves harvested or grazed per ramet or genet in the initial full model to account for variation in actual levels of grazing and harvest among plots in the grazing (unfenced) and harvest treatments. We use the terms harvest or grazing *treatment level* to refer to the plot-level treatment, and harvest or grazing *intensity* to refer to the proportion of leaves grazed or harvested at the level of the genet or ramet. Year was treated as a fixed effect because it represented time since establishment of the experiment; however, it also includes the effect of inter-annual environmental variation.

We modeled harvest and grazing intensity using data from the 20 plots open to either harvest or grazing. All other models were based on data from all 40 plots. To avoid lack of fit and heteroscedasticity of residuals when grazing intensity was modeled across both years of the study, we modeled grazing intensity separately for 2010 and 2011. Because our experimental harvest of leaves occurred just prior to monitoring, the observed intensity of leaf harvest could not have affected grazing intensities during the previous year. Therefore, we did not include leaf harvest intensity as a predictor of grazing intensity.

Full models were reduced in a backwards stepwise process, sequentially dropping the least significant fixed-effect term in the model, testing for significance with likelihood ratio tests with a threshold of $p = 0.05$. After model reduction, we tested for possible non-consumptive effects of grazing and harvest on plant growth (i.e., effects of grazing or harvest beyond that caused by the direct removal of biomass). We did this by adding the plot-level treatments (open to grazing vs. fenced and harvest vs. no harvest) as explanatory variables, along with two-way interactions between treatment and year, and two measures of ramet size (starting petiole width and stem height). A significant effect of the plot-level grazing or harvest treatment after accounting for actual levels of grazing and harvest was interpreted as indicating a non-consumptive effect. Limited sample sizes prevented us from testing for non-consumptive effects on rates of mortality or flowering. The two genets with the highest number of ramets occurred by chance in plots without harvest or fire. Plants in these plots had high leverage in the model when the number of ramets per genet was included as an explanatory variable, so this variable was omitted from the initial model of growth and added only after model reduction to test for possible density-dependent effects.

Because 18 genets did not flower during the study, and thus identification of their sex was not possible, we modeled the probability of flowering independent of sex. Sex was also not included as a factor in models of other vital rates, as we found no evidence for different rates of growth or survival by sex or interactions between sex and fire, grazing or harvest for the subset of genets with known sex (L.M. & T.T. unpublished data). All analyses were completed in R 2.13.1 (R Development Core Team 2011) using the lmer function in the lme4 package (Bates *et al.* 2011).

Results

Intensities of grazing and harvest and relationship to abiotic conditions

Canopy openness and soil moisture varied widely across plots and were not significantly correlated with any type of disturbance overall (details in Appendix B). Nearly one third (30%, n = 566) of leaves in unfenced plots were grazed in 2010; a smaller proportion (20%, n = 585) were harvested from plots open to harvest. The amount of grazing dropped in 2011, with 11% (n = 500) of leaves grazed, while both the proportion and number leaves harvested (27%, n = 462) increased (Figure B.2). Across the plots open to grazing, grazing intensity (the probability of a ramet being grazed) varied significantly with fire history, soil moisture, ramet height and the number of leaves per genet in 2010 (Table 3.1a). Larger plants with taller stems were more likely to be grazed. There was a significant interaction between fire history and soil moisture such that grazing intensities were greater in plots with fire than without fire under relatively moist soil conditions, but lower in plots with fire than without fire in plots with drier soil conditions (Figure 3.1). There was no significant effect of soil moisture or number of leaves per genet in plots with fire and no significant effect of fire overall (see Table B.2 for estimates and standard errors of non-significant main effects and covariates for all models). In 2011, when grazing levels were lower, ramet size was the only significant predictor of grazing, again with the probability of being grazed increasing with plant size (Table 3.1b).

Across ramets in harvest treatment plots, the proportion of leaves harvested varied significantly with fire history, grazing intensity, ramet size (largest petiole width), number of leaves per genet, soil moisture and year (Table 3.2). Harvest increased greatly with ramet size. Overall, increased grazing intensity reduced the proportion of leaves harvested from a ramet, and this was especially the case for ramets in no-fire plots

(Figure 3.2). As the fire by leaves-per-genet interaction shows, a greater proportion of leaves were harvested from genets with many leaves in plots with fire; the opposite was the case in plots without fire. Based on the year by soil moisture interaction the proportion of leaves harvested was greater for ramets in drier plots in 2010, but there was no effect of soil moisture in 2011.

Effects of and interactions among disturbance and abiotic factors on palm vital rates

The palm mortality rate in 2010 was 3.5%, with 14 ramets (of 397) from eight genets dying. In 2011, mortality declined to 1.3%, when five ramets (of 389) died from three genets. Palm ramet mortality was significantly affected by grazing intensity and fire history (Table 3.3). Mortality was higher among ramets in fire plots. Ramet mortality was greater in genets that experienced higher grazing, especially in the second year of the study. In addition, ramet mortality was higher in genets with more ramets. In contrast, ramets in genets with more leaves had decreased mortality.

Fire history, harvest intensity and grazing intensity all had significant effects on palm ramet growth (Table 3.4, Figure 3.3). The effects of harvest and grazing increased with palm size, such that harvest and grazing on average reduced growth of plants above a certain size (greater than ~0.6 cm for harvest and ~0.5 cm for grazing)**.** While the estimated effects of harvest and grazing on smaller plants were positive, actual rates of harvest and grazing experienced by plants of this size were very low so realized effects were essentially zero. In addition, the interaction between fire and harvesting intensity was significant, indicating that increasing levels of harvest reduced growth, especially for plants not recently exposed to fire. Except for the smallest plants, growth was reduced in the second year of the study. When the number of ramets per genet is added to the model presented in Table 3.4, the number of ramets had a significant negative effect on ramet growth ($\chi^2 = 6.110$, $df = 1$, $p = 0.013$).

Sixteen genets flowered in 2010 and 13 in 2011. Eight genets flowered in both years. One genet flowered only prior to applying the harvest and grazing treatments. Nine genets were identified as male and 13 as female. Eighteen did not flower over the three monitoring periods. Flowering increased under more open canopies and declined with increasing grazing intensities (Table 3.5). None of the six genets with more than 40% of their leaves grazed were observed flowering. Genets in fire plots had a significantly lower probability of flowering in the second year, but there was no effect of year on genets in unburned plots, and no significant effect of fire history on flowering overall.

There were no new palm seedlings observed in any of the plots over two years. Over two years, six new vegetative sprouts were produced from six different genets. None of the factors tested were significant predictors of vegetative reproduction.

Additional effects of grazing and harvest

To test for non-consumptive effects of harvest and grazing on plant growth such as from trampling, we added two sets of factors to the model in Table 3.4: 1) the intensities of harvest and grazing per genet, and 2) the harvest and grazing treatment levels (e.g., plots open to harvest or grazing versus those that were not). Each set of factors was significant even after accounting for the effect of harvest and grazing intensity on individual ramets (the consumptive effect of harvest and grazing), and therefore explained additional variation in ramet growth rates. Ramet growth declined as the proportion of leaves grazed in the genet increased ($\chi^2 = 4.787$, $df = 1$ $p = 0.02867$); this effect did not vary significantly between years. Ramet growth also declined with an increasing proportion of leaves harvested in the genet, and this effect was greater on plants with taller stems ($\chi^2 = 21.092$, $df = 2$ $p < 0.001$). Ramets in unharvested plots grew more than those in harvested plots, and the benefit of protection from harvest increased with stem height ($\chi^2 = 16.528$, $df = 2$ p < 0.001). Ramets in fenced plots grew more than those in open plots in 2010 but not in 2011 when grazing was lower ($\chi^2 = 11.162$, $df = 2$ $p = 0.004$). When both sets of factors (genet-level grazing and harvest intensities and treatment levels) were included as predictors of palm growth in the same model, the grazing treatment level remained marginally significant by likelihood ratio test (grazing + grazing:year interaction, $\chi^2 = 5.295$, $df = 2$, $p = 0.071$) , while genet grazing intensity was no longer significant ($\chi^2 = 0.594$, $df = 1$, $p = 0.441$). When both harvest treatment level and genet harvest intensity were included in the same model, genet harvest intensity remained marginally significant ($\chi^2 = 4.995$, $df = 2$, $p = 0.082$), while harvest treatment level was not ($\chi^2 = 3.217$, $df = 2$, $p = 0.200$).

Discussion

We find that *P. loureiri* demographic rates are driven by multiple interactive effects among abiotic conditions, plant size and disturbance, and that the intensities of disturbance are themselves driven by interactions between other forms of disturbance and abiotic factors (Figure 3.4). We also find evidence of non-consumptive effects of harvest and grazing on palm growth. Our results suggest that understanding and predicting the effects of environmental change on palm demography is only possible when interactive effects are included. Our integration of a manipulative field experiment with data on environmental covariates was integral to untangling the interactive effects we found, but this approach is rare, especially in tropical plant demography. We expect this approach will be valuable to determining the interactive effects among environmental drivers that are likely common to plant demographic responses to disturbance.

Interactive effects shape harvest and grazing intensities

Harvest and grazing did not occur randomly across palm individuals, but instead the intensities of these disturbances were associated with local abiotic conditions as well as the size of the palm ramets and genets. Because broom making requires palm leaves of at least ~60 cm in length, harvest intensity was greater on ramets with larger leaves. There was less harvest from genets with more leaves in no-fire plots, which, given the species' clumped growth form, may be a result of reduced ease of access to leaves in the middle of large genets. Harvesters report that one benefit of fire is that it burns off the especially spiny older leaves, making harvest easier. Local harvesters favor areas with recent fire because it induces a new flush of brighter green leaves. Increased greenness of vegetation following fire has been shown to occur in other systems (Henry *et al.* 2006). Fewer leaves were harvested from more heavily grazed ramets, suggesting that herbivory limits harvest. Our finding that this pattern was stronger in plots without fire may be a result of the reduced leaf quality (from the perspective of broom making) in areas without fire.

The clumped growth form of *P. loureiri* could also be responsible for our finding that smaller palms experienced reduced grazing, as this may make their leaves less accessible. In contrast to our expectations, and to findings in other ecosystems with both fire and ungulate grazing (Fuhlendorf *et al.* 2009; Sensenig *et al.* 2010), the intensity of grazing was not significantly higher in plots with recent fire. This may be a result of the small scale of our experiment: within a block, plots with and without fire were separated only by meters or tens of meters, which may be a finer scale than that at which the grazers and herders operate. In a concurrent study, we did detect increased grazing on palm leaves with recent fire across 14 populations separated on the order of kilometers (Chapter 4), suggesting fire may be a driver of grazing intensity but only at larger spatial scales.

The increased grazing on genets with more leaves in plots without fire in 2010 was unexpected but may be because genets with more leaves are more visible to grazers in these areas. The source of the interaction between soil moisture and fire on the intensity of grazing in 2010 is also not clear. The complex patterns of spatial and temporal variation in grazing that we observed emphasize the need for a better understanding of the drivers of this variation, especially since grazing affects multiple palm vital rates. In particular, the cause of the difference in grazing intensity between the two study years is unknown, but has important implications for palm demography.

Further investigation of the role of herbivore community composition on plant responses to grazing is also warranted. Different herbivore species may have different effects on plant vital rates depending on their grazing habits (e.g., Holdo *et al.* 2009). In addition, the presence of certain grazing species can alter rates of grazing by other species (e.g., Lagendijk *et al.* 2012). Data from our camera traps (L.M. & T.T. unpublished data) indicated that most of the grazing we observed was due to livestock. This might suggest that reducing livestock grazing would benefit palm populations. However, if reduced livestock grazing led to increased grazing by wild ungulates, as has been found elsewhere in South India (Madhusudan 2004), reductions in livestock grazing might not benefit palm populations.

Effects of and interactions among disturbance and abiotic conditions on palm vital rates

The interaction between fire and harvest on palm growth suggests that the effects of harvest on palms in areas with fire may be less negative than would have been predicted from studying the effects of fire and harvest separately. This interactive effect may result from the tendency of palms in areas with fire to have more leaves than in areas without fire (Poisson GLMM, likelihood ratio test, $\chi^2 = 3.682$, $df = 1$, $p = 0.055$): after having the same proportion of leaves harvested, palms in no-fire areas may be left with fewer intact leaves for photosynthesis. This can be considered an interaction modification effect (Didham *et al.* 2007), in which the per-unit effect of leaf harvest depends on the fire treatment level. The reductions in growth and increases in mortality in genets with more ramets show that palm vital rates are density-dependent. This suggests that disturbances that increase palm mortality – such as grazing – can be in part compensated for by increased survival and growth of remaining individuals (Maron & Crone 2006).

Despite the prevalence of palms in fire-prone vegetation, we know of no studies that compare the demography of burned and unburned palms (but see Souza & Martins 2004 for a study of palm demography before and after fire). We find that fire history affected multiple vital rates of the *P. loureiri* in contrasting ways. Palms in plots with recent fire had higher rates of mortality, but surviving individuals had higher rates of growth. The population growth rates of understory palms and other long-lived species are generally more sensitive to rates of survival than growth, though the relative sensitivity may be size-dependent (Franco & Silvertown 2004; Zuidema *et al.* 2007). This suggests that the increases in ramet growth following fire are likely to mitigate – but not fully compensate for – increased mortality in *P. loureiri*. Our results show significant impacts of fire up to two years after the fire event; however, data on the direct effects of fire events on palm vital rates are still required to fully understand the implications of fire for population dynamics. Although this has not been studied in palms, multi-year effects of fire on plant vital rates have been found in other plant species in fire-prone systems (Hartnett *et al.* 1997; Quintana-Ascencio & Morales-Hernández 1997).

The effects of grazing on palm vital rates were almost uniformly negative. Grazing – which occurred primarily on larger plants – reduced ramet growth rates, with a greater negative effect on larger plants. The increased effect of grazing on larger palms is consistent with findings from a neotropical dioecious understory palm (Endress *et al.* 2004). Also consistent with these previous findings, grazing in our study was associated with reduced *P. loureiri* flowering and, in the second year, with increased mortality. The increased mortality with increased grazing in 2011, when overall levels of grazing were lower, could be a result of the drier conditions in that year.

Except for the smallest plants, which did not produce leaves large enough to be harvested, harvest reduced ramet growth, with increasingly negative effects on larger plants. The lack of a significant effect of harvest on reproduction is surprising, as reduced vegetative and sexual reproduction due to leaf harvest has been found in other palm species (e.g., Ratsirarson *et al.* 1996; Endress *et al.* 2006; Zuidema *et al.* 2007; Martínez-Ramos *et al.* 2009). The lack of an effect of leaf harvest on palm mortality is not unexpected – other studies of palm demography have detected effects only at the highest intensities of harvest (Endress *et al.* 2006; Zuidema *et al.* 2007). However, we note that a lack of statistical significance cannot be interpreted as an acceptance of the null hypothesis of no true effect. Here, the lack of statistically significant effects of harvest and other factors and interactions could also be due to limited power given our relatively small sample size and a potentially small true effect size. Lack of significance could also be due to the limited duration of our study. With the long history of harvest at the site, more than two years of protection from harvest may be required for differences in rates of flowering or mortality to become apparent.

Increased flowering under more open canopies, as we found for *P. loureiri*, is common among understory palm species (de Steven 1989; Cunningham 1997). Because the open canopies of the ecosystems where *P. loureiri* occurs are partly maintained by frequent fires that reduce tree recruitment (Ratnam *et al.* 2011), fire may in this way indirectly benefit palm populations. In contrast with our expectations, the effects of fire, grazing and harvest did not vary significantly with light availability. The significant effect of year and its interactions with disturbance and abiotic factors suggests that additional demographic drivers in this system remain unaccounted for.

Grazing limits palm leaf harvest

While we did not find a significant interactive effect between harvest and grazing intensity on the vital rates of palm individuals, the negative correlation between actual rates of harvest and grazing intensity suggests that the overall effect of harvest depends on the rates of grazing. This form of interaction between harvest and grazing represents an interaction chain effect (Didham *et al.* 2007), in which the per-unit effect of leaf harvest is constant across levels of grazing, but the total amount of leaves harvested is less in areas with grazing than without. As a result, and in contrast to our expectations, harvest then likely has less of an effect on palm populations in areas with grazing. As more leaves are grazed, fewer intact leaves remain that can be harvested. This sub-additive effect of harvest and grazing is similar to that found for American ginseng, where deer grazing reduces plant mortality due to harvest by hiding plants from harvesters (Farrington *et al.* 2009). Given that *P. loureiri* leaf harvest across South India occurs in areas with variable amounts of grazing, and because rates of grazing and harvest are linked, understanding the impacts of harvest in this system necessitates understanding patterns of grazing as well. Acquiring a better understanding of the interactions between harvest and grazing is likely to be important for many other species, including other palms (e.g., Berry *et al.* 2011; Lopez-Toledo *et al.* 2011), that are subjected to both harvest and grazing simultaneously.

Additional effects of grazing and harvest

A common approach to simulating the effects of ungulate herbivory in plant demographic studies has been to compare demographic rates across all individuals within a grazed population to demographic rates of the subset of individuals within the same population that have escaped herbivory (e.g., Knight 2004; McGraw & Furedi 2005; Farrington *et al.* 2009). This approach does not account for any non-consumptive effects associated with herbivory, such as trampling or soil compaction. We find evidence that exposure of genets to grazing and harvest reduces the growth even of *P. loureiri* ramets that are not directly grazed or harvested. These non-consumptive effects could be physical if trampling affects ramets in genets that have been harvested or grazed, even when biomass is not removed from the ramet. These effects could also be physiological – resulting from increased carbon export to, or reduced carbon subsidies from, other grazed or harvested ramets within the same genet, as has been found in other clonal species (e.g., Chapman *et al.* 1992; Zhang *et al.* 2002). We were unable to test for these possible effects independently within our study – while some genets in plots open to grazing or harvest did not have any leaves grazed or harvested, it is likely that these genets also would have experienced fewer physical effects as well. However, we found that grazing treatment level (fenced vs. open) explained additional variation in ramet growth, even after including actual levels of grazing on the ramet and genet in the model, which would have accounted for physiological effects. This suggests that physical effects like trampling reduce ramet growth in addition to the direct consumptive effects of herbivory from biomass removal.

Our results suggest that studying herbivory using ungrazed plants within a grazed population can lead to inaccurate conclusions about the effects of this form of disturbance from at least two sources. First, this approach can bias results if the conditions that led to ungrazed plants escaping herbivory (such as smaller size or reduced leaf quality) are also associated with differences in vital rates for those individuals. In our study, smaller palms – the ones most likely to escape grazing – grew more than larger palms, even after controlling for differences in grazing, which would lead to an overestimation of the direct effects of grazing. Second, this approach will underestimate the negative impacts of grazing if, as we found, ungrazed plants are still affected by non-consumptive effects of grazing. The likely role of physical effects in our study, combined with findings of negative impacts of deer herbivory even on unpalatable plant species (Heckel *et al.* 2010), suggests that negative non-consumptive effects of herbivory are common even in non-clonal species. Studies using simulated herbivory such as clipping (e.g., Oba *et al.* 2000; Vandenberghe *et al.* 2008) may also underestimate the effects of herbivory if the non-consumptive effects of simulated herbivory differ from those of actual herbivores.

The importance of interactions among drivers to understanding plant demographic processes

Most studies of plant demography to date have been observational (Crone *et al.* 2011), and this is especially the case in tropical ecosystems. Very few experimental studies exist of interactions among multiple drivers on plant demography. Our use of a manipulative experiment integrated with measurements of disturbance intensity and abiotic factors was critical to disentangling multiple pathways by which environmental drivers can affect plant vital rates.

The prevalence of interactions we found that influenced both the intensity and the outcome of disturbance at the ramet and genet levels suggests that interactions among drivers are likely to be important for *P. loureiri* at the population level as well. As fire, livestock grazing and wild plant harvest are very common co-occurring forms of anthropogenic disturbance throughout the tropics, our findings from *P. loureiri* can provide insights into how other tropical species are likely to respond to similar disturbances.

With the short timeframe of our study, the high interannual variation in grazing intensity we observed and the likelihood of temporal variation in, and interactions between, other factors such as soil moisture and fire, we expect that long-term palm population dynamics are also affected by interactions not detected here and that interactive effects themselves vary temporally. With growing evidence to suggest that interactions among drivers are the norm rather than an exception (e.g., Schleuning *et al.* 2008; Martínez-Ramos *et al.* 2009; Hegland *et al.* 2010), further research is needed to determine in which situations the interactive effects of environmental drivers are most important to understanding and predicting plant demography. The number of possible interactions in any system is large and attempting to study them all simultaneously is neither feasible nor desirable. This is especially the case in human-managed tropical ecosystems, where interacting forms of disturbance commonly co-occur and where understanding and mitigating species declines is particularly important to conserving remaining biodiversity (Chazdon *et al.* 2009). Further studies focusing on the effects of drivers and their interactions on high-sensitivity vital rates, and on drivers likely to vary over spatial or temporal scales of interest, will be critical to meeting this need.

Table 3.1. Effects of disturbance and abiotic factors on the intensity of grazing on *P. loureiri* ramets in a) 2010 and b) 2011 from binomial generalized linear mixed-effects models.

a) 2010

Fixed effects	**Estimate**	**SE**	***Z*-value**	***p*-value**
Intercept	-0.868	0.534	-1.625	0.104
Stem height	0.232	0.057	4.098	< 0.001
Total leaves per genet	-0.018	0.031	-0.575	0.565
Soil moisture (centered)	-35.507	15.917	-2.231	0.025
Fire	0.422	0.692	-0.610	0.542
Fire x Soil moisture (centered)	39.620	18.255	2.170	0.030
Fire x Total leaves per genet	-0.123	0.0493	-2.503	0.012
Random effects	**SD**			
Block	0.001			
Split plot (Block)	0.000			
Genet (Split plot (Block))	1.101			

b) 2011

Fixed effects	**Estimate**	**SE**	***Z*-value**	***p*-value**
Intercept	-3.310	0.759	-4.362	< 0.001
Starting size (petiole width)	2.360	1.036	2.279	0.0226
Random effects	**SD**			
Block	0.388			
Split plot (Block)	0.190			
Genet (Split plot (Block))	0.914			

Table 3.2. Effects of disturbance and abiotic factors on the intensity of harvest of mountain date palm ramets from a binomial generalized linear mixed-effects model.

Fixed effects	**Estimate**	**SE**	***Z*-value**	***p*-value**
Intercept	-3.051	0.321	-9.506	< 0.001
Starting size (petiole width)	3.207	0.439	7.301	< 0.001
Soil moisture (centered)	-11.593	3.318	-3.493	< 0.001
Leaves per genet (centered)	-0.031	0.011	-2.692	0.007
Fire	-0.119	0.187	-0.636	0.525
Grazing intensity	-4.530	0.521	-3.618	< 0.001
Year (2011)	0.107	0.176	0.607	0.544
Fire x Grazing intensity	2.644	1.393	1.899	0.058
Fire x Leaves per genet	0.048	0.013	3.608	< 0.001
Year (2011) x Soil moisture	11.354	4.153	2.735	0.006
Random effects	**SD**			
Block	< 0.001			
Split plot (Block)	0.000			
Genet (Split plot (Block))	0.049			
Ramet (Genet (Split plot (Block)))	< 0.001			

Table 3.3. Effects of disturbance and abiotic factors on the mortality of mountain date palm ramets from a binomial generalized linear mixed-effects model.

Fixed effects	**Estimate**	**SE**	***Z*-value**	***p*-value**
Intercept	-4.661	1.139	-4.092	0.001
Ramets per genet	0.388	0.114	3.392	< 0.001
Total leaves per genet	-0.179	0.048	-3.748	< 0.001
Fire	1.977	0.780	2.536	0.011
Grazing intensity	0.101	1.793	0.057	0.955
Year (2011)	-1.892	0.914	-2.070	0.038
Grazing intensity x Year (2011)	8.418	4.015	2.097	0.036

Random effects	**SD**
Block	0.000
Split plot (Block)	0.000
Genet (Split plot (Block))	< 0.001

Table 3.4. Effects of disturbance and abiotic factors on the growth of mountain date palm ramets from a linear mixed-effects model.

Fixed effects	**Estimate***	**SE**	**Chi-squared**	***p*-value**
Intercept	0.160	0.040	NA	NA
Starting size (largest petiole width)	-0.410	0.122	11.088	< 0.001
$(\text{Starting size})^2$	0.226	0.102	4.772	0.029
Stem height	0.010	0.001	45.337	< 0.001
Fire	0.037	0.018	4.036	0.045
Harvest intensity	0.502	0.110	NA	NA
Grazing intensity	0.219	0.072	9.349	< 0.001
Year (2011)	0.096	0.033	11.894	< 0.001
Fire x Harvest intensity	0.104	0.052	3.876	0.049
Harvest intensity x Starting size	-0.963	0.146	42.325	< 0.001
Grazing intensity x Starting size	-0.429	0.114	14.202	< 0.001
Year (2011) x Starting size	-0.347	0.053	44.242	< 0.001
Random effects	**SD**			
Block	0.014			
Split plot (Block)	< 0.001			
Genet (Split plot (Block))	0.036			
Ramet (Genet (Split plot (Block)))	< 0.001			

*Estimates and standard errors are reported from the model fitted with restricted maximum likelihood. Chi-squared statistics and p-values are from likelihood ratio tests with each parameter removed from the maximum-likelihood based model, with all other parameters retained. It was not possible to test the significance of harvest intensity or the intercept because of the higher-order interaction between fire and harvest intensity.

Table 3.5. Effects of disturbance and abiotic factors on flowering of mountain date palm genets from a binomial generalized linear mixed-effects model.

Fixed effects	**Estimate**	**SE**	***Z*-value**	***p*-value**
Intercept	-2.560	1.201	-2.132	0.033
Canopy openness	0.0490	0.0191	2.571	0.010
Grazing intensity	-7.992	2.917	-2.740	0.006
Fire	1.368	0.914	1.498	0.134
Year (2011)	-0.0045	0.774	-0.006	0.995
Fire x Year (2011)	-2.587	1.217	-2.125	0.034
Random effects	**SD**			
Block	0.000			
Split plot (Block)	< 0.001			
Genet (Split plot (Block))	0.817			

Figure 3.1. The probability of mountain date palm ramets being grazed depended on soil moisture (mean between start and end of the annual interval) and fire history (fire in black, no fire in gray) in 2010. Lines are based on the estimated parameters presented in Table 3.1a. Points (jittered) show the observed pattern of grazing. Probabilities of grazing are graphed at mean values for canopy openness and number of leaves per genet.

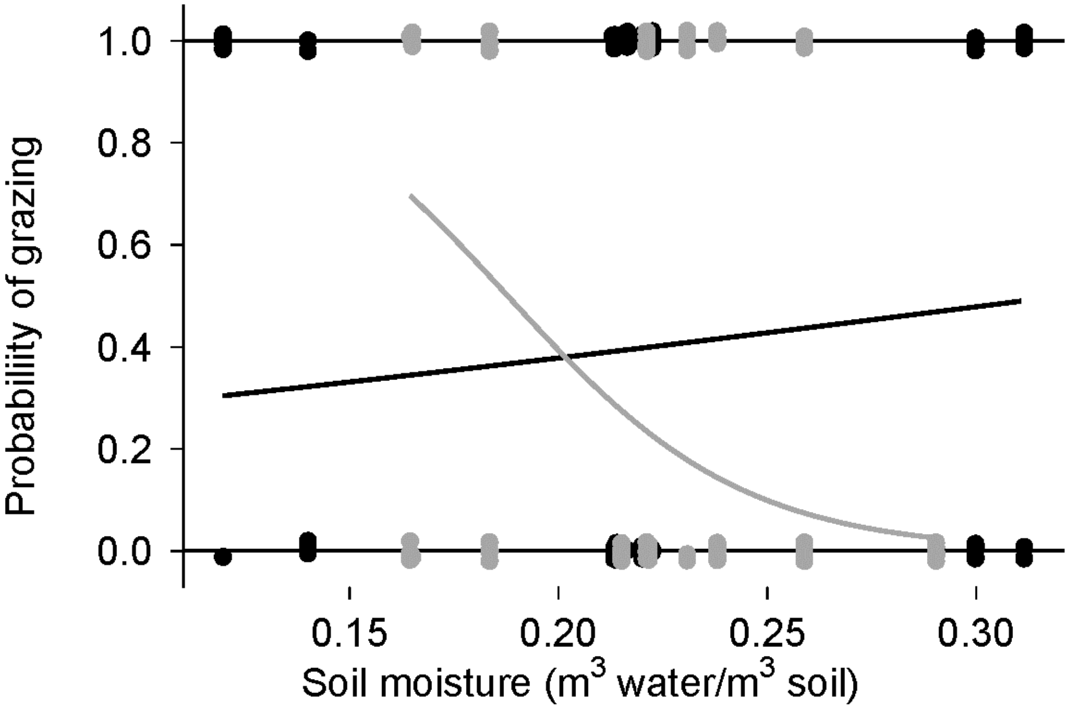


Figure 3.2. The proportion of mountain date palm leaves harvested per ramet decreased with increased grazing, especially in plots without fire. Lines (fire in black, no fire in gray) show the estimated proportion leaves harvested based on the parameters presented in Table 3.2 for 2010 at mean values for canopy openness, soil moisture, number of leaves per genet and starting size (0.6 cm). Points (jittered) show the observed proportion of leaves harvested from plants 0.6 cm in size in 2010.

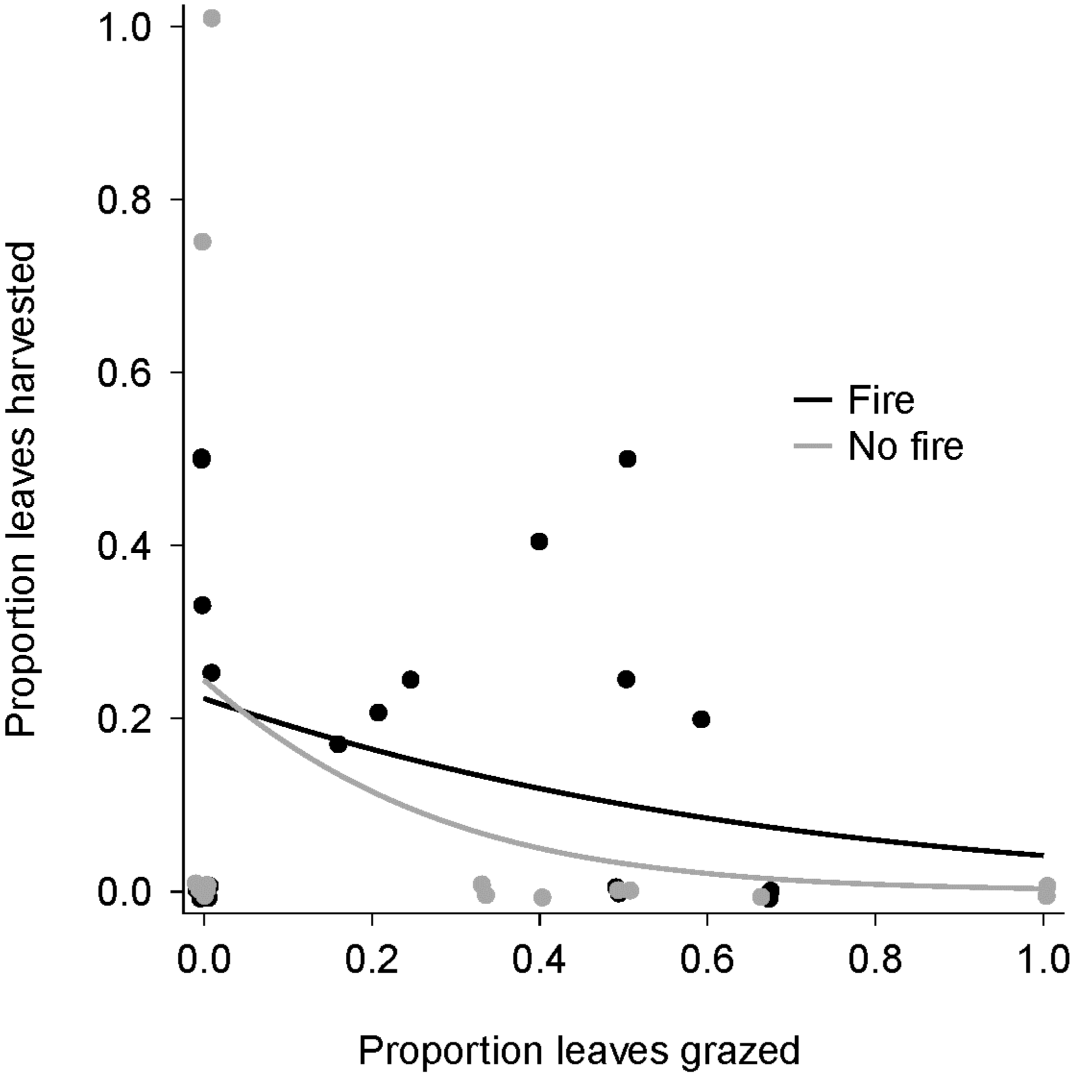


Figure 3.3. Mountain date palm ramet growth was reduced with increasing harvest intensity, especially in plots without fire. The negatives effects of harvest and grazing increased with plant size, whereas fire had a consistently positive effect on palm growth. Lines show growth by starting size (0.2, 0.6 and 1.0 cm petiole width) in 2010 as predicted from the model presented in Table 3.4 with the addition of plot-level harvest and grazing treatment effects. For each starting size, we show the effect of mean grazing and harvest intensities for plants with the mean number of leaves and median stem height.

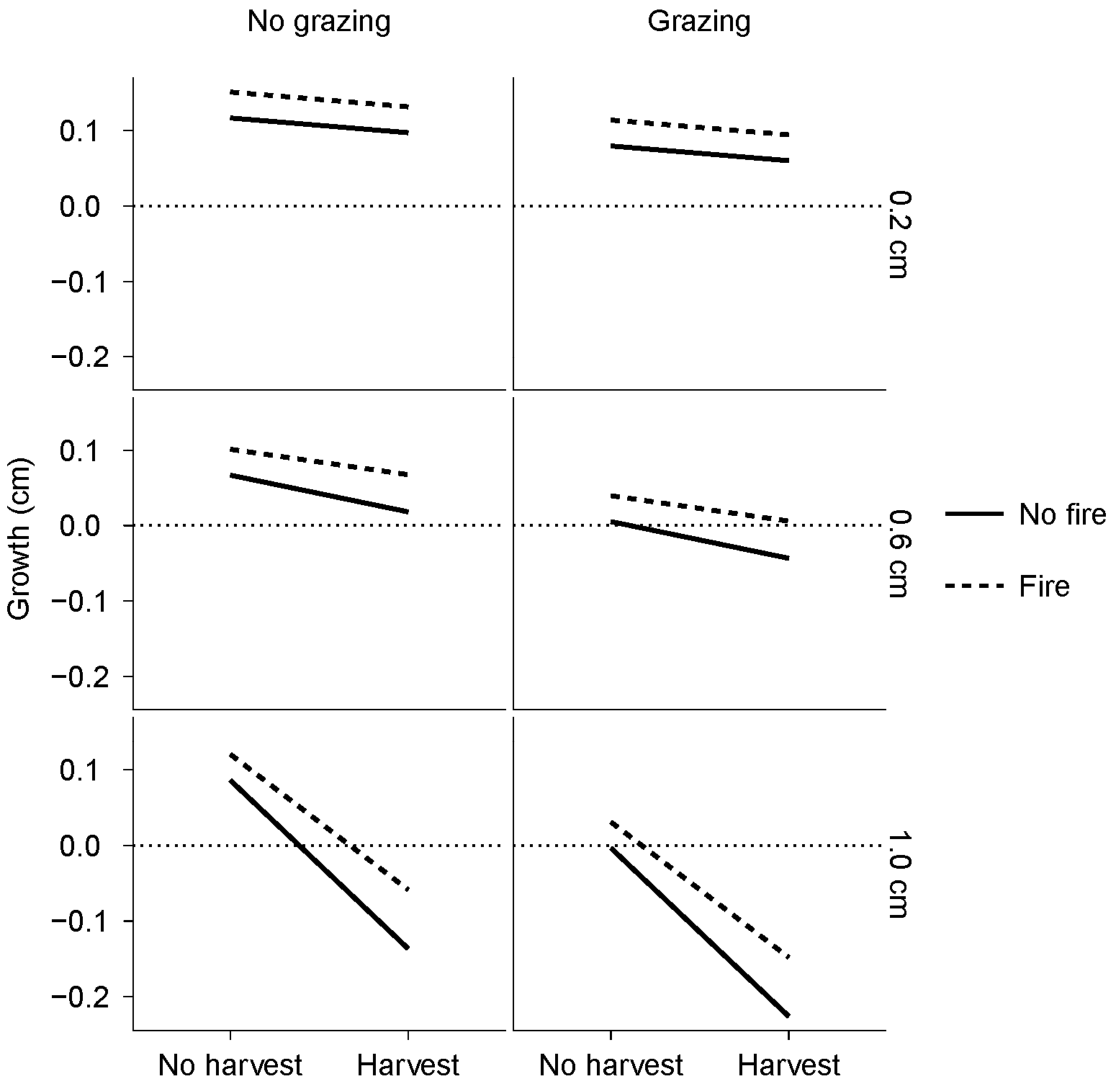
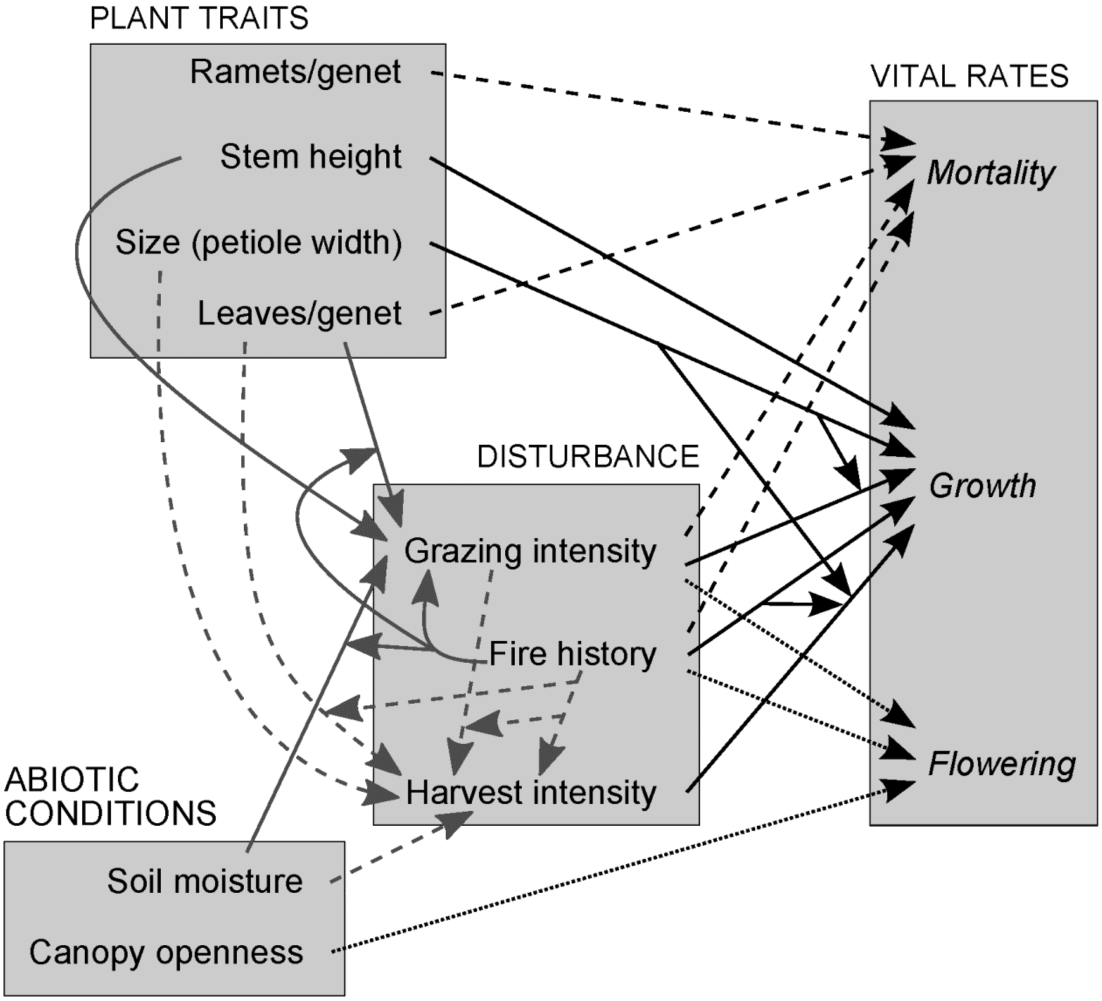


Figure 3.4. Mountain date palm vital rates are affected by disturbance, plant traits, abiotic conditions as well as interactions among these factors. The intensity of grazing and harvest a plant experiences depends on abiotic conditions, plant traits and disturbance. Black arrows show factors significantly affecting vital rates, with dashed lines for mortality, solid lines for growth and dotted lines for flowering. Gray arrows show factors significantly associated with grazing (solid) and harvest (dashed) intensities. Arrows point from predictor variables to response variables as modeled in this chapter and should not be interpreted as indicating causality.



CHAPTER 4. DISENTANGLING THE DRIVERS OF MOUNTAIN DATE PALM POPULATION DYNAMICS IN A MULTI-USE LANDSCAPE USING INTEGRAL PROJECTION MODELS

Lisa Mandle and Tamara Ticktin

Abstract

Little is known about the interactive effects of multiple forms of disturbance – natural or anthropogenic – on plant population dynamics. This gap in knowledge limits our ability to effectively manage plant populations in the face of changing disturbance regimes resulting from growing human influence on ecological processes. Fire, grazing and harvest of wild plants are three widespread and commonly co-occurring land management activities in the tropics that contribute to altered disturbance regimes with increasing human pressures. In this study, we use integral projection models to investigate the effects of and interactions between these three activities on the population dynamics of mountain date palm (*Phoenix loureiri*) in the Western Ghats, India. Our models are based on 14 palm populations and over 2,300 palm ramets monitored from 2009-2011. Our results demonstrate that fire, grazing and harvest affect both palm vital rates and projected population dynamics. We find non-linear effects of grazing and harvest on projected population growth rates (λ), with palm populations exhibiting resilience to low intensities of grazing and harvest but strong declines with increasing intensities. Palms also show resilience to fire, with increased growth compensating for reduced survival in the 1-2 years following fire. In addition, we find that intensities of grazing and harvest were higher in populations with fire in the past 1-2 years compared populations without recent fire and that intensities of harvest were lower in more intensively grazed populations. Together, these results illustrate the necessity of understanding the interactive effects of these three co-occurring forms of disturbances. Because both grazing and harvest intensities are driven by fire, managing fire frequency will be especially critical to ensuring the persistence of mountain date palm populations in human-managed ecosystems.

Introduction

Ecologists have recognized the importance of disturbance in structuring plant populations and communities for decades (Connell & Slatyer 1977; Sousa 1984; Pickett & White 1985). Numerous studies have assessed the effects of individual forms of disturbance on plant population dynamics (see review by Crone *et al.* 2011). As human activities increasingly dominate ecosystem processes (Sanderson *et al.* 2002; Ellis & Ramankutty 2008; Gardner *et al.* 2009), determining the combined effects of multiple natural and anthropogenic disturbances is critical for predicting and managing for the consequences of human-driven changes to disturbance regimes. Yet despite recognition of the importance of interactions to ecological processes (Agrawal *et al.* 2007; Didham *et al.* 2007), interactions among multiple forms of disturbance on plant population dynamics remain poorly understood, especially for long-lived species (Farrington *et al.* 2009; Midgley *et al.* 2010).

Fire, grazing and wild plant harvest are three widespread, often co-occurring forms of disturbance affecting plant populations. In many ecosystems today, these disturbances occur with greater frequency or intensity than in the past due to human activities (Asner *et al.* 2004; Bond *et al.* 2005; Kareiva *et al.* 2007). Fire and grazing regimes are recognized as having reciprocal effects on each other (Fuhlendorf *et al.* 2009; Midgley *et al.* 2010; Kirkpatrick *et al.* 2011). Importantly, grazing intensity often increases following fire (e.g., Wilsey 1996; Winter *et al.* 2011). While many studies have documented the consequences of this fire-grazing relationship for plant communities (e.g., Archibald *et al.* 2005; Collins & Calabrese 2011), much less is known about its effects on plant population dynamics (but see Staver *et al.* 2009). Understanding the population-level effects of these activities is especially important for managing the many economically important plant species that co-occur with the use of fire and in areas with grazing. Grazing has been shown in some cases to reduce the intensity of plant harvest, either by hiding plants from harvesters (Farrington *et al.* 2009) or by damaging plant parts so that they are not worth harvesting (Chapter 3). Understanding how changes in the frequency and intensity of these common forms of disturbance, and the interactions among them, affect plant population dynamics will be critical for conservation in human-managed landscapes.

In addition to the consumptive effects of disturbance through removal of biomass, many forms of disturbance may also have non-consumptive effects on plant population dynamics. Grazing, for example, may alter plant population dynamics due to trampling or compaction of soil (Rooney & Waller 2003; Heckel *et al.* 2010). Separating consumptive from non-consumptive effects in demographic studies has proved difficult (Maron & Crone 2006). Studies of the effects of grazing on plant demography often consider only consumptive effects (e.g., Knight 2004; McGraw & Furedi 2005; Farrington *et al.* 2009). However, ignoring non-consumptive effects risks under- or over-estimating the effects of disturbance.

Palms (*Arecaceae*) are a particularly useful system in which to study the effects of multiple forms of disturbance on the demography of long-lived plants because palm populations commonly experience multiple natural and anthropogenic disturbances including fire, harvest (of leaves, fruit and stems) and grazing by wild animals or livestock (Endress *et al.* 2004; Souza & Martins 2004; Pulido *et al.* 2007; Lopez-Toledo *et al.* 2011). At the same time, because palms are an important part of ecosystems around the globe and provide valuable resources for many people (e.g., Montúfar *et al.* 2011), knowledge about their responses to multiple forms of disturbance can also inform management. The effects of harvest on palm population dynamics have been well studied, though our understanding of the effects of leaf harvest come primarily from the neotropics, while studies from Asia have focused on stem-harvested rattans (Zuidema *et al.* 2007; Schmidt *et al.* 2011). Studies of the effect of herbivory and fire on palm population dynamics are much less common (Montúfar *et al.* 2011). As studies of the demographic effects of interactions among disturbances are rare across all plant species, little is known about interactions among these forms of disturbance on palms (Endress *et al.* 2004; Berry *et al.* 2011).

In this study, we examine the effects of and interactions among grazing, leaf harvest and fire on the population dynamics of mountain date palm (*Phoenix loureiri*) in the Western Ghats, India. With its high biodiversity, long history of human land use and high human densities (Chandran 1997; Cincotta *et al.* 2000; Myers *et al.* 2000), the Western Ghats region of India provides an ideal context for investigating interactions among natural and anthropogenic disturbances and the effects of human alteration of disturbance regimes.

We use integral projection models (IPMs, Easterling *et al.* 2000; Ellner & Rees 2006) with two years of data from 14 palm populations with varying histories of fire and intensities of grazing and leaf harvest. The ability to model population dynamics as a function of continuous variables, including environmental variables and individual plant variables, is a strength of IPMs and an important advance on traditional population projection matrices. IPMs have recently been used to explore the response of plant population dynamics to gradients of herbivory and resource availability (Rose *et al.* 2005; Hegland *et al.* 2010; Dahlgren & Ehrlén 2011; Rose *et al.* 2011). However, we know of no application of IPMs to understanding interactions between multiple forms of disturbance, despite the particular suitability of IPMs to such situations.

In previous research, we used a manipulative experiment to examine the effects of grazing, harvest and fire on individual palm vital rates (survival, growth and reproduction; Chapter 3). However, the way in which these impacts at the individual level scale up to influence population-level dynamics remains unknown. In addition, the manipulative experiment was carried out at a single site; whether the observed palm responses can be generalized across sites with differing histories of harvest and herbivore assemblages has yet to be determined.

In this study, we aim to answer three questions: 1) What are the effects of and interactions among grazing, harvest and time since fire on the vital rates of mountain date palm individuals and the projected dynamics of mountain date palm populations? 2) Does the intensity of grazing decline with increasing time since fire? 3) Does the intensity of harvest decline with increasing grazing intensity? In addition, we discuss the implications of our results for the persistence of palm populations in the face of these forms of disturbance.

Based on other studies of palm population dynamics (Endress *et al.* 2004; Zuidema *et al.* 2007) and our manipulative experiment examining the individual-level effects of disturbance on mountain date palm (Chapter 3), we expected to find that harvest and grazing both would reduce projected population growth rates. We expected a greater negative effect of grazing than harvest because grazing, but not harvest, was found to reduce palm survival. Survival is frequently a high-sensitivity vital rate in long-lived species such as palms (Franco & Silvertown 2004; Zuidema *et al.* 2007). For this same reason, we expected fire – both during the year of the fire and 1-2 post-fire – to have a net negative effect on palm population growth rates because of reduced survival, despite evidence of increased growth following fire. We also anticipated finding higher grazing intensities in populations with recent fire. Based on the results of our manipulative experiment, we expected that lower harvest intensities would occur with higher grazing intensities, especially in populations without fire in the past 1-2 years.

Methods

Study species and area

Mountain date palm (*Phoenix loureiri* Kunth) is widely distributed across sub-Himalayan Asia, from India through southern China into Taiwan and the Philippines, where it occurs from sea level to 1700 m in open grasslands and scrublands or forest understory (Barrow 1998). The species is dioecious and can reproduce clonally by basal suckers. Within our study area, nearly all genets had multiple genetically identical stems (ramets). Individual palms can grow up to 5 m tall, but in our study site they remain shrubby with stems less than 30 cm tall, as is common in dry and disturbed areas (Barrow 1998).

To understand the effects of disturbance on mountain date palm population dynamics, we selected 14 mountain date palm populations in savanna woodlands across five sites to represent variation in the intensities of grazing, harvest and time since fire. Our study sites encompassed three reserve forests, one protected area and a remnant forest fragment on privately owned land (Table 4.1). Commercial mountain date palm harvest occurred in the reserve forests but not the protected area or forest fragment. Sites also differed in the grazer assemblages present. The protected area was managed as a reserve forest until it was declared a wildlife sanctuary in 1973. Collection of wood from standing trees has been banned since 1987 (Shankar *et al.* 1998a), while commercial non-timber forest product extraction was banned in 2004.

Palm leaves may be browsed by both wild and domestic ungulates. Livestock from local villages were present in two reserve forest sites (Table 4.1). Wild ungulates, primarily gaur (*Bos gaurus*) and sambar deer (*Rusa unicolor*), were also present at study sites. In addition the Asian elephant (*Elephas maximus*) consumes palm leaves and the stems of young plants (Sukumar 1990), and may uproot palms. Elephants were detected in all study sites except the forest fragment, though they were not recorded from dung transects within the study plots at one reserve forest. Porcupine (*Hystrix indica*) may also consume the underground portion of the palm.

In South India, mountain date palm leaves of ~60 cm in length or longer (corresponding to leaves > ~0.5 cm petiole width) are harvested for hand brooms. Commercial harvest of mountain palm leaves by local communities takes place in reserve forests managed by the Forest Department. Ungulate grazing removes only the upper part of the palm leaf, whereas harvest removes the full leaf and part of the petiole. Ungulates preferentially graze from leaves that have not fully expanded, while harvesters collect larger, fully developed leaves (L. M. personal observation).

Ground fires, often set by local people to manage for fodder and harvested plant species, are a frequent occurrence. Fire is sometimes used to manage mountain date palm populations, as palms are perceived to produce brighter green, higher quality leaves after fire (Chapter 2). Fires are preferentially set during the dry season between February and April, in order to restrict fire to the understory (Roveta 2008). Human activity is believed to be the primary source of fires in the Western Ghats since the arrival of people in the area over 10,000 years ago (Chandran 1997; Hiremath & Sundaram 2005). Currently, within reserve forests it is rare to find areas that have not burned within the past three years; fires occur with less frequency in the protected area. The fire frequency has likely increased over the past century (Kodandapani *et al.* 2004).

Study design and data collection

Within each of the 14 study populations, we established a plot containing approximately 150 palm ramets. Plot size varied with palm density, and ranged from 12.5-200 m^2 (mean = 62 m^2, median = 42.5 m^2). Palms were measured when plots were established in July-August 2009, and then censused annually through 2011. For every ramet, at each census we measured the width of the petiole of longest leaf. We used the petiole width of the longest leaf as an indicator of plant size because most palms did not have above-ground stems and because petiole width correlates with survival, growth and reproduction in this and other palm species (e.g., Joyal 1996). For reproductive ramets we recorded the number of flowering or fruiting stalks produced and the sex of the ramet. We monitored over 2,300 mountain date palm ramets in total.

During re-monitoring in 2010 and 2011, new seedlings and vegetative sprouts were also tagged and measured. Vegetative sprouts were assumed to originate from the nearest ramet (here referred to as the "mother ramet"). We recorded the number of grazed leaves, harvested leaves and the total number of leaves (including harvested or grazed leaves that still had green petioles) per ramet. Palm leaves generally last one year (L.M. & T.T. unpublished data), so the observed number of leaves grazed and harvested was considered to be a measure of grazing and harvest intensity during the preceding year. Due to similarities in dentition between domestic and wild ungulates present at the study site, we were unable to differentiate herbivory on palms by livestock from herbivory by wild grazers. Recent elephant herbivory could be recognized where ramets had been uprooted.

Ramets within genets are connected by underground stems. In many cases, distinct genets could be identified based on patterns of growth, by exposed stems or by locating the underground stem at the end of the study. In cases where this was not feasible, we assumed that ramets separated by more than ~25 cm belonged to distinct genets based on the expert knowledge of local field assistants familiar with mountain date palm.

To account for possible environmental differences among plots that could explain differences in palm demographic rates, we measured canopy openness at the start of the study using hemispherical photos taken 1 m off the ground, with a total of eight photos per population. We analyzed photos with Gap Light Analyzer version 2 (Frazer *et al.* 1999).

Analysis of vital rates

We used linear and generalized linear mixed-effects models to model the effects of grazing, harvest, fire and important covariates on palm ramet vital rates (survival, growth, fecundity and vegetative reproduction; Table C.1). Random effects included ramets nested within genets within populations within sites, as well as year. Fixed explanatory variables included the main effects of fire, harvest and grazing, as well as covariates – ramet size (petiole width), density (ramets per genet) and canopy openness. Initial full models included all two-way interactions among grazing, harvest and fire as well as two-way interactions between grazing, harvest, fire and the covariates (ramet size, density and canopy openness). Quadratic terms were added where necessary based on checks of model residuals. We used AIC as the criterion for determining whether to drop or retain a given factor, retaining factors which reduced the AIC value of the model. Full models were reduced in a backwards stepwise process, sequentially dropping the fixed-effect term in the model that increased AIC the most. All analyses were completed in R 2.14.0 (R Development Core Team 2011) using lme4 (Bates *et al.* 2011) and nlme packages (Pinheiro *et al.* 2011).

Grazing and harvest were treated as continuous variables and measured as the proportion of leaves grazed or harvested per ramet and per genet. Fire was treated as a categorical variable with three levels: populations that burned during the dry season (usually February-April) of the study year (F0), populations 1-2 years post-fire (F12) and populations >2 years post-fire (NF). We chose these categories because of similarities in vital rates within categories and because of some uncertainty in time since fire for populations that had not burned in more than three years. Because only three populations burned during the study period, and these fires all occurred within a single site (Pillur Reserve Forest) within a single year (2010-2011), we initially excluded data from these three F0 populations from the analysis. After selecting the best set of predictors of ramet vital rates using only data from F12 and NF populations, we then re-ran the models with data from F0 populations included and tested for the effects of fire category, as well as for interactions between fire, starting size, harvest and grazing.

Ramet-level intensities of grazing and harvest were available only for surviving plants as dead ramets had no green leaves on which grazing intensity could be assessed. Because of this, we modeled survival as a function of grazing and harvest at the genet level. Both ramet- and genet-level intensities of grazing and harvest significantly affected rates of growth. We modeled sprout production as a function of genet-level intensities of grazing and harvest because genet-level measures explained more variance than ramet-level measures. This was not unexpected, given that sprouts are produced from the underground stem shared among ramets within a genet. We modeled the probability of flowering with ramet-level intensities of grazing and harvest.

Because vegetative sprouts have the potential to receive inputs of energy from the mother ramet and other ramets in the genet, they might be expected to have higher rates of survival and growth compared to seedlings. We therefore also tested whether rates of survival and growth differed between seedlings and sprouts.

We modeled the probability of fruiting using ramets known to be female. Ramets were known to be female if they fruited during the study or were within the same genet as a fruiting individual. In contrast to females whose flowering stalks elongated as fruit ripened, male ramets produced short flowering stalks that dried out during the fruiting season. Of 309 genets (excluding seedlings), 40 were known to be female, 74 were known to be male and 195 were of undetermined sex. Of 1,866 ramets with a maximum size >0.4 cm (the minimum observed fruiting size), 247 were known to be female, 604 were known to be male and 1,015 were of undetermined sex. Since an unknown portion of genets of undetermined sex are likely to be female, by excluding these from our model of fruiting probability, we have overestimated rates of fruiting. We therefore explored the sensitivity of modeled population dynamics to the rate of flowering and found that reducing the rate of flowering changed the absolute values of projected population growth rates (λ), but did not change conclusions about the relative effects of grazing, harvest and fire on palm population dynamics (Figure C.1).

Analysis of effects on population dynamics

We used integral projection models (IPMs, Easterling *et al.* 2000; Ellner & Rees 2006) to investigate the consequences of grazing, harvest, fire and their interaction on the projected population growth rates (λ) of mountain date palm ramets. Plant population dynamics have frequently been modeled with the use of population projection matrices (Caswell 2001; Crone *et al.* 2011). In these models, repeated (usually annual) measures of individual vital rates are analyzed by grouping individuals into a discrete number of stages, often based on size. The population projection matrix is determined by averaging vital rates across individuals within stages, producing the probability of an individual within one stage remaining in that stage, transitioning to another stage and/or producing new individuals in the next year. Population growth rates (λ) calculated from population projection matrices provide an estimate of the expected annual rate of population growth, with $\lambda>1$ indicating a growing population and $\lambda<1$ indicating a population expected to decline over the long term. In practice, however, λ is better used to compare relative growth rates between populations rather than to project actual future population growth (Menges 2000).

While population projection matrices are a valuable tool for understanding plant demography, they have several known limitations. The division of continuous state variables such as size into discrete categories for the construction of population projection matrices often results in artificial stages (Easterling *et al.* 2000). The number of categories used is often constrained by sample size and can influence model results (Vandermeer 1978; Moloney 1986; Chien & Zuidema 2006). There is also limited potential to incorporate variability in vital rates among individuals within stages, apart from again relying on discrete categories (e.g., Horvitz & Schemske 1995; Pfister & Wang 2005).

IPMs overcome these limitations by allowing vital rates and population dynamics to be modeled as a continuous function of plant size and by explicitly incorporating variation in fate among individuals of a given size into the model (Easterling *et al.* 2000; Ellner & Rees 2006). With IPMs, it is also possible to model the effects of other continuous factors, such as environmental conditions, on plant population dynamics. Here we use IPMs to explore population dynamics across gradients in grazing and harvest intensities.

We used a female-based model of ramet population dynamics because we found no difference in rates of survival, growth or vegetative reproduction between male and female plants, and no effect of the sex ratio on female fecundity (Caswell 2001; L.M. & T.T. unpublished data). Because we found differences in the rates of survival and growth of seedlings <0.5 cm petiole width compared to vegetative sprouts (see Table 4.2 and *Results*), we modeled seedlings <0.5 cm petiole width separately. As few solitary individuals >0.5 cm petiole width existed, we were unable to ascertain if modeled differences between solitary plants and ramets within genets above this size reflected real differences in behavior. Therefore we combined solitary palms and ramets >0.5 cm in our models.

Following Zuidema *et al.* (2010), we used a demographic kernel with four sections as the basis of our IPM:

$$\begin{bmatrix} k_{ss} & k_{sr} \\ k_{rs} & k_{rr} \end{bmatrix}$$

Each section of the kernel is a function $k(y,x)$ representing all possible transitions from size x at time t to size y at time t+1 and is composed of functions for survival, growth and reproduction (Easterling *et al.* 2000). The population is modeled as a population distribution function $n(x, t)$, representing the size distribution of ramets within a population.

The left column of the kernel represents the behavior of seedlings. The upper left-hand quadrant, k_{ss}, represents seedling survival and growth. The lower left-hand quadrant, k_{rs}, represents the growth of seedlings into ramets, which we defined to occur when a seedling reaches 0.5 cm petiole width in size. The left column of the kernel is determined by the product of the survival and growth functions for seedlings. The probability of a seedling becoming a ramet <0.5 cm petiole width in size was defined to be zero. The upper right-hand quadrant, k_{sr}, represents the production of new seedlings by ramets through sexual reproduction and is determined by the fecundity function, which is calculated as the product of 1) the survival of ramets, 2) the probability of fruiting, 3) the number of fruiting stalks per fruiting ramet and 4) the number of new female seedlings per fruiting stalk. The lower right-hand quadrant, k_{rr}, represents the survival and growth of ramets as well as the production of new ramets though vegetative reproduction. This is determined by the product of the survival and growth functions for ramets plus the size-dependent vegetative reproduction function. The vegetative reproduction function consists of the product of 1) the probability of producing a sprout, 2) the number of sprouts per sprouting ramet and 3) the size-distribution of new sprouts.

These growth, survival and reproduction functions are based on the above-mentioned statistical analyses of vital rates (see *Results* and Table 4.2). Modeled vital rates were a function of seedling or ramet starting size, genet-level grazing and harvest intensities and fire category. For vital rates that varied with ramet-level intensities of grazing and harvest, we used a multinomial model to determine predicted ramet-level rates based on genet-level rates and ramet size (Table C.2).

Although we did find evidence of effects of canopy openness and ramet density on some vital rates (Table 4.2), we focus on the effect of disturbance – grazing, harvest and fire – in this paper. We present results for IPMs with mean density and mean canopy openness observed across study populations. Density dependence had only a slight effect across the range of densities (ramets/genet) we observed (Figure C.2). Canopy openness only affected rates of growth and vegetative sprout production and did not interact with disturbance, except for slight increase in compensatory growth from grazing under more open canopies (Table 4.2).

We numerically integrated the demographic kernel using the midpoint rule (Ellner & Rees 2006) to generate IPMs across the observed range of grazing and harvest intensities, and their combination, for each of the three fire categories. We calculated the projected population growth rate (λ) for each IPM representing a distinct combination of grazing, harvest and fire category with the popbio package in R (Stubben & Milligan 2007).

Relationship between time since fire and grazing intensity

To test if the intensity of grazing declined with increasing time since fire, we used a mixed-effects logistic regression. The response variable was the number of grazed and ungrazed ramets in a population. We measured intensity as the fraction of ramets grazed because the number of leaves grazed per ramet was not recorded in 2009. Number of years since fire was the fixed predictor variable. Random effects included population (n=14) and sampling year (2009-2011). Because we were testing a specific hypothesis about the relationship between years since fire and grazing intensity, we used a likelihood-ratio test to test for a significant effect of years since fire.

Variation in harvest intensity with grazing intensity and time since fire

We again used a mixed-effects logistic regression to test if the intensity of harvest declined with increasing grazing intensities. The response variable was the number of harvested and unharvested leaves per ramet. Predictor variables were those factors found to be significant predictors of harvest intensity in our previous manipulative experiment (Chapter 3) that were also measured in this study. Those variables included ramet size (petiole width), grazing intensity (proportion of leaves grazed per ramet), fire category and a grazing-by-fire interaction. We limited this analysis to populations in which more than 5% of all leaves were harvested (n=7) to ensure that we were comparing rates of harvest among palms that could have been chosen for harvest during the study period. We also excluded populations that burned during the year (F0) due to the limited sample size. We used likelihood-ratio tests to assess the effects of grazing intensity, fire category and the grazing-by-fire interaction on harvest intensity.

Results

Survival and growth

Mountain date palm survival rates were high overall (93%, n = 2,282). A ramet's probability of survival increased with size (Table 4.2). Seedlings had a lower rate of survival than vegetative sprouts of the same size, though this difference tended to decrease with increasing size such that rates of survival were similar between individuals originating from seed and vegetatively at approximately 0.5 cm petiole width and larger (Figure 4.1a). Survival was not affected by grazing when less than 50% of leaves were grazed per genet but declined steeply with higher rates of grazing (Figure 4.1b). The trend of reduced survival with high intensity grazing was driven by two heavily grazed genets. However, we observed a similar relationship between survival and grazing in a manipulative experiment (Chapter 3) and, therefore, chose to model grazing in a stepwise fashion, with no effect below 50% leaves grazed per genet and a linear negative effect above 50% grazing (Table 4.2). We did not detect a significant effect of harvest on survival.

Rates of survival tended to be lowest in populations that burned during the year, intermediate in populations 1-2 years post-fire, and highest in populations >2 years post-fire (Figure 4.1c, Table 4.2). Although this trend was not significant, the trend of reduced survival with recent fire matched that of our manipulative experiment (Chapter 3). Because of the high sensitivity of long-lived plants to small changes in the rates of survival (Zuidema *et al.* 2007), we retained the fire effect in our model of survival in order to explore its potential impact on population dynamics. We also found evidence that survival rates were lower for ramets in large genets (Table 4.2).

Starting size was a significant predictor of a ramet's size in the following year (Table 4.2). Smaller ramets tended to grow, while larger ramets tended to shrink (Table 4.2, Figure 4.2a). Seedlings had lower growth rates than ramets of the same size that were produced vegetatively, though this difference again disappeared by the time seedlings reached 0.5 cm petiole width (Figure 4.2b). Ramet growth was significantly affected by grazing at both the ramet and genet levels. Ramets that were directly grazed at low intensities (10% leaves grazed per ramet) had increased growth relative to ungrazed ramets, but reduced growth with heavy grazing (Table 4.2, Figure 4.2c). Ramets in highly grazed genets grew less, independent of the level of direct grazing on the ramet (Table 4.2).

We found significant effects of both ramet- and genet-level harvest intensities on ramet growth (Table 4.2). We also found a significant harvest-by-size interaction (Figure 4.2d). Smaller ramets grew more with low intensities of harvest but grew less at high intensities. Harvest had a consistently negative effect on larger ramets that increased with harvest intensity. As with grazing, ramets in heavily harvested genets grew less, independent of the level of direct harvest on the ramet. This non-consumptive effect of harvest was less than that of grazing.

We found a significant effect of time since fire on the growth of palm ramets and a fire-by-starting-size interaction (Table 4.2). Small ramets in plots 1-2 years post-fire grew more than ramets that burned during the year and ramets >2 years post-fire. However, larger ramets grew more (or shrank less) in populations that burned (Figure 4.2a). Ramets 1-2 years post-fire consistently grew more than ramets >2 years post-fire (Table 4.2).

Vegetative reproduction

A total of 72 ramets produced at least one new sprout over the study period. The probability that a ramet produced a vegetative sprout increased with low-intensity grazing at the genet-level (> ~10% leaves grazed, Table 4.2, Figure 4.3a). However, with higher intensity grazing, sprout production declined and no sprout production was observed in genets with greater than 30% grazing. Ramet-level intensities of harvest and grazing did not significantly predict rates of vegetative reproduction. Vegetative reproduction did not vary significantly with fire category. We also found evidence of reduced sprout production in more open canopies (Table 4.2).

We observed a total of 89 new sprouts over two years. Ramets that produced new sprouts ("mother ramets") produced a mean of 1.25 sprouts each. We did not detect a significant effect of harvest, grazing, fire or other covariates on the number of sprouts produced.

The size of new sprouts was significantly affected by the size of the mother ramets, with larger mother ramets producing larger vegetative sprouts (Table 4.2, Figure 4.3b). The variance in sprout size also increased exponentially with the size of the mother ramet (Table 4.2). Sprouts produced in genets with more ramets were smaller in size than sprouts produced in genets with fewer ramets (Table 4.2).

Sexual reproduction

A total of 41 female ramets flowered in 2010 and 2011, producing 63 fruiting stalks. We found that the probability of flowering increased with ramet size (Table 4.2, Figure 4.4). The minimum observed fruiting size was 0.4 cm petiole width. Harvest reduced the probability of flowering (Figure 4.4a). We also found that rates of flowering were higher with recent fire (Figure 4.4b).

The number of fruiting stalks per flowering plant ranged from 1 to 4 (mean = 1.54, median =1). We did not detect a significant effect of harvest, grazing, fire or other covariates on the number of stalks produced. All new seedlings were 0.1 cm petiole width in size or else did not possess a fully expanded leaf, so their size could not be measured. We found no significant difference in behavior between the two types of seedlings and therefore assigned all new seedlings to a size of 0.1 cm petiole width.

We observed a total of 18 new seedlings across eight populations and two years, equivalent to 1 new seedling per 48 m^2 over two years. We detected no new seedlings in six populations from two sites (both reserve forests). With so few new seedlings, it was difficult to assess the effects of harvest, grazing, fire or covariates on seedling production. We observed an average of 0.28 new seedlings per fruiting stalk in the prior year. In areas with high mountain date palm harvest (reserve forest populations), this ranged from 0.034 seedlings/stalk 1-2 years post-fire to 1.0 seedling/stalk >2 years post-fire. In areas without high harvest (the protected area and forest fragment), we found 0.53 seedlings/stalk 1-2 years post-fire and 0.43 seedlings/stalk >2 years post-fire. No new seedlings were observed in the three populations exposed to fire during the previous year, but only two fruiting stalks were observed. Because of the uncertainty of the contribution of harvest history and fire to the production of seedlings, we modeled population dynamics both with the overall average value and with observed values for harvest and fire combinations. We assumed that half of new seedlings were female.

Population dynamics

Integration of models of survival, growth and reproduction suggested that mountain date palm populations can support low intensities of harvest (< ~20% leaves harvested per genet) and grazing (< ~15% leaves grazed per genet) without reducing projected population growth rates (λ). However, higher intensities of these activities could have negative effects on long-term population persistence. Our models of population dynamics also suggested that palm populations experience increased growth 1-2 years post-fire, but reduced growth in years with fire, as well as reduced >2 years post-fire (Figure 4.5).

The modeled effect of harvest on projected population growth rates depended on time since fire. Projected population growth rates of populations >2 years post-fire changed only slightly with changes in harvest intensity (Figure 4.5a). In populations that burned within the year or were 1-2 years post-fire, projected population growth rates increased slightly with low-intensity harvest and then declined with increasing harvest intensities. When the observed variation in number of seedlings/fruiting stalk with harvest intensity and time since fire was incorporated into the model, the negative effect of harvest occurred at much lower harvest intensities (Figure 4.5b).

As with harvest, low-intensities of grazing were associated with slight increases in projected population growth rates (Figure 4.5c). Projected population growth rates declined with higher intensities of grazing and especially with >50% leaves grazed per genet, beyond which grazing reduced rates of survival.

The combined effects of harvest and grazing varied with fire category (Figure 4.6). Projected population growth rates were highest in populations with 1-2 years post-fire and low intensities of harvest and grazing. However, high intensities of harvest or grazing reduced projected population growth rates in these populations. Again, the degree to which population growth rates declined with increasing harvest intensity depended on the estimated production of new seedlings (Figure 4.6b and d).

Relationship between fire and grazing

As expected, we found the proportion ramets grazed in a population was highest shortly after fire and declined with increasing time since fire (Figure 4.7). With the low re-occurrence of fire in our focal populations during the study period, years since fire and sampling year were significantly correlated ($r = 0.352$, $p = 0.02$). Because of this, the effect of years since fire on the proportion of ramets grazed was significant without sampling year included as a random effect in the model ($\chi^2 = 1085$, $df = 1$, $p < 0.001$), but not with sampling year ($\chi^2 = 1.33$, $df = 1$, $p = 0.25$).

Effects of grazing and fire on harvest intensity

As predicted from the results of our manipulative study (Chapter 3), harvest intensity declined with increasing grazing intensity ($\chi^2 = 14.10$, $df = 1$, $p < 0.001$). In contrast with the manipulative experiment, the effect of grazing on harvest intensity did not vary with fire category (grazing-by-fire interaction, $\chi^2 = 0.005$, $df = 1$, $p = 0.94$). However, the intensity of harvest was greater in areas 1-2 years post-fire compared to areas >2 years post-fire ($\chi^2 = 4.47$, $df = 1$, $p = 0.03$).

Discussion

Our results demonstrate that mountain date palm populations likely have the capacity to support – and may even benefit from – low intensities of grazing (< ~15% leaves grazed per genet) and harvest (< ~20% leaves harvested per genet). However, higher intensities of harvest and of grazing (especially ≥ 50% leaves grazed per genet) reduced palm population growth rates substantially. In addition, palm populations appeared to perform best 1-2 years post-fire but worse in years in which they burned or after >2 years post-fire. This suggests that fire return interval is a critical component of the palm's long term population dynamics.

The use of integral projection models (IPMs) proved especially valuable for understanding the effects of harvest and grazing across the gradient of intensities at which they occurred in the study populations, as the effects of these activities on population dynamics were non-linear. Modeling both mountain date palm vital rates and population dynamics revealed that compensatory ramet growth contributed to the resilience of mountain date palm populations to fire and to low intensities of grazing and harvest (Figure 4.2 a,c,d). However, this compensatory response had limits. High intensities of grazing and harvest reduced ramet growth and contributed to the negative population-level effects of these disturbances with increasing intensities. Modeling grazing and harvest intensities as factors, as would have been necessary with traditional population projection matrices, could have masked some of the changes in the effects of these activities across this gradient. Knowing the threshold intensities beyond which harvest and grazing negatively affect mountain date palm populations is important to preventing these activities from threatening long-term population persistence. A limited capacity for compensatory response to disturbance, at both the population and individual levels, is likely to be important for understanding and managing the responses of other plant species to changing disturbance regimes.

Compensatory growth and sprout production contributes to resilience to low-intensity grazing

Increased sprout production and growth of ramets under low-intensity grazing led to an increase in projected population growth rates (λ) with increased grazing up to ~10% leaves grazed per genet. The increase in clonal reproduction with this low-intensity grazing is evidence of another mechanism, in addition to compensatory growth, that likely contributes to mountain date palm's resilience to disturbance. This is consistent with findings from other clonal palms, which increased sprout production following disturbance (de Steven 1989) and for which clonal reproduction can buffer the effects of disturbance on population growth rates (Sampaio & Scariot 2010). At higher intensities, however, grazing reduced sprout production and growth of mountain date palm ramets.

Projected population growth rates declined especially sharply after grazing intensity increased beyond 50% of leaves per genet and began to cause declines in survival. Though there have been relatively few studies quantifying the population-level effects of large mammalian grazers on plants, a review of these suggests that where grazers have consumptive effects – as is the case with mountain date palm – the overall effect of grazing on population dynamics is negative (Maron & Crone 2006). The non-linear effect of grazing on λ in mountain date palm contrasts with the relatively steady decline with increasing grazing intensity found for the shrub *Vaccinium myrtillus*, the only other IPM of mammalian grazing to date (Hegland *et al.* 2010). However, grazing intensities used in the IPM for *Vaccinium myrtillus* were population-level measures of inferred grazing based on pellet counts. Our vital rate models were based on ramet-level measures of grazing intensity and projected population growth rates are modeled assuming equal intensities of grazing across genets and across ramets of a given size. With an understanding of individual-level effects of grazing as our models provide, it will be possible to explore the consequences of heterogeneity in grazing intensities within populations and its implications for populations' resilience to disturbance. Realistically, intensities of grazing vary among individuals within populations, and this variation might result in a smoother decrease in projected population growth rates with increasing population-level grazing intensity. Further modeling is planned to investigate the effect of intra-population variation in grazing and harvest intensities.

Compensatory growth contributes to resilience to low-intensity harvest

Harvest increased the growth of small ramets, contributing to increased projected population growth rates (λ) with increased harvest up to ~5% leaves harvested per genet. As harvest intensity increases beyond 5% leaves harvested per genet, λ declined due to reduced rates of fruit production and reduced growth of large ramets in mountain date palm. The increased rate of ramet growth that occurred both with low-intensity harvest and grazing is similar to increased leaf production following defoliation found in *Geonoma congesta*, another clonal understory palm species (Chazdon 1991).

The overall trend of reduced mountain date palm ramet growth with increasing size we found for mountain date palm also occurred in *Geonoma congesta*. At least part of the negative relationship between growth and size that we observed could also be due to regression to the mean resulting from measurement error. A ramet whose initial size is underestimated, yielding a small initial size, will tend to show more growth as the estimated measurement the following year is equally likely to underestimate or overestimate its true size. The reverse is true for ramets whose initial size is overestimated. Because repeated measures on individuals is an inherent part of demographic studies, regression to the mean is likely to contribute to patterns of growth observed in other models of population dynamics, though its effects have not been explored.

Palm leaf harvest has been recognized to have a high potential for sustainability, as harvest generally has little effect on high-sensitivity vital rates, such as survival (Zuidema *et al.* 2007; Schmidt *et al.* 2011). Consistent with our manipulative experiment (Chapter 3), we did not find support for an effect of leaf harvest on mountain date palm ramet survival. This contributes to the lack of a modeled negative effect of harvest rates of up to 85% on projected population growth rates in populations >2 years post-fire. However, it is still possible that non-significant differences in survival rates with harvest could have population-level consequences given the high sensitivity of survival for long-lived plant species. The documented effects of defoliation on other understory palms is mixed, with some species showing reduced survival at high intensities of harvest and other species exhibiting no change in survival with harvest (Zuidema *et al.* 2007).

Reduced flowering with harvest was evident in this study and is a common effect of harvest in other palm species (Ratsirarson *et al.* 1996; Zuidema *et al.* 2007). We did not detect a significant effect of harvest on flowering rates in our previous manipulative experiment (Chapter 3). Also in contrast with our manipulative experiment, the effect of harvest intensity on ramet growth did not vary with time since fire. These two differences might be related to the harvest history of the manipulative experiment location, where unharvested palms had a history of recent previous harvest, whereas in this study, populations without harvest had likely been unharvested for longer periods of time.

Fire reduces survival but increases growth and flowering

As expected, fire was associated with reduced survival but increased growth of surviving ramets. We also found increased rates of flowering following fire. Contrary to what we expected, the integrated effects of fire at the population level resulted in the highest projected population growth rates 1-2 years post-fire. The lowest projected population growth rates occurred in populations that burned during the year with high intensities of harvest or grazing. It is important to interpret the effect burning with caution, however, as it is based on only three populations within a single site that burned during the same year, and its relative effect compared to other fire categories depended on assumptions about seedling production (Figure 4.5a and b). Studies of the effect of fire on palm demography are rare, despite the prevalence of palms in fire-prone ecosystems. Our results are consistent with the findings of Souza and Martins (2004), in which rates of mortality of *Attalea humilis* seedlings and juveniles increased following fire but that population dynamics were largely resilient to fire.

Our findings also provide an explanation for the local perception that mountain date palm populations benefit from fire (Chapter 2). Palm ramets that survive burning experience increased growth, and this increased growth is likely observable by local leaf harvesters. Burned populations also appear to experience reduced survival. The difference in survival is slight – only a few percentage points – and may be difficult to perceive, but it is still important to palm population dynamics. Whether the net effect of fire increases or reduces palm population growth rates over the long term is likely to depend on the frequency of fire, and the trade-off between increased growth and flowering and reduced survival that time since fire represents, as well as the effects of fire on subsequent intensities of grazing and harvest.

If the ecosystems in which mountain date palms occur are to be managed for conservation of native biodiversity, the implications of fire frequency for other species within the community must also be considered, as not all species in a community respond to fire in the same way or have the same optimal fire return interval (Menges 2007). As previous research on tree communities in dry forests in South India has shown, frequent fires can increase the density of some species, while reducing overall species diversity (Saha & Howe 2003). Models of the population dynamics of the tree species and economically important NTFP, *Phyllanthus emblica*, which co-occurs with mountain date palm in the Western Ghats, suggest that this species may decline under the 2-3 year fire return intervals that are currently occurring in the region (Sinha & Brault 2005).

Non-consumptive effects of grazing and harvest

We found reduced ramet growth with increasing intensities of genet-level grazing after statistically controlling for the direct ramet-level effects of grazing. In other words, ungrazed ramets in genets with no grazing grew more than ungrazed ramets in genets in which other ramets were grazed. While this could be due in part to shared resources among ramets within a genet, results from our manipulative experiment (Chapter 3) suggest that the negative effects of grazing on palm demography are due in part to non-consumptive effects. This suggests that negative effects of grazing on palm demography are due in part to non-consumptive effects. Non-consumptive effects are the effects of grazers apart from the direct effects of biomass removal, and potentially include trampling and changes to soil properties. We also found evidence of non-consumptive effects of harvest (Table 4.2). The smaller estimated effect size of genet-level harvest intensity compared to genet-level grazing intensity indicates that the non-consumptive effects of grazing are greater than those of harvest. These results are consistent with our findings for this species from a manipulative experiment (Chapter 3), and with findings of non-consumptive effects of grazing on non-clonal plant species (e.g., Heckel *et al.* 2010), which suggest the non-consumptive effects of herbivory are likely to be common. The effects of ungulate herbivory on plant demography have often been simulated by comparing the demographic rates across all individuals within a grazed population to demographic rates of the subset of individuals within the same population that have escaped herbivory (e.g., Knight 2004; McGraw & Furedi 2005; Farrington *et al.* 2009). This approach will underestimate the negative impacts of grazing if, as we found, ungrazed individuals are negatively affected by non-consumptive effects of grazing.

Sensitivity of mountain date palm population dynamics to fecundity rates

Reductions in flowering have generally been projected to have little effect on long-term palm population dynamics because fecundity tends to be a low-sensitivity vital rate (Zuidema *et al.* 2007). Our findings for mountain date palm differ from those for other palm species, and long-lived plant species in general, in that mountain date palm projected population growth rates were sensitive to estimates of flowering rates and seedling recruitment (Figure 4.6d). We plan to carry out prospective and retrospective analyses (i.e., elasticity analysis and life table response experiments) to further clarify which vital rates contributed to the observed effect of harvest on mountain date palm population dynamics. Accurately determining the fecundity rates is especially challenging for long-lived species because rates as often small and highly variable across years (Wright *et al.* 2005). In cases where disturbances are expected to change fecundity rates and population dynamics are sensitive to these changes, obtaining precise estimates of fecundity rates will be particularly important.

We found evidence of an interaction between fire and harvest on palm fecundity. High intensities of harvest caused declines in projected population growth rates with recent fire but had less of an effect on populations >2 years post-fire (Figure 4.5a). However, the degree to which harvest caused declines in projected population growth rates depended on assumptions about the effect of harvest on seedling recruitment (Figure 4.5a and b). We observed few new seedlings in reserve forests sites with a history of harvest burned within the past two years. With such a small sample size, it is unclear if the lack of new seedlings is due to harvest. Palm leaf harvesters in some areas cut fruiting stalks to tie together bundles of harvested leaves (L.M. personal observation). If fruiting stalks are cut before fruit mature, this might reduce seedling recruitment. According to harvesters, flowering stalks are not a preferred method for tying palm leaf bundles. Substituting alternative materials (e.g., cord made of grasses) could reduce pressure on palm populations if the removal of fruiting stalks truly is limiting seedling recruitment. Seeds collected from harvested sites had high viability and good germination rates when sown in a common garden (L.M. & T.T. unpublished data). This suggests reduced seedling recruitment could potentially be offset by outplanting seeds.

Intensity of grazing affected by time since fire

While we did not find any statistical interactions between grazing and fire in models of palm vital rates, we did find evidence that grazing intensity depends on time since fire (Figure 4.7) Although the effect of time since fire was confounded with year in our study, increased grazing with more recent fire would be consistent with findings from other savanna and grassland ecosystems (Wilsey 1996; Fuhlendorf *et al.* 2009; Winter *et al.* 2011).

Importantly, we observed that high intensities of grazing following fire occurred even at sites without livestock, indicating that wild herbivores are also responding to fire and that livestock are not solely responsible for this trend. In areas with livestock grazing, it might be expected that reductions in grazing could benefit palm populations and, therefore, palm leaf harvesters. However, if reduced livestock grazing led to increased grazing by wild ungulates, as has been found elsewhere in South India (Madhusudan 2004), reductions in livestock grazing might not reduce total grazing on mountain date palm.

With little information on the relationship between fire and grazing of wild herbivores in India (but see Sankaran 2005), interpretation of the observed relationship between fire and grazing is necessarily speculative. Different herbivore species in East Africa have been found to respond differently to fire, with relative preference for burned patches dependent on body size (Wilsey 1996; Sensenig *et al.* 2010). Fire may also influence the heterogeneity of grazing within a landscape (Archibald & Bond 2004). Further investigation of the effect of different herbivores and herbivore assemblages and the relationship between herbivory and fire in this system will be critical to understanding not only the population dynamics of mountain date palm, but also other savanna woodland species in India.

Intensity of harvest varies with grazing intensity and time since fire

In addition to the apparent relationship between fire and grazing, the intensity of harvest was greater in populations with recent fire. Harvesters reported a preference for harvesting in recently burned areas (Chapter 2). Plants recovering from fire have brighter green leaves, which are considered higher quality. Fire also removes old, senescing leaves, improving access to new leaves for harvest.

While the intensity of harvest is likely to increase with recent fire, this pattern is complicated by the relationship between harvest and grazing intensity. Our findings of reduced harvest intensity with increasing grazing intensity in this study and our manipulative experiment (Chapter 3) suggest that grazing can limit leaf harvest, as grazed leaves have no worth to harvesters who require full, intact palm leaves for brooms.

Ultimately, our results suggest that although the highest palm population growth rates are expected in populations with recent fire and very low grazing and harvest intensities, mountain date palm populations may rarely experience this combination of conditions because of the preference of harvesters and herbivores for recently burned areas. Understanding how the intensities of harvest and grazing and their effects vary under different fire return intervals will be crucial if these systems are to be managed both for their benefits to humans through palm leaves and cattle fodder and for their conservation value in terms of plant and animal diversity.

Further directions

Prospective and retrospective analysis will contribute to better understanding how observed changes in vital rates with grazing, harvest and fire contribute to changes in projected population growth rates, and aid in assessing possible management strategies to minimize the negative impacts of harvest. In addition, while the effects of density dependence were slight, inclusion of density dependence in modeled population dynamics could provide a more realistic assessment of population dynamics in the face of disturbance (Silva Matos *et al.* 1999). It is possible, for example, that mountain date palm populations are somewhat more resilient to high-intensity grazing than the models presented here illustrate, if reduced survival from high-intensity grazing is offset by increased survival of remaining individuals, as is suggested by our model of survival (Table 4.2).

Given the substantial effects of disturbance (grazing, harvest and fire), as well as evidence of negative density dependence, exploration of the transient dynamics of mountain date palm populations is likely to yield results that are more relevant for understanding the species' real-world dynamics than the long-term projections presented here (Ezard *et al.* 2010). While transient dynamics have been frequently modeled with population projection matrices (Stott *et al.* 2011), IPMs are expected to provide a better representation of these dynamics (Easterling *et al.* 2000). In addition, while high intensities of harvest and grazing might be sustainable from a ramet-level perspective, these activites could have substantial effects on the structure and total biomass of mountain date palm populations. Other studies have found that even when harvest does not threaten population persistence, it can shift population structure such that remaining individuals are too small for harvest and overall population biomass is greatly reduced (e.g., Guedje *et al.* 2007). Given that harvest and grazing lead to reductions in size of surviving ramets, and that harvest requires ramets with leaves > 60 cm, such a shift could occur in mountain date palm as well. The application of IPMs to modeling the transient dynamics and structure of mountain date palm populations under different harvest and grazing intensities and fire return intervals is a high priority for future research.

Table 4.1. Characteristics of study sites, including the presence (+) and absence (-) of commercial mountain date palm harvest and grazer species. Sites are presented in order of occurrence from west to east.

Site:	*Pillur Reserve Forest*	*Palaniappa Estate Forest Fragment*	*Sathyamangalam Reserve Forest*	*BRT Wildlife Sanctuary*	*Male Mahadeshwara Hills Reserve Forest*
No. plots:	4	2	2	4	2
No. ramets measured	670	297	365	666	334
Commercial harvest of mountain date palm:	+	-	+	-	+
Herbivores present in plots[a]**:**					
Livestock	-	-	+	-	+
Elephant[b]	+	-	+	+	-
Gaur	+	+	+	+	+
Sambar deer	+	+	+	+	+
Range of years since fire (2010/2011)	1-2/0-3	1-3/2-4	1-3/2-4	2-6/3-7	1-2/2-4
Elevation (m)	725-800	1600-1700	1450-1475	1100-1400	1285-1300

[a] Based on dung transects in plots from 2010-2011

[b] Elephant dung did not appear within study plots in MM Hills, but elephants were observed at the study site during this time.

Table 4.2. Estimated coefficients from mixed-effect models of the probability of survival, rate of growth, probability of flowering, probability of producing a sprout and mean sprout size for mountain date palm ramets.

Fixed effects	**Estimate**	**SE**
Probability of surviving to t+1		
Intercept (F0)	2.53	0.647
Recent fire (F12)	0.394	0.419
No fire (NF)	0.641	0.507
Seedling	-2.10	1.02
Ramets per genet[a]	-0.274	0.208
Size at start[b]	2.41	0.456
Size at start[b] x seedling	4.17	3.60
Grazing (genet) >0.5	-29.0	5.43
Size at t + 1 of surviving ramets[c]		
Intercept (F0)	0.161	0.0295
Recent fire (F12)	0.0945	0.0259
No fire (NF)	0.0428	0.0296
Seedling	-0.152	0.0309
Size at start[b] (F0)	0.777	0.0511
Size at start[b] x F12	-0.147	0.0467
Size at start[b] x NF	-0.179	0.0567
Size at start[b] x seedling	0.291	0.0585
Canopy openness[d]	0.00130	0.000791
Grazing (ramet)	0.311	0.0425
Grazing (ramet)^2	-0.370	0.0555
Grazing (ramet) x canopy openness[d]	0.00325	0.00113
Grazing (genet)	-0.157	0.0400
Harvest (ramet)	0.554	0.0386
Harvest (ramet)^2	-0.266	0.0351
Harvest (ramet) x size at start[b]	-0.345	0.0434
Harvest (genet)	-0.0813	0.0238
Probability of flowering at time t		
Intercept (recent fire, F12)	-8.02	1.15
No fire (NF)	-2.414	0.515
Size[b]	9.09	1.31
Harvest (ramet)	-3.31	1.54
Probability of producing a sprout		
Intercept	-4.66	0.231
Grazing (genet)	18.8	10.6
Grazing (genet)^2	-173	103
Canopy openness[d]	-0.0291	0.0123
Mean sprout size at t + 1[e]		
Intercept	0.223	0.0629
Starting size of mother ramet[b]	0.202	0.102
Ramets per genet[a]	-0.0731	0.0268

[a] Log-transformed and centered

[b] Petiole width of the longest leaf

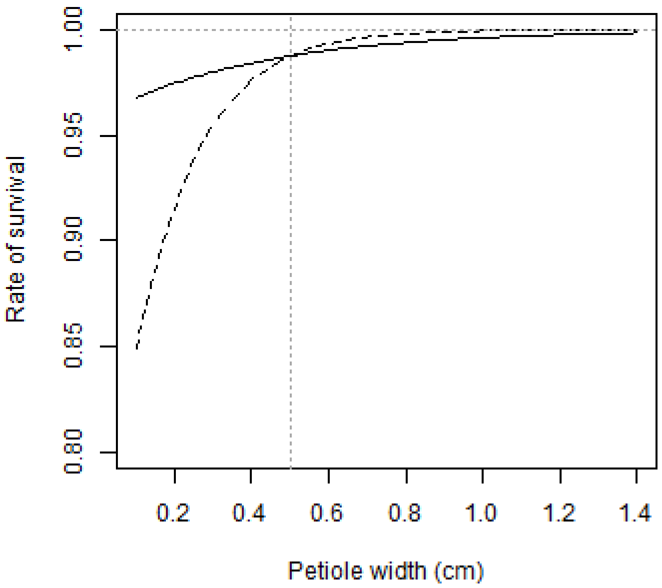
[c] Variance around the growth curve, $\sigma^2 = 0.0181$

[d] Centered

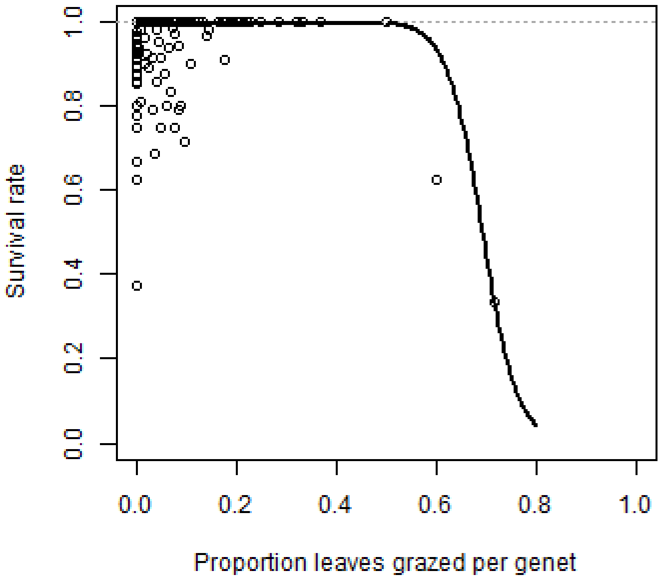
[e] Variance around the predicted sprout size, $\sigma^2 = 0.00567*\exp(2.86*\text{starting size of mother ramet})$

Figure 4.1. Modeled rates of mountain date palm ramet survival varied a) between seedlings (dashed) and ramets (solid) by size; b) with grazing intensity; and c) with fire category (thin dashed – exposed to fire in the past year, thin solid – fire within the past 1-2 years, thick solid – no fire within 2 years) by size. The vertical dashed line in panel a at 0.5 cm width indicates the size above which single individuals were considered to have the same rate of survival as vegetatively produced ramets. Points in panel b show the raw observed rates of ramet survival per genet by grazing intensity.

a)



b)



c)

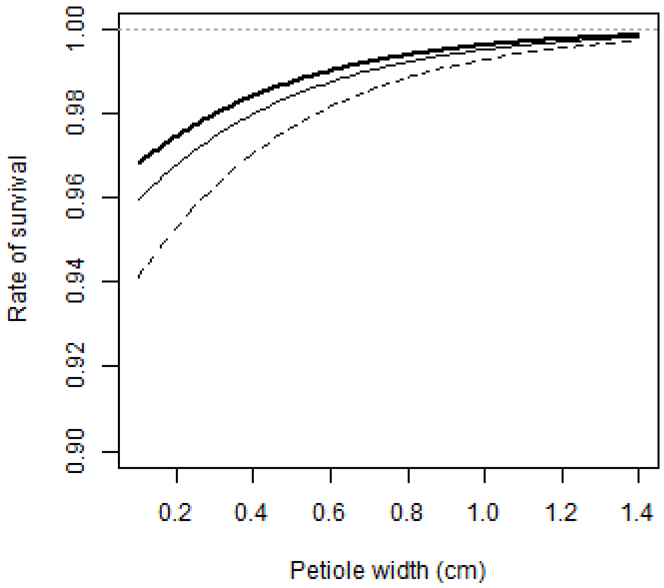
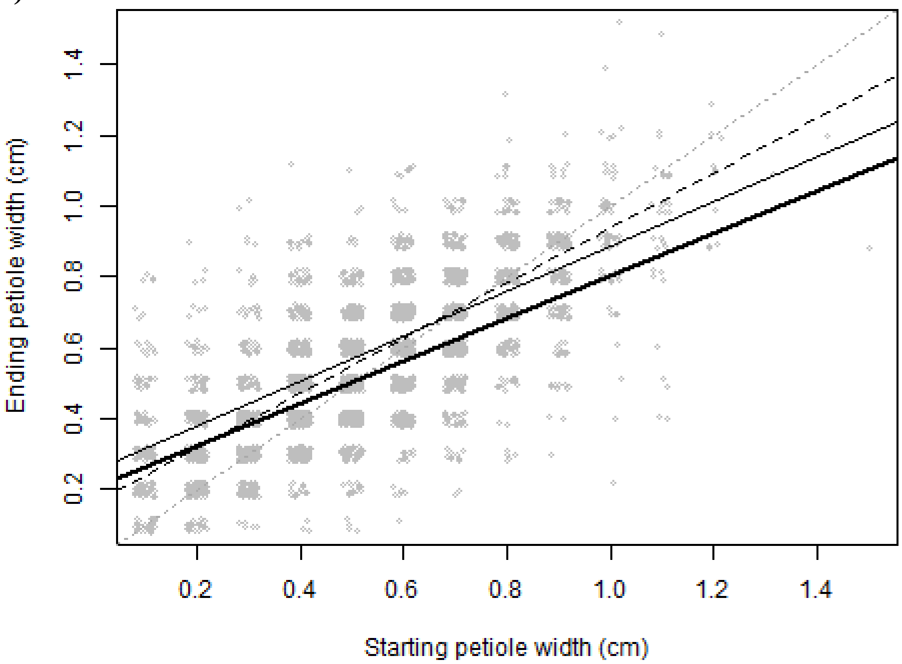
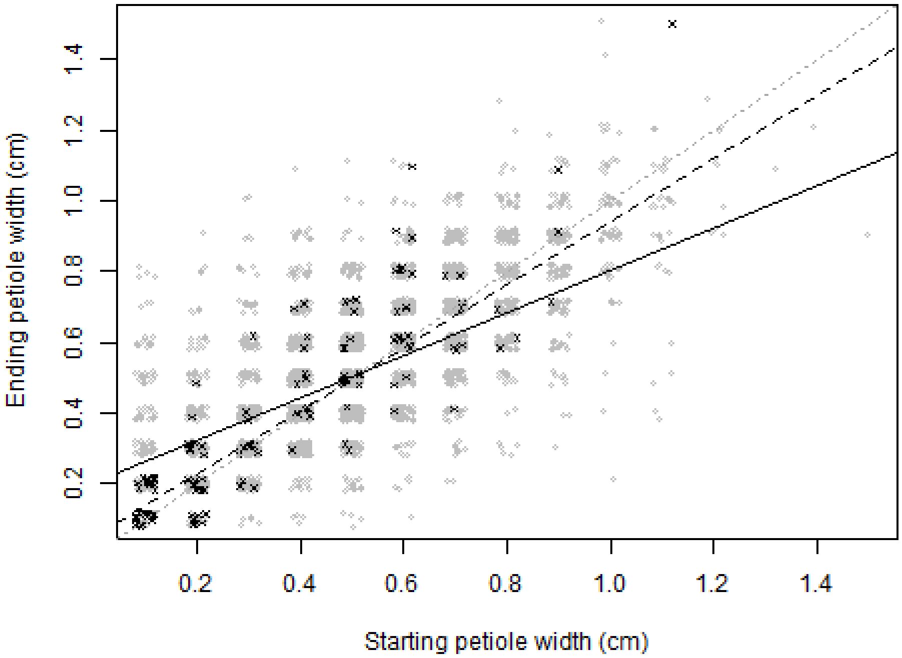

Rate of survival
0.90
0.92
0.94
0.96
0.98
1.00
0.2
0.4
0.6
0.8
1.0
1.2
1.4
Petiole width (cm)

Figure 4.2. Modeled variation in mountain date palm ramet size as a function of starting size and a) fire category (thin dashed – burned during the year, thin solid – 1-2 years post-fire, thick solid – >2 years post-fire); b) seedlings (dashed) and ramets (solid); c) genet-level grazing intensity; and d) genet-level harvest intensity. Points show jittered raw growth data. The gray dotted 1:1 line indicates no change in plant size, with points above indicating growth and points below indicating shrinkage. In panel b, points from ramets are shown as gray circles, while points from seedlings or solitary individuals are shown as black crosses.

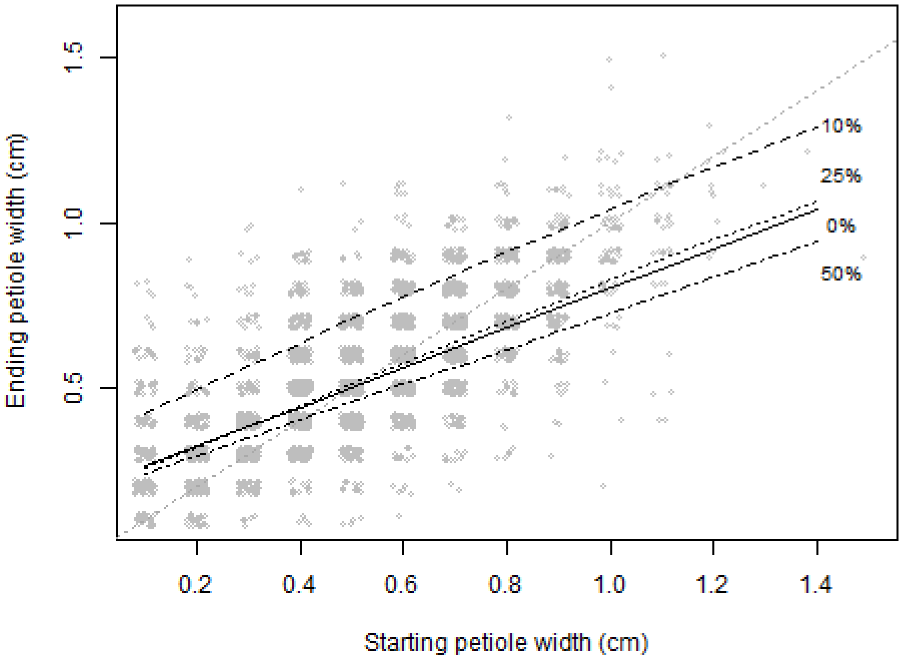
a)



b)



c)


Ending petiole width (cm)
0.5
1.0
1.5
Starting petiole width (cm)
0.2
0.4
0.6
0.8
1.0
1.2
1.4
10%
25%
0%
50%

d)

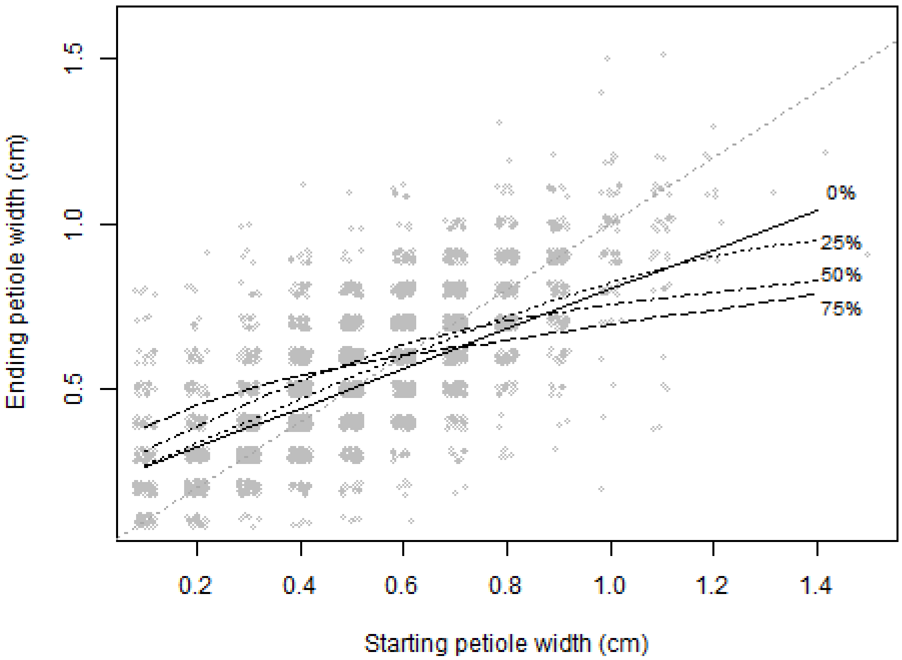
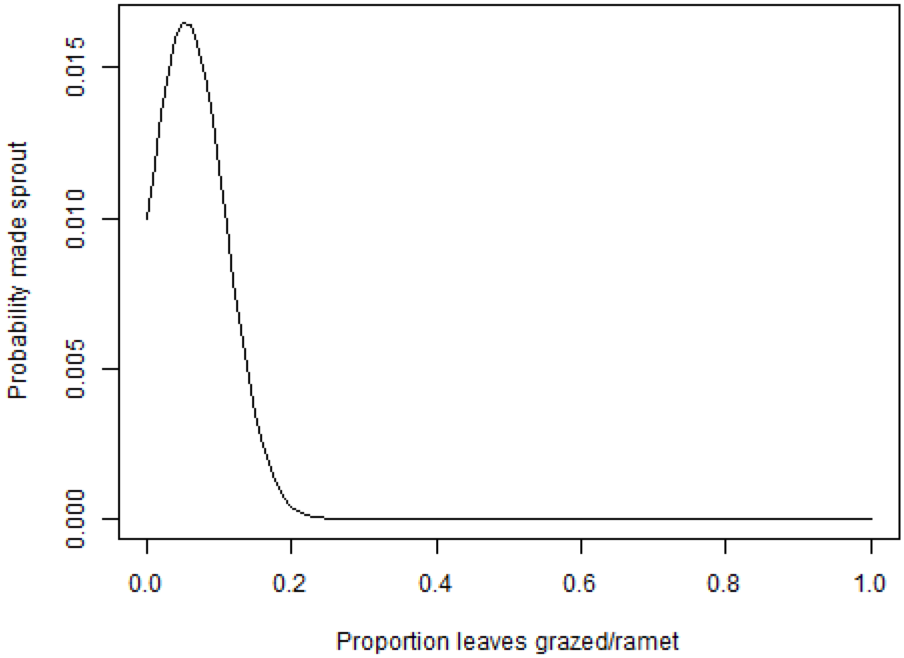

Ending petiole width (cm)
0.5
1.0
1.5
Starting petiole width (cm)
0.2
0.4
0.6
0.8
1.0
1.2
1.4
0%
25%
50%
75%

Figure 4.3. Modeled rates of sprout (new ramet) production varied with grazing intensity (a), while the mean and variance of sprout size varied with the size of the mother ramet (b).

a)



b)

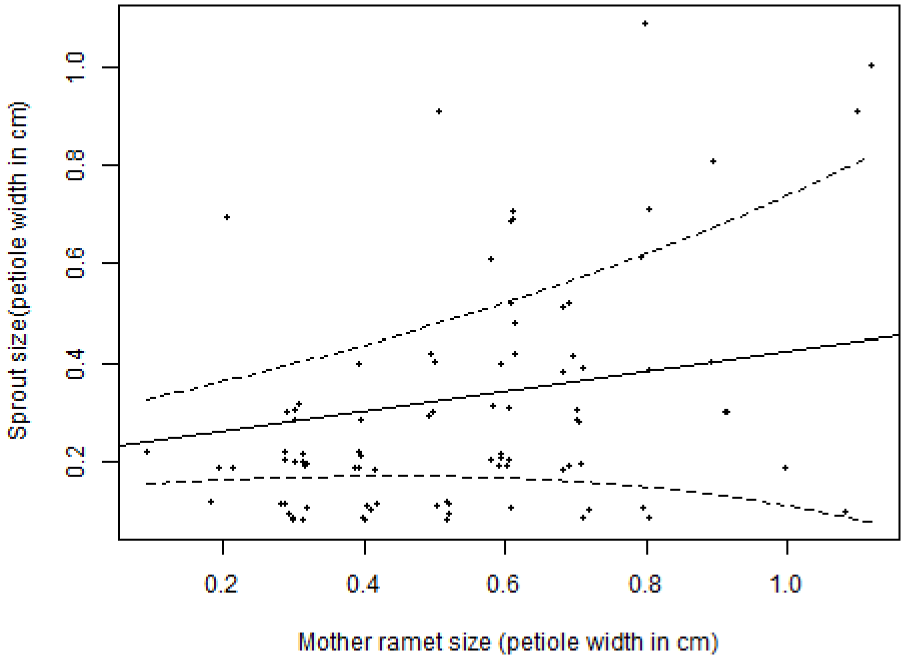
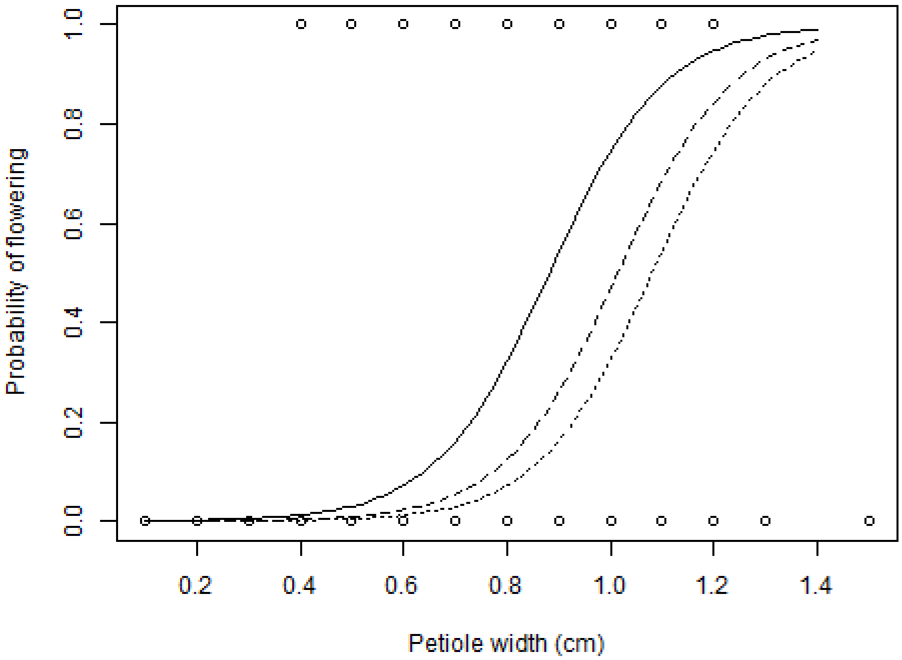


Figure 4.4. The modeled probability of mountain date palm ramet flowering a) declined with increasing harvest intensity (solid line – no harvest, dashed line – 25% harvest, dotted line – 50% harvest); and b) increased 1-2 years post-fire (thin line) compared to populations >2 years post-fire (thick line).

a)



b)

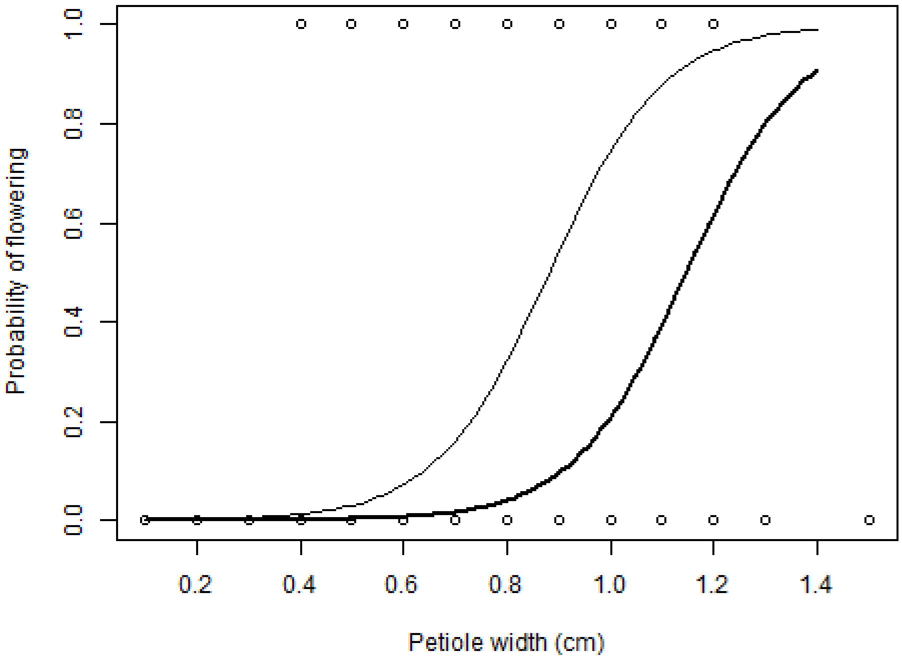
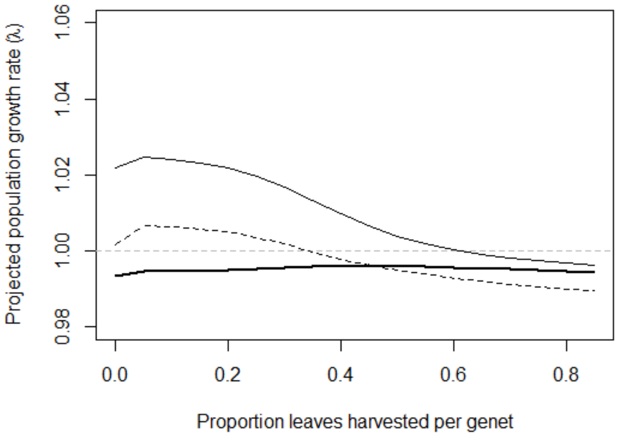
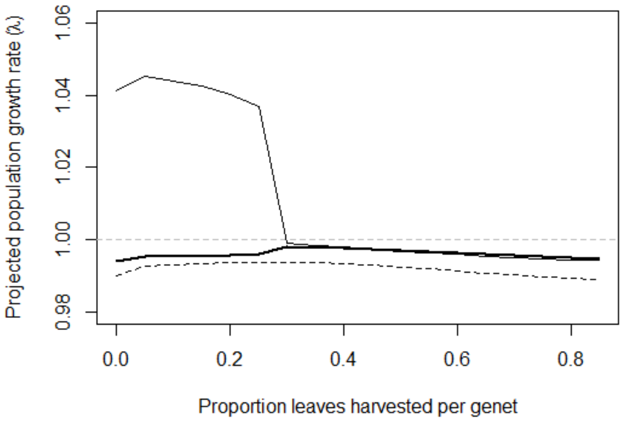


Figure 4.5. The effects of harvest (a and b) and grazing (c) on palm population dynamics by fire category (dashed – burned during the year, thin solid –1-2 years post-fire, thick solid – >2 years post-fire). Panel a shows the effects of harvest assuming an average seedling recruitment across all populations, while panel b shows the effects of harvest using observed seedling recruitment rates by fire category and harvest history (with high harvest rates of recruitment beginning at 30% harvest intensity).

a)



b)



c)

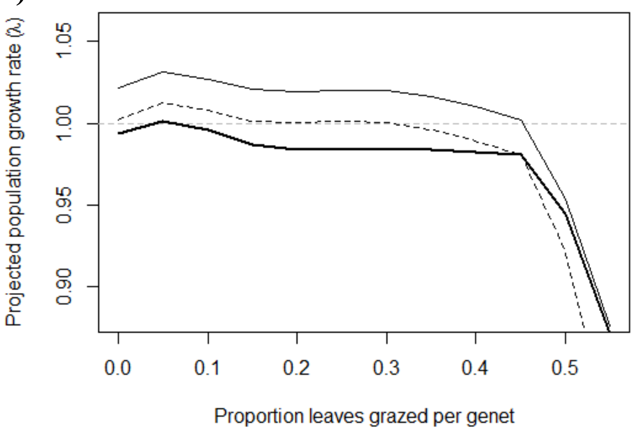


Figure 4.6. The interactive effects of harvest and grazing on the projected population growth rates (λ) of mountain date palms as modeled for populations a) >2 years post-fire, b) 1-2 years post-fire, and c) burned during the year, assuming no effect of harvest or fire on seedling recruitment rates. Panel d shows λ for populations 1-2 years post-fire using observed seedling recruitment rates by fire category and harvest history (with high harvest rates of recruitment beginning at 30% harvest intensity).

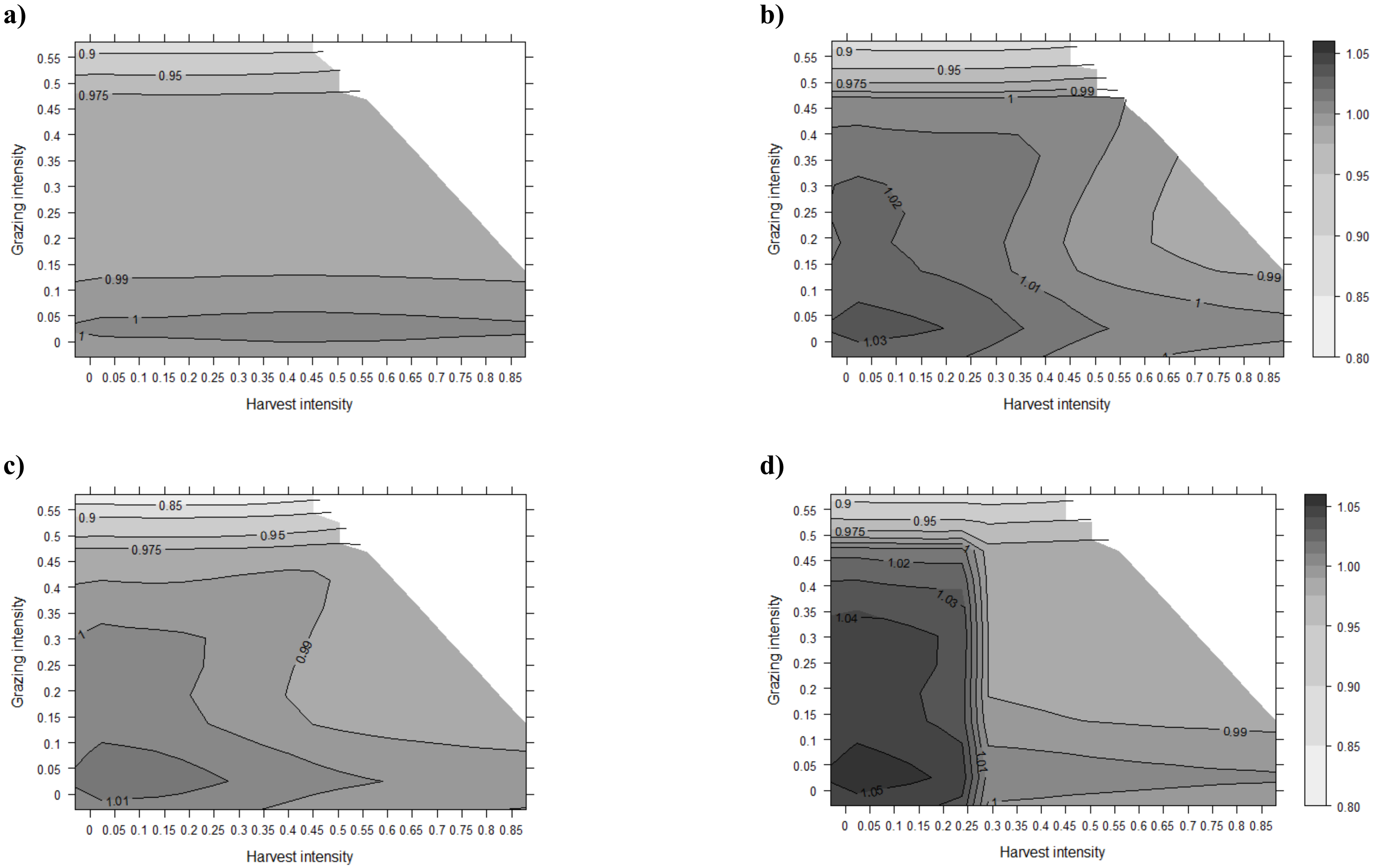
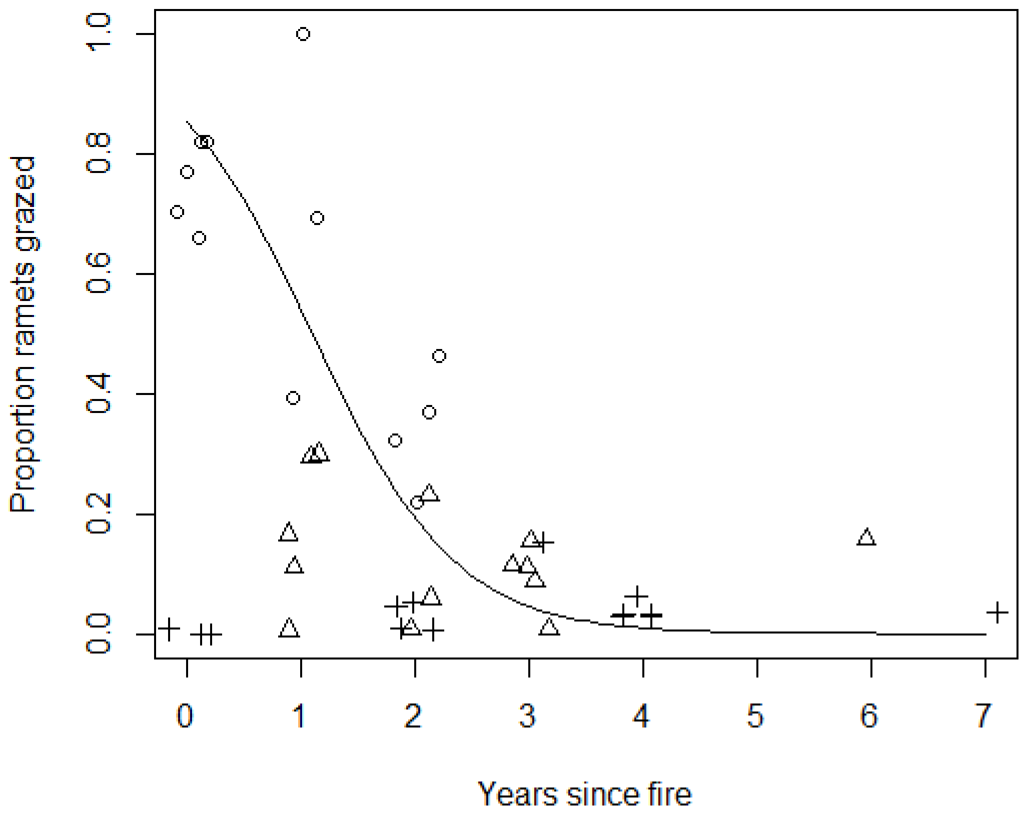


Figure 4.7. Proportion of mountain date palm ramets grazed per population as a function of time since fire. Points are observed proportions jittered to minimize overlap and differ in shape by year (circle = 2009, triangle = 2010, cross = 2011).



CHAPTER 5. SHIFT IN PLANT DIVERSITY FROM OVERSTORY TO UNDERSTORY WITH HUMAN LAND USE IN A SEASONALLY DRY TROPICAL ECOSYSTEM

Lisa Mandle and Tamara Ticktin

Abstract

Most of the world's remaining terrestrial biodiversity exists in tropical ecosystems affected by human activities. Understanding the conditions under which human land use is compatible with the maintenance of tropical diversity is critical for effective conservation efforts. Despite the threats to seasonally dry tropical ecosystems, little is known about the impact of human land use change on their conservation value. We used savanna woodlands within the Western Ghats biodiversity hotspot as a case study to understand the effects of human land use on plant diversity. We investigated the effects of three common land-use activities – biomass extraction, livestock grazing and ground fire – on plant richness, diversity and the geographic ranges of species present. Overall species richness and diversity were similar across sites with and without biomass extraction and livestock grazing. Understory diversity and richness increased with livestock grazing. Overstory diversity, tree seedling diversity and tree seedling richness decreased with more recent fire. We found no effect of biomass extraction on species richness or diversity. Areas with biomass extraction tended to have more common species and fewer narrowly-distributed species than areas with fewer human activities, though this difference was not statistically significant ($p = 0.148$). Our results suggest that a mosaic of protected areas along with areas managed for biomass extraction and livestock grazing would be an effective way to balance the conservation of plant diversity with local communities' needs while maintaining overall levels of plant species diversity in these savanna woodlands.

Introduction

Tropical ecosystems are valued for the diversity of species they harbor and the ecosystem services they provide, but these species and services are threatened by ongoing land use change (Bradshaw *et al.* 2009). Tropical ecosystems with low levels of human influence are few and are inadequate for preserving remaining biodiversity (Gardner *et al.* 2009). Human-managed landscapes must be incorporated into conservation strategies.

To effectively conserve remaining biodiversity, it is critical to determine to what degree conservation of biodiversity is possible in human-managed tropical systems (Chazdon *et al.* 2009).

The Western Ghats region of India provides a highly suitable location to assess the compatibility between human land use and biodiversity. The Western Ghats is the most densely populated of all biodiversity hotspots (Cincotta *et al.* 2000; Mittermeier *et al.* 2005).The region has a long history of human land use, with humans present for over 12,000 years (Chandran 1997), as well as traditional conservation practices such as the recognition of sacred groves (Gadgil & Vartak 1976). The high densities of both people and biodiversity make understanding the interactions between land use and diversity especially important.

In addition, understanding the compatibility between human land use and biodiversity conservation is particularly salient given the recent passage and implementation of India's Forest Rights Act, which recognizes local communities' rights to manage natural resources and biodiversity and provides for joint management of these resources with the state (Bawa *et al.* 2011). This represents a substantial change in government policy, which historically sought to exclude local communities from forest areas while managing forests for commercial products such as timber (Saxena 1999). While the Forest Rights Act may lead to some degree of land use change, it provides an opportunity for information about the effects of human land use on biodiversity to be incorporated into management decisions at a local level. It also provides an opportunity for decisions about how to balance human needs with biodiversity conservation to be made in a more participatory manner.

Previous research has shown that human-managed areas can contribute to the conservation of native plant, bird, insect and mammal diversity (e.g., Estrada & Coates-Estrada 1997; Gascon *et al.* 1999; Mayfield & Daily 2005; Ranganathan *et al.* 2008; Anand *et al.* 2010). However, these studies have focused primarily on tropical moist forests. Less is known about the compatibility of human land use and conservation in seasonally dry tropical ecosystems. Although tropical dry forests, savannas and woodlands harbor lower levels of plant diversity than humid forests, these ecosystems are centers of land conversion and fragmentation, provide important provisioning and regulating ecosystem services, and are less protected than moist forests (Murphy & Lugo 1986; Chape *et al.* 2005; Balvanera *et al.* 2010). As a result their conservation in human-managed landscapes is especially critical. In the Western Ghats, seasonally dry tropical ecosystems are important sources of fuelwood, livestock fodder and non-timber forest products (NTFPs) for local communities (Davidar *et al.* 2010), as well as critical habitat for endangered megafauna (Das *et al.* 2006). We cannot expect to predict or effectively cope with biodiversity losses from land use change if these seasonally dry tropical ecosystems are ignored.

The diversity of species within an ecosystem is just one of several criteria used to assess conservation value (Gadgil 1992). The identity of species is also important, with more value often accorded to rare species, including species that are endemic or narrowly distributed, because of the greater possibility of their permanent extinction. In addition, over the short term, species invasions can increase biodiversity at local scales (Sax *et al.* 2007), but invasion by non-native species does not increase an ecosystem's conservation value. Assessing the conservation value of human-managed lands therefore requires accounting for possible differences in commonness, rarity and invasiveness within communities, in addition to overall levels of diversity.

In this study, we assessed the degree to which three very common forms of human land use (specifically, biomass extraction of fuelwood and NTFPs, livestock grazing and ground fire) are compatible with the maintenance of plant diversity in savanna woodland ecosystems in the Western Ghats, India. We focused on the effects of these forms of land use because of their prevalence in tropical forests in Asia and throughout the tropics (FAO 2010). We addressed three research questions:

1) Does plant species richness and diversity vary with land use (specifically, biomass extraction, livestock grazing and fire)?
2) Does the breadth of the geographic range of species (as a proxy for rarity and species-based conservation value, Gadgil 1992) vary with land use?
3) What are the implications of these findings for the conservation of native plant diversity with human land use in the savanna woodlands of the Western Ghats?

Given the long history of our focal forms of land use in the Western Ghats, we expected they would result in little change in diversity and richness. We expected that more intensive land use would be associated with more common, widely distributed species and fewer narrowly distributed species.

Methods

Study sites & design

Our study was located in savanna woodlands of the southern Western Ghats in the South Indian states of Tamil Nadu and Karnataka. Study sites encompassed three reserve forests, one protected area and a remnant forest fragment on privately owned land (Table 5.1), representing a range of land use intensities. The forest fragment was adjacent to Pillur Reserve Forest and formed the western study region. Biligiri Rangaswamy Temple Wildlife Sanctuary adjoins Sathyamangalam Reserve Forest and is within 45 km of Male Mahadeshwara Hills Reserve Forest, forming the eastern study region. The study regions were separated by ~75 km. We treated the study area as two regions to account for possible differences in species pools and differences in climate resulting from the precipitation gradient from the Western Ghats rain shadow.

We ranked sites in land use intensity (LUI) from 1 to 3 (Table 5.1) based on levels of biomass extraction (commercial NTFP harvest and fuelwood collection or not), and livestock grazing (present or absent). The protected area and forest fragment were ranked 1 because commercial biomass extraction did not occur there (though low levels of extraction may occur), nor did livestock grazing. Pillur Reserve Forest was ranked 2 because biomass extraction but not livestock grazing occurred there. Sathyamangalam and Male Mahadeshwara Hills reserve forests were ranked 3 because both biomass extraction and livestock grazing were present. See Appendix D for additional information on the assessment of biomass extraction and livestock grazing intensities.

The protected area was managed as a reserve forest until it was declared a wildlife sanctuary in 1973. Collection of wood from standing trees has been banned since 1987 (Shankar *et al.* 1998a), while commercial NTFP extraction was banned in 2004. Ground fires, often set by local people to manage for fodder and harvested plant species, are a frequent occurrence. Within reserve forests, it is rare to find areas that have not burned within the past three years; fires occur with less frequency in the protected area. The fire frequency has likely increased over the past century (Kodandapani *et al.* 2004).

Within each of the five study sites, we established two to four 20 x 20 m study plots, selected to represent variation in fire history within the sites (Table 5.1). We established a total of eight plots in reserve forests, four in the protected area and two in the forest fragment. To maximize the similarities in community composition, we located our plots in areas with populations of the mountain date palm (*Phoenix loureiri*), which is harvested commercially from the reserve forest sites but not currently from the protected area or remnant forest fragment.

Data collection

Community composition surveys

We measured the overstory and understory in 2010 and seedlings only in 2011. For the overstory, we counted the number of stems > 1 cm diameter breast height (dbh) within the full plot and recorded dbh. The understory community was measured in eight 1 x 1 m subplots with a stratified-random placement (two plots within each quadrant of the full plot). We recorded the percent cover category by species for all shrubs and forbs whose maximum size was < 1 cm dbh based on visual estimation. The total percent cover of grasses and sedges was also recorded but without identification to species. Non-vascular plants were omitted. All estimates were carried out by the same observer. Percent cover categories included ≤ 1%, 1-5%, 5-10%, 10-20% and subsequent 10% ranges. Individuals < 1 cm dbh of tree species were not included in the understory community but were instead measured as part of the seedling community. The seedling community was defined as individuals < 1 cm dbh or without a dbh (technically seedlings and saplings) of tree species reaching a maximum size of > 1 cm dbh, and was measured in 25 randomly placed 1 x 1 m subplots. The number of seedlings per species was recorded per subplot. Individuals with multiple stems were counted as a single seedling. Seedlings < 1 cm dbh arising from root suckers or resprouting from the base of coppiced trees were not included. Scientific names and growth forms were determined by botanists R. Ganesan, S. Rehel and R. Laden, and with the assistance of local floras (Gamble *et al.*

1967; Matthew 1983, 1995) for trees, shrubs and forbs (Appendix E). Families were determined from Stevens (Stevens 2011).

Species distributions

We used biogeographic distribution as an estimate of species' range size and divided species into five categories: 1) pantropical or widespread in temperate and tropical regions, 2) in Asia and at least one other continent, 3) widespread in Asia, 4) limited to India and adjoining countries, 5) limited to India and Sri Lanka, or more narrowly distributed. The limited number of narrowly distributed species prevented splitting category 5 further.

Environmental conditions

We measured several environmental factors to account for variation in abiotic conditions that could affect plant species richness and diversity. We determined the elevation of each plot with a barometric altimeter on a Garmin e-Trex Vista H handheld GPS unit. In addition, we measured canopy openness using the average of five hemispherical photos taken 1 m off the ground in each plot, analyzed with Gap Light Analyzer version 2 (Frazer *et al.* 1999). For each plot, we extracted 19 bioclimatic variables from WorldClim 1.4 representing mean climate conditions between 1950-2000 with measures of temperature, precipitation and their seasonality (Hijmans *et al.* 2005).

Data analysis

Environmental conditions

All analyses were conducted in R version 2.13.2 (R Development Core Team 2011). To reduce the number of inter-correlated environmental variables, we used principal components analysis (PCA) to summarize the variation across the 19 bioclimatic variables and elevation. The first two PCA axes accounted for 95% of the variation in the data, so we extracted the plot scores on these axes to create the variables PC1 and PC2, representing climatic conditions across plots. Plots with positive scores for PC1 tended to be cooler, at higher elevations and with more precipitation. Plots with positive scores for PC2 had more precipitation and less seasonal variation in precipitation and temperature.

Species diversity and richness

We calculated species richness and the Shannon-Wiener diversity index (H') for the overstory, understory and seedling communities by plot using the R package vegan (Oksanen *et al.* 2011). Species abundances were measured as basal area for the overstory, percent cover for the understory and number of individuals for seedlings. Other diversity indices yielded similar rankings among plots, so we present results only from the Shannon-Wiener index. To assess how well our sampling approximated the species richness of each location, we generated species accumulation curves and compared them to the estimated richness of the total species pool at each site, calculated using the first-order jackknife estimation (Oksanen *et al.* 2011). Species accumulation curves were generated by randomly sampling stems (overstory) or subplots (understory and seedlings) from all stems or subplots respectively, within a plot. Because the relative species richness observed among plots was similar to the relative projected richness of the species pool (Figure 5.1), we used observed richness in subsequent analyses.

We used an information-theoretic approach to determine relationship between land use and observed species richness and diversity. To assess the relative importance and impact of environmental factors and land use (biomass extraction, livestock, fire and LUI) on species diversity and richness, we developed a set of 16 candidate models for each component of the community (overstory, understory and seedlings). Candidate models were linear mixed-effect models developed using the lmer function in the lme4 package for R (Bates *et al.* 2011). All models included site as a random factor in order to account for the spatial structure among study plots. Models additionally included environmental variables that could potentially influence richness or diversity, as well as the land use variables of interest as fixed effects. We initially tested site nested within region as the random component of the models, but incorporating regional differences never improved the model by AICc, and so region was omitted.

We included four groups of candidate models: 1) site alone (one model), 2) site + environmental conditions (seven models: elevation, PC1, PC2, PC1 + PC2, canopy openness, grass cover, years since fire), 3) site + land use (four models: biomass extraction, livestock, biomass extraction + livestock, and ranked LUI), and 4) site + environmental conditions + land use (four models: biomass extraction, livestock, biomass extraction + livestock, and ranked LUI each added to the site + environmental conditions model with the lowest AICc). For all candidate models in the set, we calculated AICc, differences in AICc (ΔAICc) and AICc weights using the R package AICcmodavg (Mazorelle 2011). We ranked models according to AICc and considered all models with $\Delta\text{AICc} \leq 2$ to have strong support (Anderson 2008).

To determine the contribution of non-native invasive species to observed patterns in understory diversity, we reran the understory analyses omitting the seven species present in our study plots that are classified as invasive non-native species within India (*Ageratina adenophora, Ageratum conyzoides, Asclepias curassavica, Bidens pilosa, Chromolaena odorata, Lantana camara* and *Oxalis corniculata*; Reddy *et al.* 2008; Appendix E).

Species distributions

To test whether the breadth of the biogeographic distribution of species differed with land use (no use [LUI 1] vs. moderate use [LUI 2 and 3]), we used a Poisson generalized linear model (GLM) with number of species per distribution category per plot as the response variable. Our null model included distribution category, region and the distribution category x region interaction as predictor variables. We included region as a factor to account for potential differences in the breadth of species distributions between the two study regions, due to differing climatic conditions and species pools. We assessed the effect of land management by comparing the log-likelihood chi-square (G^2) values between the null model and a model with an additional distribution category x land use interaction. A significant chi-square test ($p < 0.05$) indicates that the number of species per distribution category differed significantly between areas with and without moderate land use, after accounting for differences between regions. We followed this general test of the effect of land use on biogeographic distribution with pre-planned contrasts using Z tests to test for differences in the number of species with land use in each of the five distribution categories. We hypothesized that areas with moderate land use would have greater numbers of widely distributed species (distribution categories 1 and 2) and fewer narrowly distributed species (distribution categories 4 and 5). We considered areas with greater numbers of narrowly distributed species to be more valuable from a conservation perspective.

Results

Environmental conditions

Canopy openness ranged from 20 to 70%, with a mean of 50%. Canopy openness, elevation and PC1 were all significantly positively correlated (canopy-elevation: r = 0.749, df = 12, p = 0.002; canopy-PC1: r = 0.546, df = 12, p = 0.043; elevation-PC1: r = 0.843, df = 12, $p < 0.001$). Plots with livestock grazing had 40% more open canopies (62 vs 45% open; t = -3.025, df = 11.006, p = 0.012). Livestock grazing was negatively correlated with PC2 scores (-0.197 vs. 0.079; t = 2.766, df = 11.356, p = 0.018). All other correlations among environmental variables and between environmental and land use variables were not significant at the p = 0.05 level.

Species richness and diversity

Across the 14 plots, we found 147 species, of which 141 were identified to family, 133 to genus and 106 to species (Appendix E). Identified species came from 43 families and 104 genera.

Overstory species richness declined with increasing canopy openness and overstory species diversity was lower in areas with recent fire (Figure 5.2). The seedling community also exhibited both decreased species richness and diversity with recent fire (Figure 5.3).

The understory in locations with livestock grazing had higher levels of both species richness and diversity, compared to locations without livestock (Figure 5.4). Linear mixed effects models revealed that increased canopy openness contributed to increased understory species richness, whereas increased grass cover contributed to increased understory species diversity, after accounting for the effect of livestock grazing (Appendix F). The effects of grass cover and canopy openness appear to be distinct, as there was no direct correlation between grass cover and canopy openness (r = 0.070, df =

12, $p = 0.812$). After eliminating the seven non-native invasive understory species from the analysis, the trend of increased richness and diversity with livestock grazing remained (Figure 5.4), but livestock grazing was less strong of a predictor of species richness (Appendix F).

We did not find support for an effect of biomass extraction or increasing land use intensity on the diversity or richness of the overstory, tree seedling or understory plant communities. Overstory and tree seedling richness and diversity did not differ significantly between areas with and without livestock grazing.

Understory and overstory richness and diversity were negatively correlated, although this trend was not significant (richness: $r = -0.393$, $df = 12$, $p = 0.165$; diversity: $r = -0.349$, $df = 12$, $p = 0.221$). Overstory and seedling richness and diversity were not significantly correlated, nor were understory and seedling richness and diversity.

Species distributions

Areas with moderate land use (i.e., reserve forests, LUI 2 and 3) tended to have more common species and fewer narrowly distributed species than areas with less human activity (Figure 5.5). Although this difference was not statistically significant overall ($\Delta G^2 = 8.158$, $df = 5$, $p = 0.148$), it was consistent across both regions. Pairwise contrasts were marginally significant for category 2, species found in Asia and at least one other continent ($p = 0.059$), but otherwise not significant (1: $p = 0.316$, 3: $p = 0.605$, 4: $p = 0.466$, 5: $p = 0.102$).

Discussion

No decrease in species diversity and richness with moderate land use

Overall, we found that areas managed for biomass extraction and livestock grazing in savanna woodlands of the Western Ghats had similar levels of plant species diversity and richness to areas protected from these activities. This suggests that these kinds of land uses are compatible with the maintenance of plant species diversity. There are at least two possible non-exclusive explanations for this observed trend. Areas with livestock grazing had more open canopies, so increased understory light availability in these locations may have reduced competition for light at the surface, permitting a greater diversity of understory species to coexist (Grace 1999). This mirrors the findings of Mayfield and Daily (2005) in which understory species richness in Costa Rica increased with canopy openness, except at the highest levels of openness and disturbance found in open pastures. In addition, livestock grazing might reduce the standing biomass of grasses, leading to a greater diversity of understory forbs, as has been found in other systems with long histories of ungulate grazing (Collins *et al.* 1998).

Non-native invasive species contributed to increased understory plant diversity at the plot level. The increase in local diversity with invasion is frequently observed in plant communities, though it is unclear if such a pattern would hold over the long term (Sax *et al.* 2007). In this study, less than 5% (7/147) of observed species were non-native invasives, meaning the overall contribution of non-native invasive species to levels of diversity and richness was small. Omitting non-native invasive species from the analysis did not change the pattern of increased understory species richness and diversity in areas with livestock grazing, which illustrates that patterns of species richness and diversity were not driven by non-native invasive species.

These results point to the conservation value of areas where human land use leaves much of the native vegetation structure intact. These findings are consistent with a study of rattan harvest in Indonesia, in which harvest does not involve felling trees and retains high diversity (Widayati & Carlisle 2012). The maintenance of tree cover and structural complexity is also considered key to agroforestry systems' ability to conserve high levels of native biodiversity compared to agricultural mono- or poly-cultures (Tscharntke *et al.* 2005; Bhagwat *et al.* 2008). Our findings also suggest that when biomass extraction is linked to reduced tree diversity (Shankar *et al.* 1998a; Arjunan *et al.* 2005; Kumar & Shahabuddin 2005), felling of trees (e.g., for fuelwood and timber harvest) may be a primary cause. Other studies have found that maintenance of natural vegetation structure within human-modified landscapes also promotes a diversity of vertebrate and invertebrate species (Anand *et al.* 2010; Winfree *et al.* 2011), and so moderate land use that maintains tree cover may be able to support diverse animal communities as well.

We expect this trend may be common in places like India and elsewhere in Asia and Africa, which have a long history of human land use, and where species sensitive to these forms of disturbance would already have been eliminated (Balmford 1996). Given the prevalence of these kinds of human-managed ecosystems in the tropics, it is important to recognize their potential to contribute to the maintenance of tropical biodiversity, especially compared to the more extreme forms of land conversion common to the Western Ghats and elsewhere, such as non-native timber plantations, coffee and tea plantations and agricultural monocultures.

The relationship between time since fire and overstory diversity, tree seedling diversity and tree seedling richness suggests that frequent fire may reduce the diversity of tree species in the savanna woodland ecosystems we studied. This is consistent with findings from other tropical dry forests in India where annual fires reduced tree seedling diversity by favoring species capable of resprouting from the roots (Saha & Howe 2003). Given that fires in the study area are often set to promote harvest of non-timber forest products (NTFP) and improve fodder for livestock (Hiremath & Sundaram 2005), these activities may indirectly contribute to reduced tree diversity. At the same time, most of the plant diversity of these savanna woodland ecosystems is found in the understory and would likely not persist under more closed canopies (Ratnam *et al.* 2011). While the history of fire in Indian forests remains a controversial subject, fire has been used as a management tool in these areas for millennia (see Hiremath & Sundaram 2005 and references therein). As understory species diversity is lower in areas with less open canopies, elimination of fire in these systems could lead to increased canopy cover and overstory species diversity at the expense of reduced understory diversity. The relationships among fire, tree cover, plant diversity and ungulate herbivory are complex (Collins *et al.* 1998; Peterson & Reich 2007; Fuhlendorf *et al.* 2009; Mayer & Khalyani 2011), and research to date has come primarily from the Americas and Africa. Given the increasing frequency of fire in the study area (Kodandapani *et al.* 2004; Shaanker *et al.* 2004a), this relationship deserves further study in the Indian context. Specifically, it is important to determine what frequency of fire might contribute to maintaining understory species diversity and provision of NTFP and fodder to local resource users, without eliminating canopy cover and compromising other ecosystem processes and services.

Land use and conservation of rare species

In addition to having similar overall levels of species richness and diversity, the lack of significant difference in biogeographic distribution between areas managed for biomass extraction and nearby areas with fewer human activities suggests these areas contain similar kinds of plant species and that reserve forests have high conservation value. However, we found that areas managed for biomass extraction tended to have, at the plot level, more widely-distributed species and fewer narrowly distributed and endemic species compared to nearby areas with fewer human activities. Though not statistically significant, this pattern is particularly notable given both our small sample size and the fact that biomass extraction previously occurred within the protected area (Shaanker *et al.* 2004a). It is unlikely that the protected area location was chosen specifically for its endemic plant diversity relative to neighboring areas – the diversity and density of large mammals and the presence of tropical moist forest were the primary factors used to select the protected area's location (Barve *et al.* 2005). Further investigation is warranted to determine the nature of turnover in species composition between areas with different land use intensities, and therefore the role of protected areas in conserving rare species.

The trend of increasing numbers of widely distributed species with more intensive land use, though again not statistically significant, is consistent with previous studies that have found that human activities can lead to biotic homogenization (McKinney & Lockwood 1999; Olden *et al.* 2004). The implications of biotic homogenization for ecosystem function and ecosystem services are not known, though it is speculated that homogenization may reduce ecosystem stability and resilience (Olden 2006; Clavel *et al.* 2011). Our findings suggest the need for further study to determine if and to what degree biotic homogenization is occurring with moderate intensity land use, and to understand the consequences of biotic homogenization for human well-being and native species conservation.

Balancing biodiversity conservation and land use in the Western Ghats

Ultimately, our results suggest that areas with moderate intensities of biomass extraction and livestock grazing can conserve a comparable degree of plant species diversity relative to savanna woodlands without biomass extraction and livestock grazing in the Western Ghats. Given the prevalence of these forms of land use and the lack of areas that have not been exposed to anthropogenic disturbance in India, recognizing the potential for these areas to contribute to conservation objectives is critical to effectively managing existing diversity without unnecessarily compromising local livelihoods. At the same time, we find evidence of some trade-offs between managing for human benefits from ecosystem services and the maintenance of native plant biodiversity in savanna woodlands. Fire is used to manage areas for both livestock grazing and harvest of NTFP. Increasing fire frequency associated with these activities may reduce both tree cover and tree species diversity.

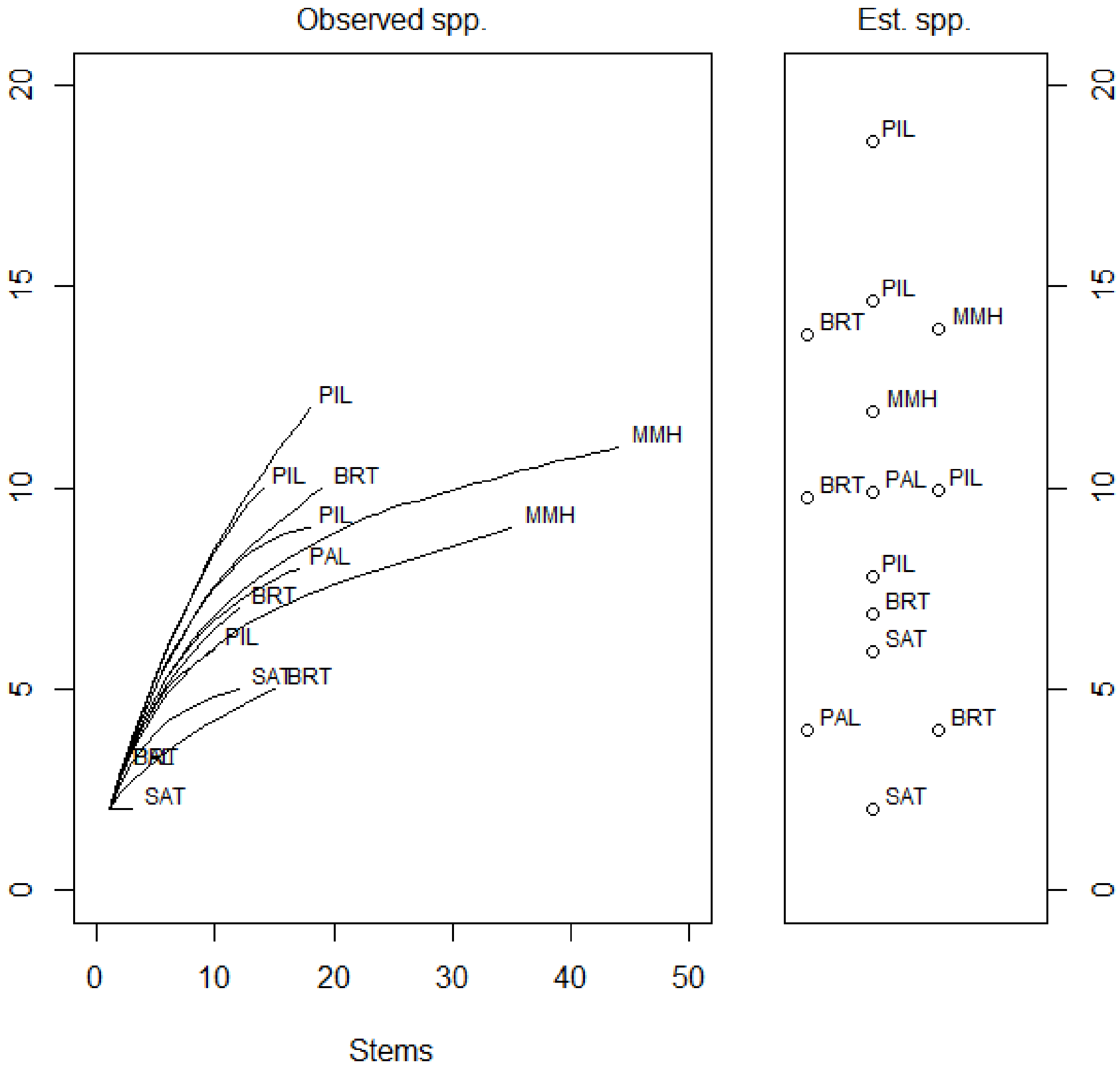
Our results suggest that promoting a mosaic of land management practices would be an effective way to balance the need to protect plant diversity with the potential for these ecosystems to provide direct benefits to local communities while maintaining high levels of plant species diversity. Protected areas with reduced human land use may more effectively conserve tree cover and tree diversity, while areas subject to moderate land use could still maintain substantial overall plant diversity and provide connectivity between protected areas, while additionally providing benefits to local people. Such a model of management represents a departure from India's historic forest policy that attempted to exclude local communities and local resource use from forests (Saxena 1999). However, India's Forests Rights Act, which requires that traditional forest resources are jointly managed by local communities and the state, may provide an opportunity to experiment with different models of conservation and management (Bawa *et al.* 2011). The decision about how to balance local benefits from biodiversity with conservation is ultimately a choice to be made by societies (DeFries *et al.* 2004). Ecological studies such as this one provide a valuable source of information about the nature of trade-offs between land use and biodiversity conservation, information that is lacking throughout much of the tropics (Chazdon *et al.* 2009).

Table 5.1. Characteristics of savanna woodland study sites in the Western Ghats, India, including the presence (+) and absence (-) of biomass extraction and livestock grazing within each site. Sites are presented from west to east.

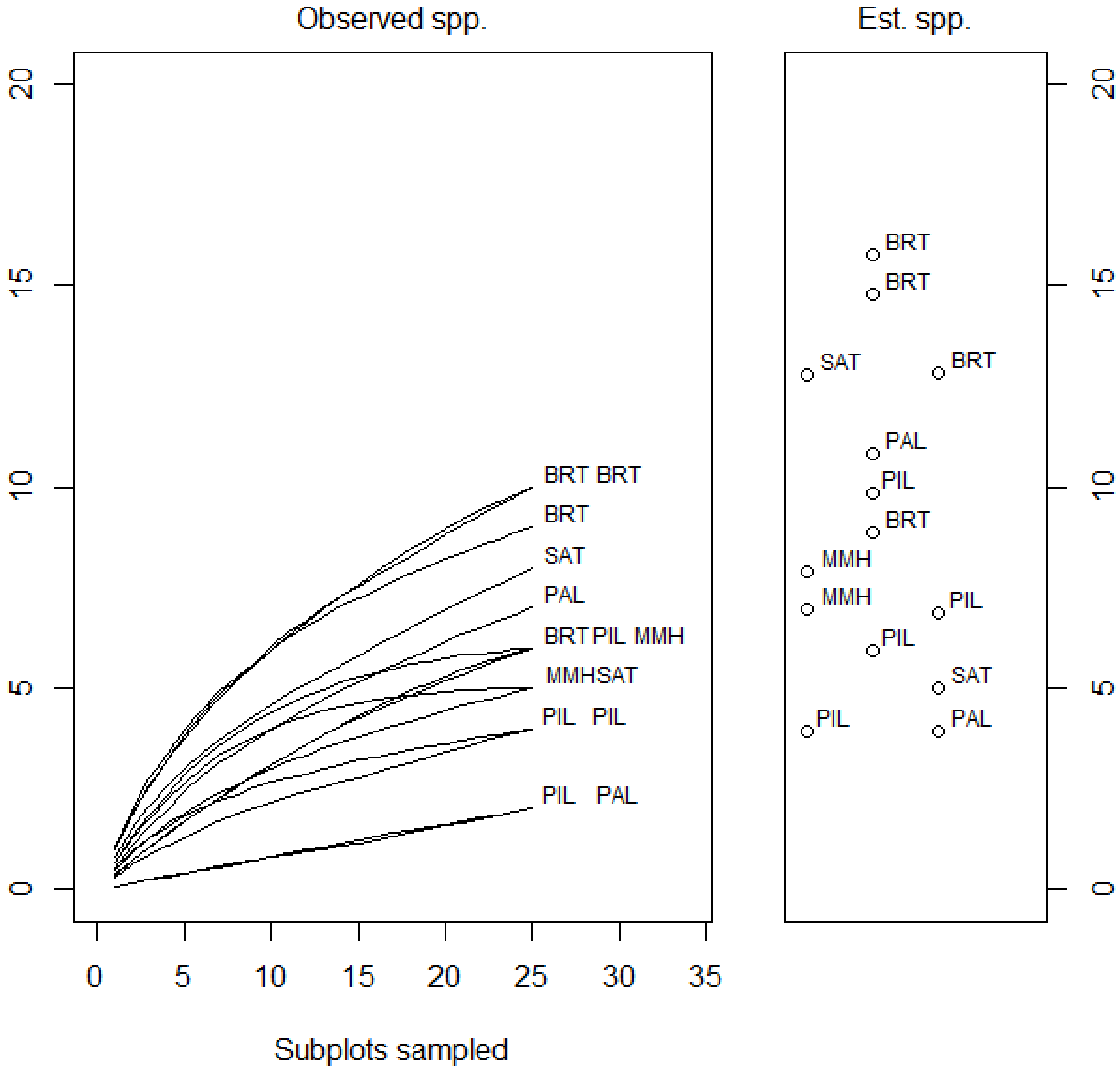
Region:	West		East		
Site:	*Pillur Reserve Forest*	*Palaniappa Estate Forest Fragment*	*Sathyamangalam Reserve Forest*	*BRT Wildlife Sanctuary*	*Male Mahadeshwara Hills Reserve Forest*
No. plots:	4	2	2	4	2
Biomass extraction:	+	-	+	-	+
Livestock grazing present in plots:	-	-	+	-	+
Range of years since fire (2010/2011)	1-2/0-3	1-3/2-4	1-3/2-4	2-6/3-7	1-2/2-4
Land use intensity (LUI) rank:	2	1	3	1	3
Elevation (m)	725-800	1600-1700	1450-1475	1100-1400	1285-1300

Figure 5.1. Species accumulation curves (left panel) and estimated species pools (right panel, jittered) for (a) overstory, (b) seedling, and (c) understory plant communities by plot. Plots are labeled by site (PIL – Pillur Reserve Forest, PAL – Palaniappa Estate forest fragment, SAT – Sathyamangalam Reserve Forest, BRT – BRT Wildlife Sanctuary, MMH – Male Mahadeshwara Hills Reserve Forest; see Table 5.1 for more information).

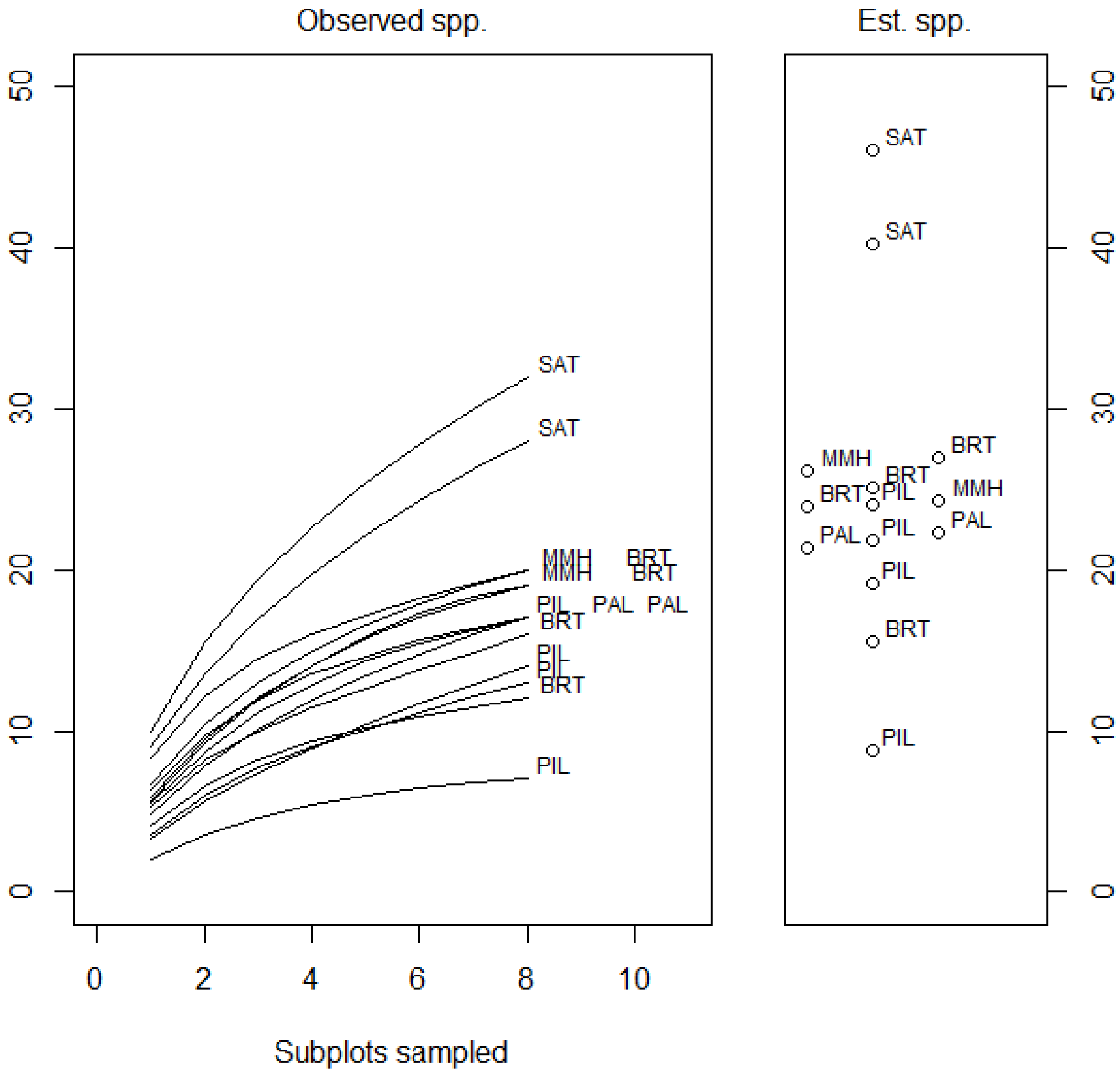
a)



b)


Observed spp.
Est. spp.
0
5
10
15
20
0
5
10
15
20
25
30
35
Subplots sampled
BRT BRT
BRT
SAT
PAL
BRT PIL MMH
MMHSAT
PIL PIL
PIL PAL
BRT
BRT
SAT
BRT
PAL
PIL
BRT
MMH
MMH
PIL
PIL
SAT
PIL
PAL

c)



Observed spp.
Est. spp.
Subplots sampled
0
10
20
30
40
50
0
2
4
6
8
10
SAT
SAT
MMH
MMH
BRT
BRT
PIL
PAL
PAL
BRT
PIL
PIL
BRT
PIL
SAT
SAT
MMH
BRT
BRT
PIL
PAL
PIL
PIL
BRT
MMH
PAL
BRT
PIL

Figure 5.2. Overstory species richness declined with canopy openness (top) and overstory species diversity declined with more recent fire (bottom). The trend in diversity with fire was driven primarily by the plot with 6 years since fire and one of the plots with 1 year since fire.

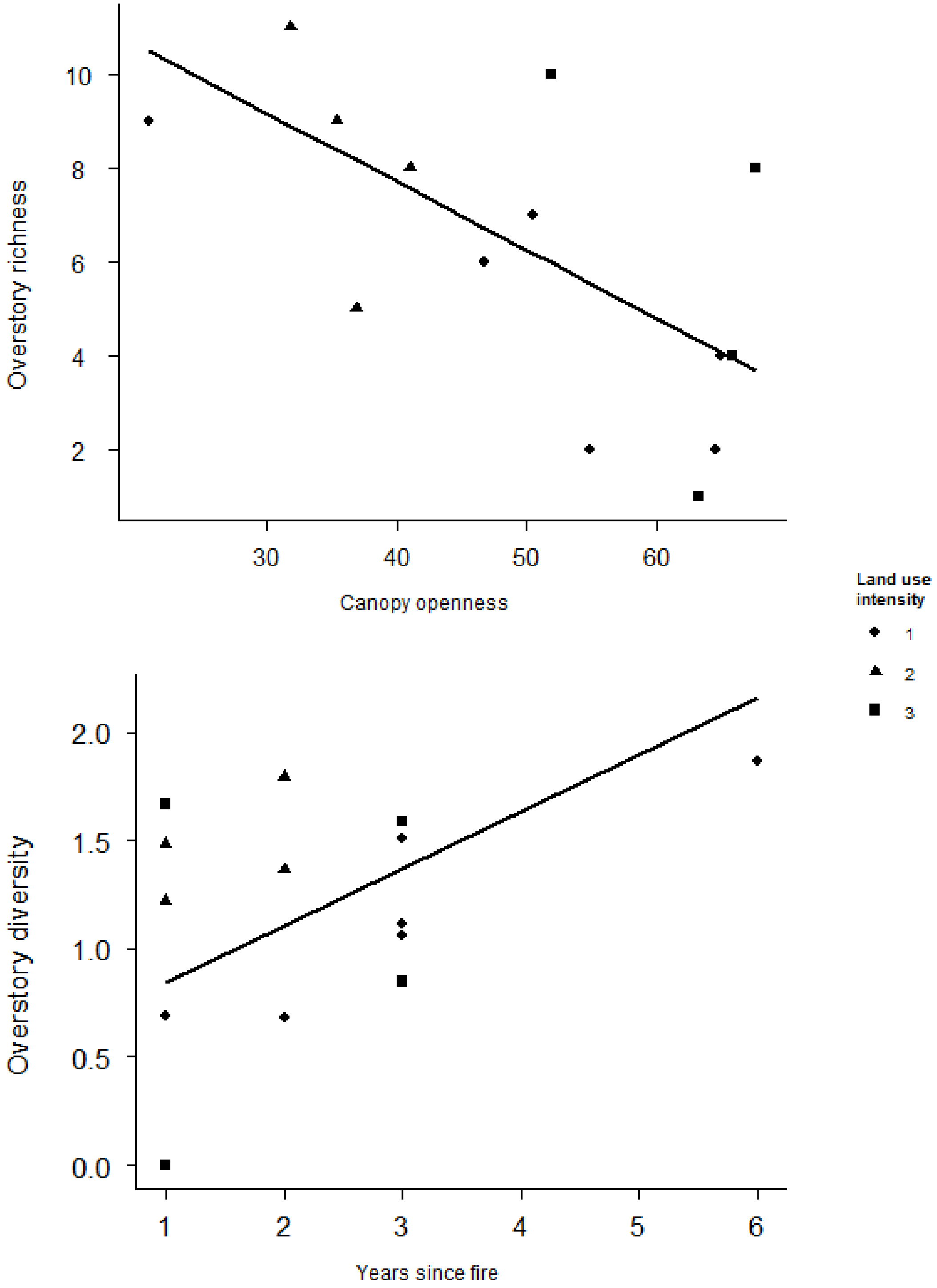


Figure 5.3. Seedling richness (top) and diversity (bottom) increased with time since fire

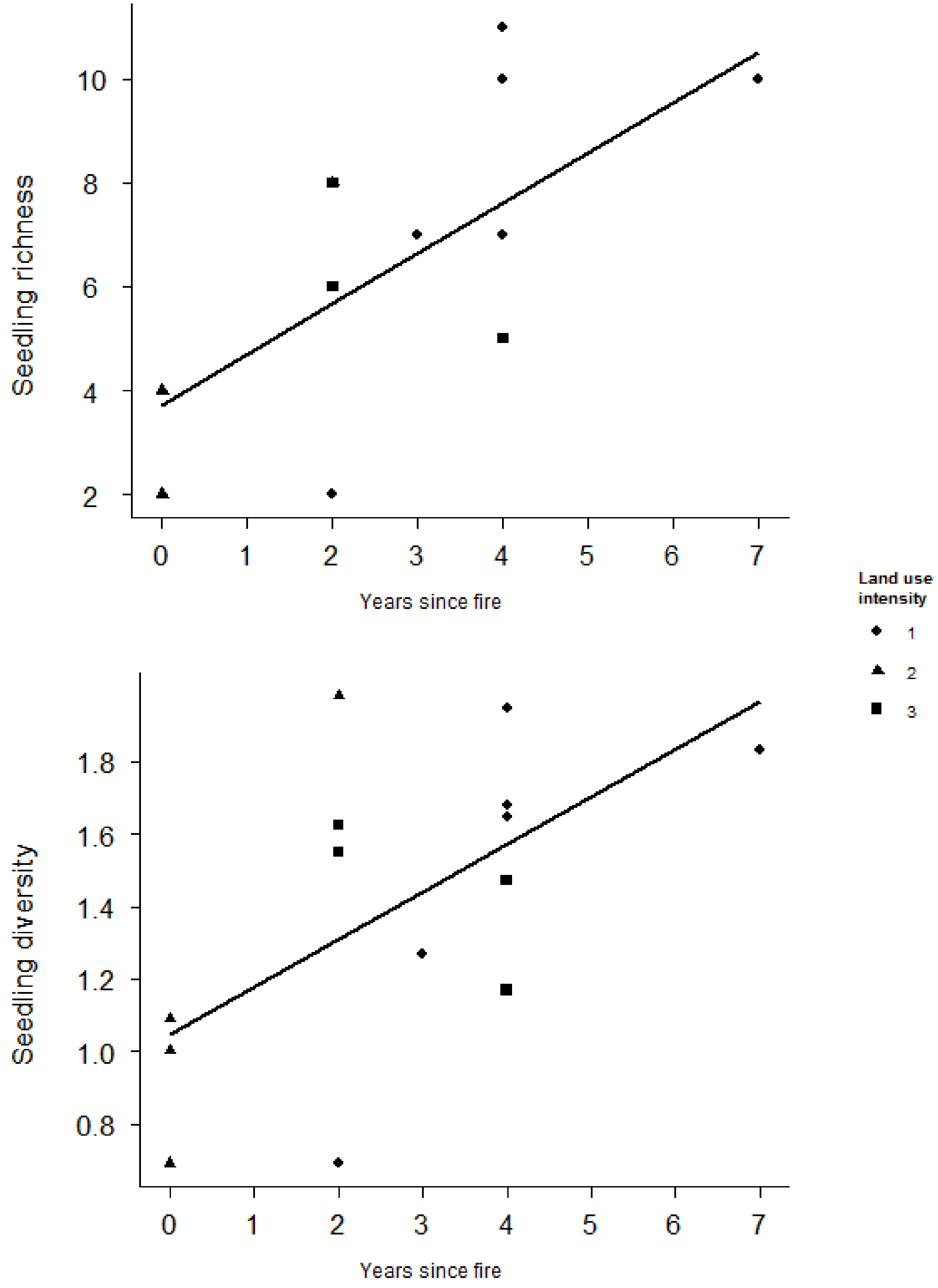


Figure 5.4. Boxplots, with jittered points overlaid, of understory richness (top) and diversity (bottom) for plots without (n = 10) and with (n = 4) livestock grazing, with and without non-native invasive species included in the analysis.

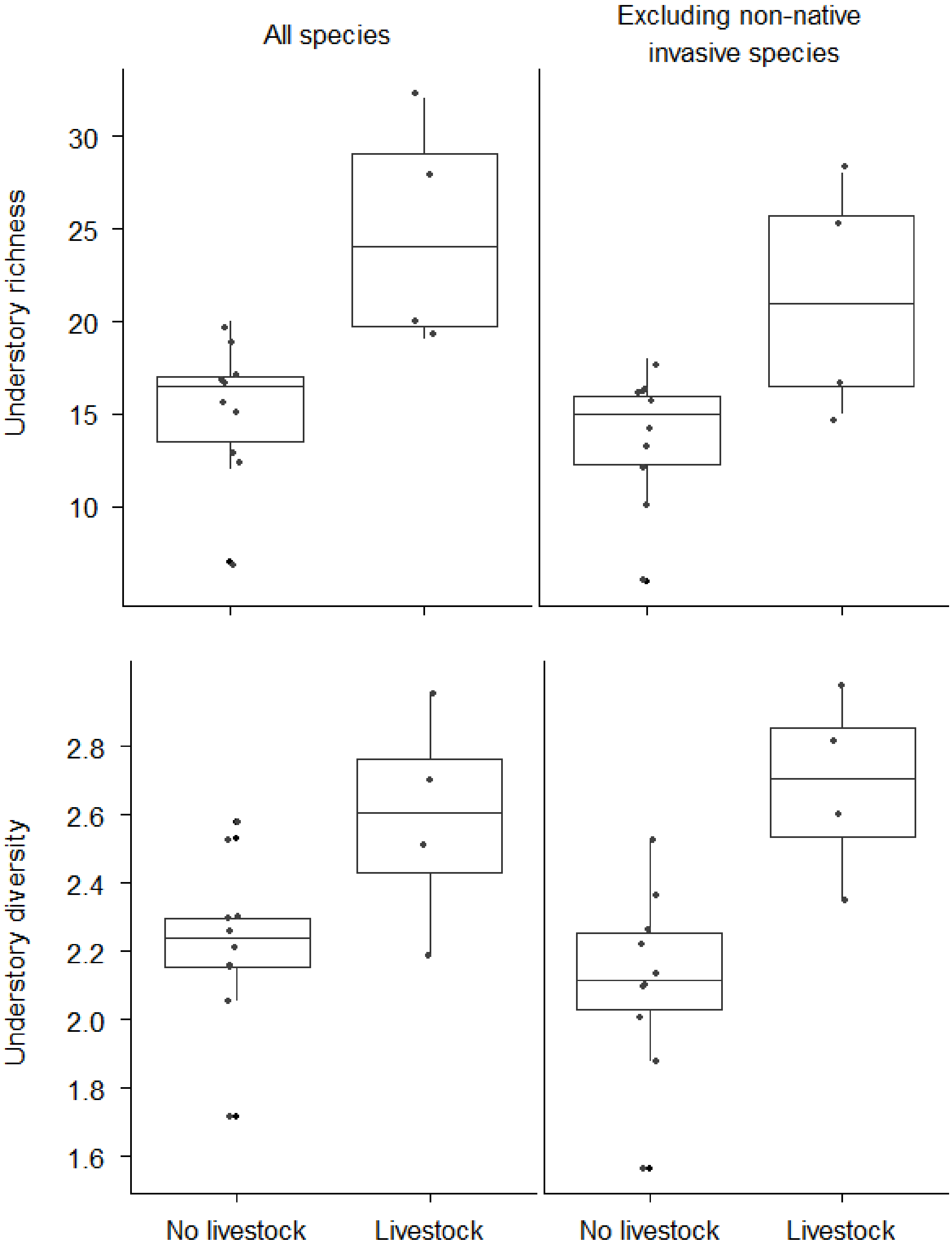
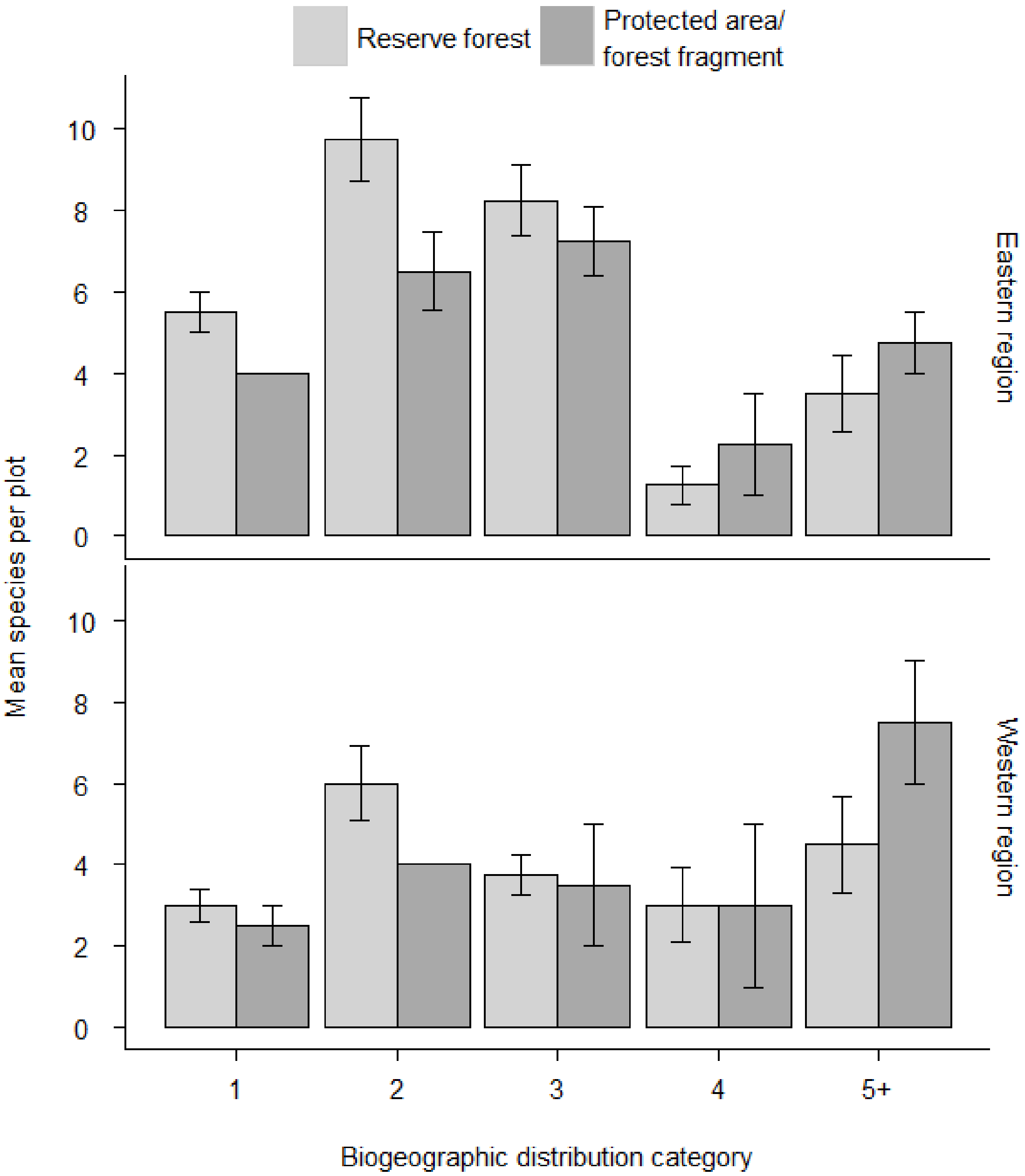


Figure 5.5. Number of species (mean per plot ±1 SE) per biogeographic distribution category across land use types and by region. Biogeographic distribution categories range from pantropical or widely distributed throughout temperate and tropical regions (1) to endemic to India and Sri Lanka, or more narrowly distributed (5+). Widely distributed species tend to be overrepresented and narrowly distributed species tend to be underrepresented in reserve forests with moderate land use (LUI 2 in the eastern region and LUI 3 in the western region) compared to areas with more limited human activities (protected area/forest fragment, LUI 1).



CHAPTER 6. MODERATE LAND USE ALTERS FUNCTIONAL COMPOSITION BUT MAINTAINS FUNCTIONAL DIVERSITY IN A SEASONALLY DRY TROPICAL ECOSYSTEM

Lisa Mandle and Tamara Ticktin

Abstract

There is growing recognition of the importance of managing for functional diversity to improve conservation of ecosystem functions and services. However, most studies to date have assessed the effects of extreme changes in land use (e.g., timber extraction or conversion of forests for agriculture) on functional diversity. Little is known about whether moderate changes in land use are compatible with the maintenance of functional diversity. Understanding the consequences of widespread forms of moderate land use, such as non-timber forest product (NTFP) and fuelwood harvest or livestock grazing, is especially important in the tropics, where high biodiversity co-occurs with growing human populations heavily dependent on local ecosystems. We assessed differences in plant functional composition and functional diversity across savanna woodlands with varying degrees of human land use in the Western Ghats, India. Across these moderate forms of land use, we found no overall decline in functional diversity with land use intensification. We found shifts in functional composition associated with biomass extraction, livestock grazing and time since fire and mixed effects of these activities on functional diversity. Livestock grazing increased understory functional diversity, while biomass extraction reduced the functional diversity overstory species. Our results suggest that current bans on extraction of NTFP in protected areas in India do little to increase the conservation value in terms of functional diversity of these areas while significantly reducing local benefits. Our results also provide a novel source of evidence to support to the idea that we need to rethink the conservation value of these human-managed landscapes, especially those with moderate-intensity land use in the tropics. Conservation policy and resources in India, and elsewhere in the tropics, might be more productively directed towards reducing the more extreme forms of land use change and restoring degraded land rather than restricting more moderate land use activities such as those considered here.

Introduction

Human land use is the primary threat to plant biodiversity worldwide (Brummit & Bachman 2010). Changes in plant communities resulting from land use intensification are expected to have significant consequences for ecosystem function and ecosystem services (Foley *et al.* 2005). There is therefore growing recognition that conservation strategies need to include conservation of functional diversity, not simply species diversity (Díaz *et al.* 2006; Cadotte 2011).

Functional traits are the characteristics of individuals and species that influence ecosystem-level properties and processes (Petchey & Gaston 2006). Functional diversity is the variation in functional traits within a community. Increased functional diversity is expected to maximize the long-term stability and resilience of ecosystem function (Díaz & Cabido 2001; Loreau *et al.* 2001). A greater diversity of effect traits – traits that determine plants' effect on ecosystem processes (Lavorel & Garnier 2002) is expected to result in increased productivity and resource-use efficiency (Díaz & Cabido 2001). The diversity of response traits – those associated with plants' response to environmental change – is considered an important indicator of a community's resilience to disturbance and environmental change (Elmqvist *et al.* 2003).

Land management has the potential to alter ecosystem processes not only through changes in functional diversity but also through shifts in functional composition (Tilman *et al.* 1997). Empirical studies have frequently found that functional composition (i.e., functional trait values), rather than functional diversity, determines important ecosystem properties and processes such as net primary productivity, decomposition, soil carbon and nitrification (e.g., Garnier *et al.* 2004; Laughlin 2011). Current ecosystem service provision – often a primary land management goal – may therefore be determined largely by functional composition (Díaz *et al.* 2006). However, management aimed at maximizing certain functional traits over the short term might compromise future ecosystem resilience and provision of ecosystem services (Foley *et al.* 2005).

Land management may alter functional composition and functional diversity by changing community assembly processes and environmental filters (Mayfield *et al.* 2010). The effects of management on functional composition and functional diversity are potentially distinct (Figure 6.1). Land use intensification might alter the degree of competition and ecological filtering in structuring plant communities without altering the functional traits selected for, leading to increases or decreases in functional diversity without changes in functional composition (Figure 6.1a). For example, promoting a subset of valued timber species within a formerly diverse forest could reduce functional diversity without changing the mean functional composition of the community. Alternatively, land use aimed at promoting certain valued functional traits could potentially lead to a shift in functional composition without changes in overall functional diversity (Figure 6.1b). This might be observed if a forest is converted to a treeless pasture, but the reductions in tree diversity are compensated for by increases in understory diversity. Finally, land use might simultaneously alter both functional composition and functional diversity by changing what traits are selected for as well as the intensity of ecological filtering or competition (Figure 6.1c). As land use intensification often results in the simplification of ecosystems stemming from attempts to increase benefits from a subset of species within the community, it seems likely that changes in land management will commonly involve both shifts in functional composition and changes in functional diversity (Figure 6.1c). Indeed, this pattern was found in the conversion of North American grasslands to agriculture (Lin *et al.* 2011) but has not yet been investigated in other ecosystems.

One major constraint to developing functional diversity-based recommendations relevant to conservation and management decisions is the limited distribution of studies to date, both across ecosystem types and in terms of the history and nature of land-use intensification. Changes in functional composition and functional diversity with land use have been explored predominantly in contexts of substantial land use change, such as conversion of tropical moist forest to pasture (Mayfield *et al.* 2005; Mayfield *et al.* 2006) and conversion of temperate grasslands for agriculture (Lin *et al.* 2011). The effects of less extreme changes in land use – for example fuelwood collection, non-timber forest product (NTFP) harvest or livestock grazing that occur without forest clearing – on functional composition and diversity are not known. Understanding the effects of finer-scale changes can provide valuable information about the degree of land use that may be compatible with the maintenance of functional diversity.

In addition, existing studies of plant functional diversity and land use change in the tropics are largely limited to moist forest ecosystems (e.g., Laliberté *et al.* 2010). Despite the low levels of protection and high levels of human land use change experienced by tropical dry forests, woodlands and savannas (Murphy & Lugo 1986; Chape *et al.* 2005), to date there are few studies on functional diversity in these ecosystems. These ecosystems evolved with disturbance regimes and environmental constraints different from moist forests, and therefore can be expected to respond differently to changes in the frequency and intensity of anthropogenic disturbances.

Finally, most studies of plant functional diversity have come from areas with more recent human presence (specifically, the Americas and Australia; Flynn *et al.* 2009; Laliberté *et al.* 2010; Mayfield *et al.* 2010). With a longer history of human presence, ecosystems in Asia and Africa might experience different effects of land use change on diversity if disturbance-sensitive species have already largely been eliminated from the flora. In this case, land outside of protected areas could contribute to conservation of remaining biodiversity more effectively in these places than in areas with a relatively short history of anthropogenic disturbance. Determining the conservation value of human-managed ecosystems is especially important in Asia, which has a relatively low designation of protected areas (Chape *et al.* 2005) along with large and growing human populations.

We asked if different kinds of human land use activities – specifically biomass extraction of fuelwood and NTFPs, livestock grazing and ground fire – are associated with changes in the functional composition and functional diversity of tropical savanna woodland plant communities within the Western Ghats, India. The Western Ghats is the biodiversity hotspot with the greatest human population density (Cincotta *et al.* 2000), making it especially critical to reconcile biodiversity conservation and human land use. We focused on biomass extraction, livestock grazing and fire because of their prevalence in Asia and the tropics (FAO 2010). In addition, these forms of land use leave much of the native overstory intact.

We addressed two questions:

1) Do the functional composition and functional diversity of plant communities differ in areas with different land uses?

2) What are the implications of these findings for conservation of functional diversity?

Based on previous studies of the relationships between functional traits and disturbance, we developed a series of hypotheses about the effects of our focal land uses on functional traits (Table 6.1). Given that our three focal land use-activities occur without forest clearing and given the long history of the three focal land use activities in India, we did not expect large changes in functional diversity with these kinds of land use change, in contrast with findings from many ecosystems in the Americas with a shorter history of human presence. We did expect to observe shifts in functional composition with differences in land use history.

Methods

Study sites & design

Our study was located in savanna woodlands of the southern Western Ghats in the South Indian states of Tamil Nadu and Karnataka. Our study sites encompassed three reserve forests, one protected area and a remnant forest fragment on privately owned land, which represented a range of land use intensities (Table 6.2). We ranked sites in land use intensity (LUI) from 1 to 3 (Appendix D) based on levels of biomass extraction (commercial NTFP harvest and fuelwood collection or not) and livestock grazing (present or absent).

Within each of the five study sites, we established two to four 20 x 20 m study plots with a total of eight plots in reserve forests, four in the protected area and two in the forest fragment. To ensure comparisons among similar vegetation types, we located our plots in areas with populations of the mountain date palm (*Phoenix loureiri* Kunth), whose leaves are harvested commercially from the reserve forest sites but not currently from the protected area or remnant forest fragment. Study plots were selected to represent variation in fire history within sites (Table 6.2).

Data collection

We surveyed the overstory, understory and seedling plant communities within each study plot (Appendix G.1). We compiled species-level functional trait data from the literature for a selection of functional effect and response traits for the plants recorded in the community composition surveys (Table 6.3; Appendix G.2). Traits were selected based on previously documented relationships with ecosystem processes and response to disturbance (Cornelissen *et al.* 2003).

Data analysis

Functional composition

To analyze variation in functional composition among plots, we calculated community-level weighted mean trait values (CWMs), weighted by species abundance (Laliberté & Legendre 2011). Abundance was measured as basal area for the overstory, percent cover averaged over subplots for the understory, and total number of individuals for the seedling community. All analyses were conducted in R version 2.13.2 (R Development Core Team 2011). CWMs were calculated using package FD (Laliberté & Shipley 2011).

We used an information-theoretic approach to assess the relative importance and impact of environmental factors and land use history on functional composition. For each trait for which we had a hypothesis about the effect of fire, biomass extraction, livestock grazing and/or LUI (Table 6.1), we developed a set of candidate models. Candidate models were linear mixed-effects models developed using the lmer function in the lme4 package (Bates *et al.* 2011). All models included site as a random factor. Models additionally included environmental variables that could potentially influence trait composition as well as the land use variables of interest as fixed effects. We represented environmental variation that could affect plant community composition with the first two axes of a PCA of 19 bioclimatic variables and elevation (Appendix G.3). Candidate models were simple (Appendix G.4), including at most four fixed effects and no interactions because of the sample size of 14 plots. For all models in the candidate set, we calculated AICc, ΔAICc and AICc weights using the package AICcmodavg (Mazorelle 2011). We ranked models according to AICc and considered models with ΔAICc ≤ 2 to have strong support.

Functional diversity

We calculated two measures of functional diversity: functional dispersion (FDis, Laliberté & Legendre 2011) and functional evenness (FEve, Villéger *et al.* 2008). We calculated FDis and FEve separately for effect and response traits for the overstory, understory and seedling components of the community. FDis is the mean distance in multi-dimensional functional trait space of individual species to the centroid of all species within a community. FDis has a minimum of zero in communities with a single species. High functional effect dispersion is associated with increased productivity and resource use efficiency (Díaz & Cabido 2001). High functional response dispersion is an indicator of ecosystem resilience (Elmqvist *et al.* 2003).

FEve is a measure of the evenness of the species abundance distribution in multi-dimensional trait space. Communities with high functional evenness are expected to be better able to maintain productivity and ecosystem function in the face of environmental fluctuation and to be better able to adapt to new environmental conditions (Hillebrand *et al.* 2008). FEve increases when functional distances among species are more regular or when abundance is more evenly distributed among species. FEve ranges from 0 to 1 and is undefined for communities with fewer than three species. FDis and FEve are independent measures of functional diversity, and both are unbiased by species richness (Laliberté & Legendre 2011). We calculated FDis and FEve, weighted by species abundance, with package FD (Laliberté & Shipley 2011; Appendix G.5).

To determine which environmental and land use variables contributed to variation in functional diversity among sites, we used the same information-theoretic approach used from our analysis of functional composition. We included all 16 possible candidate models (Appendix G.4) in each candidate model set. Although changes in functional diversity could in part be due to the presence or absence of particular trait combinations and not solely the result of changed variation in individual functional traits, for each strongly supported model (i.e., ΔAICc ≤ 2) showing effects of land use variables on functional trait dispersion, we investigated the effects of these variables on the variability of individual functional traits (Appendix G.6). To determine if observed patterns in understory diversity were driven by the presence of alien invasive species, we re-ran the understory analyses omitting the seven species classified as invasive alien species within

India (Reddy *et al.* 2008) and present in our study plots (*Ageratina adenophora*, *Ageratum conyzoides*, *Asclepias curassavica*, *Bidens pilosa*, *Chromolaena odorata*, *Lantana camara* and *Oxalis corniculata*).

Results

Functional composition

Overstory

There was a shift towards shorter overstory species in locations with livestock grazing and with high levels of grass cover (Table 6.4). The relative abundance of wind-dispersed species decreased with increasing land use intensity, and was lower with biomass extraction after accounting for the effects of elevation (Table 6.4). Concurrently, the prevalence of endozoochorous species increased with increasing land use intensity and with biomass extraction (Figure 6.2). We did not find support for hypothesized differences in functional composition among sites with different land uses for physical defenses, resprouting capacity, wood density or seed mass. We were unable to test for differences in clonal reproduction because of the limited representation of the trait. No sites had exozoochorous overstory species.

Understory

We found an increased prevalence of species with physical defenses in areas with livestock grazing as well as an increased prevalence of endozoochory (Table 6.4). However, support for these effects was due entirely to non-native invasive species. We also found lower mean understory species seed mass in areas with biomass extraction, livestock grazing and increasing land use intensity, both with and without non-native invasive species included in the analysis (Table 6.4).

Contrary to our expectations, we found reduced representation of species capable of clonal reproduction in areas with livestock grazing (Table 6.4). Support for this effect disappeared when non-native invasive species were omitted. We did not find support for hypothesized differences in resprouting capacity, wind dispersal or exozoochory.

Seedlings

There was an increased abundance of seedlings of endozoochorous species in locations with livestock grazing (Table 6.4). We did not find support for hypothesized differences in clonality, resprouting capacity, maximum height, physical defense, wood density, seed mass or wind dispersal. Too few plots contained seedlings of exozoochorous species to test for differences in composition.

Functional diversity

Overstory

The functional diversity of effect traits of overstory species did not differ with land use. The functional dispersion of response traits was reduced in areas with biomass extraction, after accounting for the effects of elevation (Table 6.4). The functional evenness of response traits was unchanged.

Reduced variation in overstory species dispersal mechanisms in areas with biomass extraction contributed to the reduced functional dispersion. The increased prevalence of endozoochory with biomass extraction was coupled with reduced variability in this trait ($p = 0.007$, $\chi^2 = 7.286$, $df = 1$). The reduced prevalence of wind dispersal also led to reduced variation $p = 0.007$, $\chi^2 = 7.234$, $df = 1$).

In contrast, we found increased variation in pollination traits with biomass extraction (Table 6.4). Bird-pollinated overstory species were present only in areas with biomass extraction. We also found increased variation in seed mass with biomass extraction ($p = 0.041$, $\chi^2 = 4.176$, $df = 1$), though no change in mean seed mass ($p = 0.434$, $\chi^2 = 0.611$, $df = 1$).

Understory

Within the understory, the functional dispersion of both effect traits and response traits increased in areas with livestock, after accounting for the negative effects of grass cover (Figure 6.3). There was reduced functional evenness of effect traits in locations with biomass extraction and in plots with more recent fire, partly a result of non-native invasive species (Table 6.4). We found little support for an effect of land use on the evenness of response traits.

Increases in functional dispersion were associated increased variation in several functional traits, a result of these traits' increased prevalence. Shifts in functional composition moved CWMs for several binary traits closer to 0.5, leading to increased variance within the community. The increase in physical defenses due to non-native invasive species associated with livestock resulted in increased variance ($p = 0.040$, $\chi^2 = 4.207$, $df = 1$). Areas with livestock grazing had increased prevalence and variance of butterfly-pollinated species ($p = 0.004$, $\chi^2 = 8.188$, $df = 1$; $p = 0.005$, $\chi^2 = 7.993$, $df = 1$) and thrip-pollinated species ($p < 0.001$, $\chi^2 = 14.525$, $df = 1$; , $p < 0.001$, $\chi^2 = 11.330$, $df = 1$), as well as endoozoochory ($p = 0.028$, $\chi^2 = 4.847$, $df = 1$; $p = 0.043$, $\chi^2 = 4.064$, $df = 1$). The increased variation in butterfly pollination and endozoochory, but not thrip pollination, was due to the non-native invasive species *Lantana camara*.

Seedlings

Seedling communities in plots with more recent fire exhibited a greater dispersion of effect traits, but land use did not have substantial effects on the dispersion of response traits Table 6.4). We found support for increased functional evenness of effect traits with increasing land use intensity and with biomass extraction. Functional evenness of seedling response traits increased with biomass extraction and in areas with recent fire.

The increased dispersion of seedling effect traits was associated with an increased prevalence of, and therefore variation in, leguminous tree seedlings ($p < 0.001$, $\chi^2 = 413.495$, $df = 1$; $p = 0.002$, $\chi^2 = 9.986$, $df = 1$) and tree seedlings with semi-evergreen phenology ($p = 0.003$, $\chi^2 = 8.704$, $df = 1$; $p = 0.004$, $\chi^2 = 8.175$, $df = 1$) in areas with recent fire.

Discussion

Land use and balancing conservation objectives

Balancing current and future human well-being with the conservation of biodiversity and ecosystem function requires establishing which forms of land use are compatible with the maintenance of functional diversity. We found that overall, the savanna woodlands in this study that are managed with moderate intensity for the provision of ecosystem goods to local communities, specifically biomass extraction and livestock grazing, harbored similar levels of functional diversity to adjacent areas that are protected from these activities. While different forms of land use had mixed effects on the functional diversity of different components of the plant community (overstory, understory and tree seedlings), we found no overall decline in functional diversity with increasing land use intensity.

From a functional diversity perspective, savanna woodland areas managed for these local benefits have high conservation value. This is likely especially true compared to competing land uses such as timber, coffee and tea plantations, or agricultural monocultures. Areas with NTFP extraction also retained high levels of species diversity, despite the overall lack of a relationship between functional diversity and species diversity (Chapter 5, L.M. & T.T. unpublished data). These results suggest that current bans on extraction of NTFPs in savanna woodlands of some protected areas in India may do little to increase the conservation value in terms of species and functional diversity of these areas while significantly reducing local benefits.

Conservation policy and resources in India, and elsewhere in the tropics, might therefore be more productively applied towards reducing the more extreme forms of land use change and restoring degraded land rather than restricting more moderate land use activities. Our results lend support to the idea that India's controversial Forest Rights Act is compatible with conservation, at least in the savanna woodland ecosystems studied here. The Forest Rights Act devolves management rights of large areas of forests to the local communities that have traditionally used them. Moderate intensities of traditional management practices are likely compatible with the maintenance of high levels of plant functional diversity and species diversity in these savanna woodlands.

Shifts in functional composition with land use indicate environmental filtering

The shifts in functional composition with differences in land use found in our study (Table 6.4) indicate that land use activities are serving as environmental filters in several ways. The increased prevalence of endozoochorous species in the understory and seedling communities with livestock grazing is one example of this. Livestock may be acting as dispersers and ungulate-dispersed species may be better able to persist with livestock grazing than species with other dispersal mechanisms. Our findings are similar to those from a tropical semi-deciduous forest in Brazil in which animal-dispersed species predominated in forest stands with intensive livestock trampling (Toniato & de Oliveira-Filho 2004). This finding highlights the importance of considering the identity of dispersers within broader biotic dispersal categories. A plant community composed of livestock-dispersed species might not support important wild animal dispersers such as primates and birds, and would therefore be of lower conservation value, especially if the livestock-dispersed species are invasive. The increase in physical defenses with livestock grazing is also consistent with the global trend of decreased palatability of species with grazing in systems with a long grazing history (Díaz *et al.* 2007).

The increased prevalence of endozoochory and decreased prevalence of wind dispersal within the overstory in areas with biomass extraction and with increasing land use intensity suggests another environmental filter on plant communities. The increase in endozoochory with land use intensification is contrary to previous studies that have found increases in abiotic dispersal mechanisms with human activity due to declines in disperser populations from habitat degradation and hunting (e.g., Terborgh *et al.* 2008). In our case, the mechanism underlying the pattern we observed is not clear, and highlights the need for a better understanding of the effects of moderate-intensity land uses on functional composition and diversity.

Although the maximum height of overstory species was lower in savanna woodlands with livestock grazing, we found no effect of livestock on understory or seedling maximum height with grazing. The difference in trends between the overstory and tree seedlings suggests that livestock grazing may be limiting the recruitment of taller tree species, but that these species are not dispersal limited. Decreased overstory height and increased canopy openness in areas with livestock grazing indicates these locations have less aboveground woody biomass, and potentially store less carbon than areas without livestock grazing. This could affect the value of these areas should local communities or the Indian government include these lands in carbon offset programs such as REDD+.

Changes in functional diversity with land use

We found no overall reduction in functional diversity with land use intensification, but some land use activities did alter the diversity of some components of plant community (Table 6.4). Diverse responses of different components of a community to land use seem to be common (Laliberté *et al.* 2010) and may indicate inherent trade-offs within processes of community assembly that could affect attempts to manage for overall levels of functional diversity.

Shifts in functional composition associated with human land use were often – but not always – accompanied by changes in functional diversity (Figure 6.1c). The reduction in overstory response dispersion with biomass extraction suggests these areas may have reduced resilience to environmental change (Elmqvist *et al.* 2003). Reduced response dispersion of the canopy may be due in part to management activities which favor only certain kinds of species reaching the canopy – for example, species not preferred for fuelwood. However, seedling and understory response diversity were not reduced with biomass extraction. This suggests that management practices which allow a greater diversity of seedlings to reach the overstory would allow a diverse overstory to regenerate. One way to achieve this would be to create access to alternative fuel sources – such as natural gas – that could reduce fuelwood extraction from these areas (Davidar *et al.* 2010).

We found mixed responses of functional evenness to land use differences, with understory effect evenness decreasing with biomass extraction and land use intensity while seedling response evenness increased. FEve decreases when dominant species are more functionally similar. Fire and biomass extraction may increase environmental filtering of understory species, limiting the functional traits that are successful in those conditions (Zobel 1997). The increased functional evenness of seedlings with biomass extraction and with fire is surprising, as it is expected that these factors would select for species with a suite of traits that allow them to tolerate anthropogenic disturbance, such as resprouting capacity (Lavorel & Garnier 2002). However, fire and biomass extraction may reduce competition between seedlings and understory species, allowing for a more even distribution in abundance among species, resulting in increased functional evenness. Although livestock were associated with shifts in the functional composition of the overstory and seedling communities, we did not find a substantial effect of livestock on their functional diversity (Table 6.4, Figure 6.1b). If environmental filtering is considered analogous to a sieve (Keddy 1992) this finding suggests that for tree species, livestock grazing changes where (in trait space) the sieve's holes are located, but not the mesh size, at least within the set of functional traits we considered.

The increased functional dispersion of understory communities with livestock grazing – a trend not driven by non-native invasive species – suggests that in ecosystems with long histories of ungulate grazing and human land use, some livestock grazing might contribute to the maintenance of forb diversity. A reduction in standing grass biomass with grazing is one possible mechanism. In this study, sites with livestock grazing had on average 30% less grass cover, though this trend was not significant (*t*-test: $p = 0.3085$, $df = 8.036$); grass cover was also associated with reduced understory functional dispersion.

Our finding that the non-native invasive species *Lantana camara* contributed to increased functional diversity points to the need for caution if functional diversity is to be adopted as a management target. Even non-native invasive species, like lantana, that possess novel combinations of functional traits will eventually reduce functional diversity if they become too prevalent within a community. If maximizing functional diversity becomes a target for management and restoration, the identity of species must also be considered. Otherwise, management aimed at promoting functional diversity could counterproductively promote non-native species, also leading to homogenization across communities (Sax & Gaines 2003).

Future directions for functional diversity and conservation in human-managed systems

While our study is one of the first to examine the effects of these moderate forms of land use on plant functional diversity, if these findings hold in other systems, they suggest the need to rethink the conservation value of lands managed for these moderate intensity land uses in the tropics. Further studies in areas with long histories of human land use, and where land use maintains a standing canopy, are needed to test the generality of our findings and to determine what levels of human activities are compatible with the maintenance of functional diversity.

Table 6.1. Predicted effects of land use on functional traits of savanna woodland plant communities in the Western Ghats. Arrows indicate the predicted direction of change with land use, which we analyzed in this study. “NP” indicates that we did not predict a directional change in the trait and so did not test for changes with a particular land use.

Trait	Predicted change with land use				Sources
	Biomass extraction	Livestock grazing	Fire	LUI	
Height	↓	↓	↓	↓	Weiher *et al.* 1999[a] Lavorel *et al.* 2007[a,b] Díaz *et al.* 2007[a, b]
Physical defense	NP	↑	NP	NP	Díaz *et al.*, 2007[a, b]
Wood density (tree seedlings and overstory only)	↓	↓	↓	↓	ter Steege & Hammond 2001[a] Gurvich *et al.* 2005[a]
Clonality	↑	↑	↑	↑	McIntyre *et al.* 1999[b] Bond & Midgley 2001[a] Saha & Howe 2003[a] Díaz *et al.* 2007[b]
Resprouting capacity	↑	↑	↑	↑	McIntyre *et al.* 1999[b] Bond and Midgley 2001[a] Díaz *et al.*, 2007[b]
Seed mass	↓	↓	↓	↓	Westoby *et al.* 2002[a, b]
Wind dispersal	↑	↑	↑	↑	Howe & Miriti 2004[a, b]
Endozoochory[c] (internal animal dispersal)	↑/↓	↑/↓	↑/↓	↑/↓	Howe & Miriti 2004[a, b]
Exozoochory[c] (external animal dispersal)	↑/↓	↑/↓	↑/↓	↑/↓	Howe & Miriti 2004[a, b]

[a] Reference refers to overstory and tree seedlings/saplings

[b] Reference refers to understory

[c] The mixed predictions for animal dispersal result from two conflicting predictions. On the one hand, animal-dispersed species (like wind-dispersed species) have high potential for long-distance dispersal, and thus may be better able to colonize disturbed sites. On the other hand, anthropogenic disturbance is often associated with loss of animal dispersers due to hunting and/or habitat fragmentation, and so may reduce the prevalence of these species.

Table 6.2. Characteristics of study sites. Sites are presented from east to west.

Site:	*Pillur Reserve forest*	*Palaniappa Estate Forest Fragment*	*Sathyamangalam Reserve forest*	*BRT Wildlife Sanctuary*	*Male Mahadeshwara Hills Reserve forest*
No. plots:	4	2	2	4	2
Biomass extraction	+	-	+	-	+
Livestock grazing present in plots:	-	-	+	-	+
Range of years since fire (2010/2011)	1-2/0-3	1-3/2-4	1-3/2-4	2-6/3-7	1-2/2-4
Land use intensity (LUI) rank:	2	1	3	1	3
Elevation (m)	725-800	1600-1700	1450-1475	1100-1400	1285-1300

Table 6.3. Traits used in the analysis of functional composition and diversity. A trait was included for an aspect of the community (overstory, understory or seedling) if data was available for at least 50% of the species and if the trait varied among species. See Appendix G.2 for information on trait data sources.

Functional trait	*Trait type (Effect/Response)*	*Community aspect (Overstory/ Understory /Seedling)*	*Variable type*	*Unit*
Growth form[a]	E	O/U/S	Categorical (single value per species)	–
Leaf phenology[b]	E	O/S	Categorical, ordered (single value per species)	–
Maximum height	E	O/U/S	Continuous	m
Wood density	E	O/S	Continuous	g/cm^3
Legume (nutrient uptake strategy)	E/R	O/U/S	Binary (single value per species)	–
Raunkiaer life form[c]	E/R	U	Categorical (single value per species)	–
Clonality	R	O/U/S	Binary (single value per species)	–
Dispersal mode[d]	R	O/U/S	Categorical (multiple values possible per species)	–
Physical defense	R	O/U/S	Binary (single value per species)	–
Pollination syndrome[e]	R	O/U/S	Categorical (multiple values possible per species)	–
Resprouting ability	R	O/U/S	Binary (single value per species)	–
Seed mass	R	O/U/S	Continuous	g/1000 seeds

[a] From Cornelissen (2003): climber, dwarf shrub, erect-leafy, hemiparasite, palmoid, short basal, shrub, tree, tussock

[b] Evergreen, semi-evergreen, deciduous

[c] Chamaephyte, geophyte, hemicryptophyte, phanerophyte, therophyte

[d] Ballistic, endozoochory, exozoochory, passive, water, wind

[e] Bee, beetle, bird, butterfly, fly, mammal, moth, thrip

Table 6.4. Observed effects of land use on functional composition and functional diversity of overstory, understory and seedling communities. Details of candidate model sets and model results are in Appendix H (functional composition) and Appendix I (functional diversity).

	Overstory	Understory	Seedlings
Shifts in functional composition			
Biomass extraction	↓ wind dispersal ↑ endozoochory ↑ bird pollination*	↓ seed mass	—
Livestock	↓ maximum height	↓ seed mass ↑ physical defense[†] ↓ clonality[†] ↑ endozoochory[†] ↑ butterfly pollination*[†] ↑ thrip pollination*	↑ endozoochory
Fire	—	—	↑ legume* ↑ semi-evergreen*
LUI	↓ wind dispersal ↑ endozoochory	↓ seed mass	—
Shifts in functional diversity			
Biomass extraction	↓ response dispersion	↓ effect evenness	↑ effect & response evenness
Livestock	—	↑ effect & response dispersion	—
Fire	—	↓ effect evenness	↑ effect dispersion ↑ response evenness
LUI	—	—	↑ effect evenness

† Shifts due solely to non-native invasive species; details in Appendix J.

* Shifts determined from post hoc tests to determine the sources of change in functional dispersion

Figure 6.1. Conceptual diagram of possible effects of human land use on functional composition and functional diversity. Human land use might alter current and future ecosystem function by a) reducing or increasing functional diversity (i.e., the amount of multi-dimensional functional trait space occupied by a community) without altering functional composition (i.e., the position of a community within functional trait space), b) altering functional composition without altering functional diversity, or c) altering both functional diversity and functional composition.

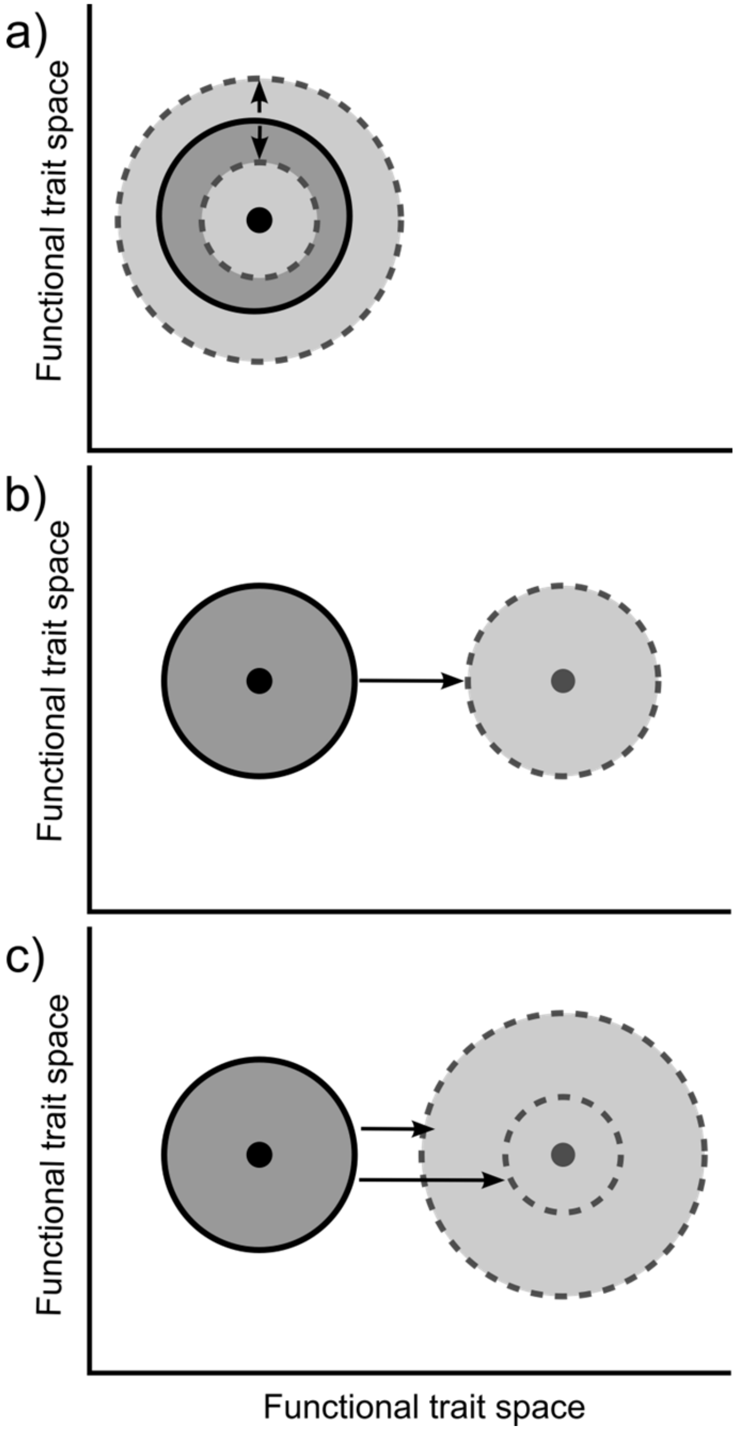


Figure 6.2. Box and dot plots of basal-area weighted proportion of overstory species with wind dispersal and endozoochory by land use intensity (LUI). To control for trends in dispersal mode with alititude, we show the residuals from a model with elevation; therefore, the y-axis shows the proportion of wind dispersal or endozoochory by land use intensity, relative to what would be predicted by a plot's elevation.

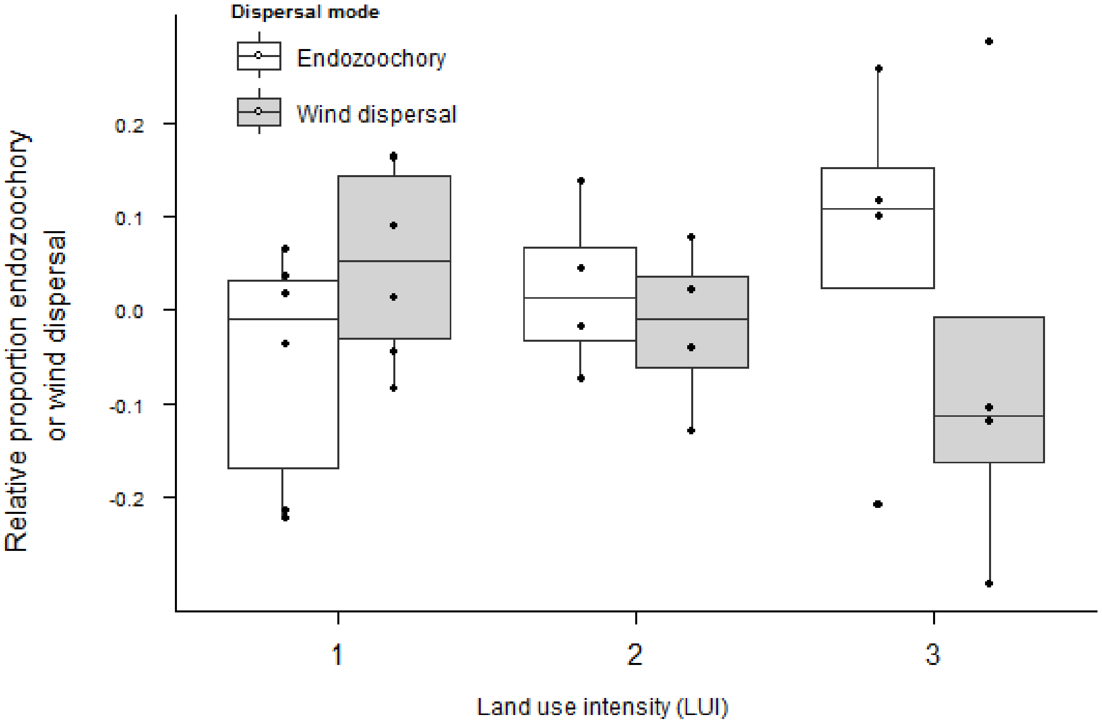
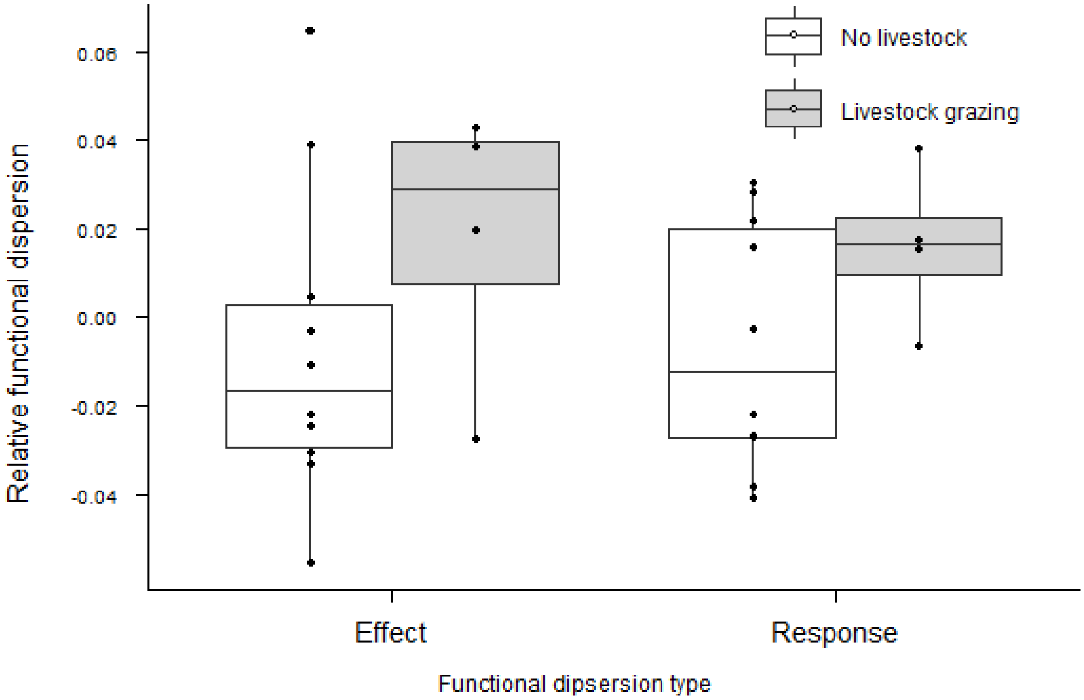


Figure 6.3. Combined box and dot plots of effect and response dispersion of understory communities with and without livestock. To control for trends in dispersion with grass cover, we show the residuals from a model with grass cover; therefore, the y-axis shows functional dispersion relative to what was predicted by a plot's grass cover alone.



CHAPTER 7. CONCLUSIONS

My dissertation examines the consequences of three widespread and commonly co-occurring forms of disturbance in human-managed tropical landscapes – fire, grazing and non-timber forest product (NTFP) harvest – on the population ecology of mountain date palm (*Phoenix loureiri*) and on the composition and diversity of surrounding savanna woodland plant communities. Here, I synthesize my findings from the previous chapters, discussing their implications for managing these systems both for mountain date palm leaf harvest and conservation of native biodiversity. I also describe the contributions of this research to the fields of plant population ecology, community ecology and conservation biology. Finally, I discuss some of the limitations of this study and suggest further avenues of research that could improve our understanding of and capacity to manage for trade-offs between ecosystem services and biodiversity conservation.

Main findings

I used a manipulative experiment to test for effects of and interactions among fire, grazing and leaf harvest on mountain date palm individuals. With data from an observational study of 14 palm populations with varying land-management histories, I developed integral projection models (IPMs) to investigate how differences in time since fire as well as grazing and harvest intensities affect mountain date palm population dynamics. I also compared the composition and diversity – both species diversity and functional diversity – of the plant communities surrounding the 14 palm populations to understand how differences in land management history affects the prospects for conservation of species and ecosystem processes in these landscapes.

Overall, mountain date palm individuals and populations appear to be resilient to fire and to at least low intensities of harvest and grazing. I found evidence of several mechanisms underlying this resilience. Palm individuals had higher growth rates in the 1-2 years following fire than individuals >2 years post-fire (Chapters 3 and 4). Palm individuals also exhibited increased growth following low intensities of grazing and harvest (Chapter 4). With density-dependent mortality rates, mortality of palm individuals from fire or high intensity grazing may be at least partially offset by increased survival of remaining individuals (Chapters 3 and 4). Increased vegetative reproduction with low-intensity grazing (< ~10% leaves per genet) provides an additional mechanism by which palm populations can buffer the effects of disturbance (Chapter 4).

Both grazing and harvest had non-consumptive effects on mountain date palm individuals in addition to the effects resulting from loss of biomass (Chapters 3 and 4). Specifically, palm individuals that escaped grazing and harvest in areas where grazing and harvest occurred had lower growth rates than individuals in areas without grazing and harvest. The non-consumptive effect of grazing was consistently greater than the non-consumptive effect of harvest. Non-consumptive effects are likely due in part to trampling (Chapter 3).

My manipulative experiment revealed that the demographic rates of mountain date palm individuals were driven by multiple interactive effects among abiotic conditions, plant size and disturbance (Chapter 3). Furthermore, the intensities of one disturbance often depended on the concurrent intensities of other forms of disturbance. Grazing intensity reduced palm leaf harvest (Chapters 3 and 4), and the intensities of grazing and harvest were highest with recent fire in the observational study (Chapter 4). The capacity of mountain date palm populations to persist with leaf harvest will likely depend primarily on fire return interval because of the increases in harvest and grazing intensity following fire. Understanding the effects of harvest on mountain date palm population dynamics and the potential for sustainable leaf harvest requires an explicit consideration of co-occurring land management activities as well as the environmental conditions in which harvest occurs.

My studies of the surrounding savanna woodland plant communities suggest that moderate human land use in the forms of NTFP harvest and livestock grazing can be compatible with maintenance of a large degree of native plant diversity. This finding was true for both species diversity and functional diversity (Chapters 5 and 6). Species richness and diversity were similar across areas with and without commercial mountain date palm leaf harvest (Chapter 5). Areas with livestock grazing exhibited greater understory diversity both in terms of species richness and diversity and functional diversity (Chapters 5 and 6). Areas with more recent fire had lower levels of overstory diversity and tree seedling diversity and richness. Understory diversity was higher under more open canopies. Together, these results suggest that frequent fire may reduce tree cover and diversity, at the same time allowing a greater diversity of plant species to exist in more open understories.

I also found that areas currently managed for harvest of mountain date palm leaves (as well as other NTFPs and fuel wood) tended to have more common species and fewer narrowly-distributed species than areas with fewer human activities, though this was not statistically significant (Chapter 5). Further study is warranted to determine if protected areas with minimal human activities do provide additional conservation benefits to rare species in savanna woodlands. Promoting a mosaic of land management practices could be an effective way to balance conservation objectives with local communities' needs. Under such a system, protected areas could better preserve tree cover and diversity, and areas subject to moderate land use can both maintain substantial diversity and enable connectivity between protected areas, while providing benefits to local people.

Evidence of trade-offs between management for palm leaf harvest and conservation of native plant diversity

Overall, my findings suggest that there is a high capacity for these savanna woodlands to support some degree of mountain date palm leaf harvest while maintaining high levels of native plant diversity. However, I also find evidence of some trade-offs between these two management aims.

Like many understory palms, mountain date palm appears to benefit from more open canopies, exhibiting increased growth (Chapter 4) and increased rates of flowering (Chapter 3). Mountain date palm is generally known to occur in disturbed and fire-prone areas (Barrow 1998). In addition exhibiting increased growth rates following fire, mountain date palms may also benefit indirectly from fire though its maintenance of more open canopies (Mayer & Khalyani 2011; Ratnam *et al.* 2011). Based on my studies of community structure and composition, recent fire was associated with reduced tree diversity both of seedlings and in the overstory. Perhaps intuitively, the diversity of overstory species was also lower in areas with more open canopies. While too frequent fire may have negative consequences for palm populations, and therefore mountain date palm leaf harvest, it seems unlikely that the optimum fire return interval for mountain date palm populations would also maximize tree diversity or cover. Taken together, these results suggest a trade-off between maximizing the growth of mountain date palm populations and maximizing tree species diversity, mediated by the relationship between fire and canopy openness.

Understory diversity was unaffected by the history of harvest at the study site, but increased in areas with more open canopies. This suggests that while managing for mountain date palm harvest may reduce tree diversity, this can be offset by increases in understory diversity. Indeed, the greatest contribution to the plant diversity of savanna woodlands often comes from forbs in the understory (Ratnam *et al.* 2011). For a conservation community largely interested in maintaining tree cover (e.g., Davidar *et al.* 2010), this may not be a desirable trade-off. It is, however, a trade-off likely common to the harvest of other understory species that benefit from increased understory light availability (e.g., Kathriarachchi *et al.* 2004; Ticktin & Nantel 2004; Schmitt *et al.* 2010). This trend suggests that harvest of understory NTFP species may best provide incentives for conservation of plant diversity in more open habitats such as secondary forests and savanna woodlands, as compared to dense forest.

Contribution to the scientific literature

My dissertation focuses on the effects of three forms of disturbance that are widespread and commonly co-occur in human-managed tropical systems: fire, grazing and NTFP harvest. Despite the importance of these disturbances and their potential interactive effects, relatively few studies have tested for such interactions. In my dissertation, I examined the effects of and interactions among of these disturbances on mountain date palm individuals and populations. I also assessed their effects on surrounding plant communities.

NTFP harvest routinely occurs with other human land management activities, including fuelwood collection, livestock grazing and fire (e.g., Endress *et al.* 2004; Gaoue & Ticktin 2007; Schmidt *et al.* 2007). Many species harvested for NTFP occur across, and are harvested from, a range of environmental conditions. Despite this, few studies have assessed how harvest might interact with these co-occurring activities (see review by Ticktin 2004; but see Farrington *et al.* 2009; Schmidt 2011; Sinha & Brault 2005) or how the effects of harvest might vary under different environmental conditions (but see Gaoue & Ticktin 2007; Martínez-Ramos *et al.* 2009). My dissertation uses both a manipulative experiment and a regional observational study to understand the interactions between harvest, fire and grazing across varying environmental conditions. My findings confirm the necessity of considering harvest in the context of other co-occurring land uses because of importance of multiple interactions among land-management activities, as well as with abiotic environmental conditions.

Integral projection models (IPMs) allow population dynamics to be modeled as a function of continuous variables, such as environmental gradients, and represent an important advance on traditional population projection matrices. My use of IPMs proved especially valuable for understanding the effects of harvest and grazing, as these activities had non-linear effects on mountain date palm population dynamics. Modeling both palm vital rates and population dynamics revealed that compensatory growth contributed to the resilience of mountain date palms to fire and to low intensities of grazing and harvest, but that this compensatory growth had limits. Modeling grazing and harvest intensities as factors, as would have been necessary with population projection matrices, could have masked some of the changes in the effects of these activities across this gradient. Knowing these limits of compensatory responses is important to preventing harvest and livestock grazing from threatening mountain date palm populations. The IPMs I developed in this dissertation are, as far as I am aware, the first application of this tool to studying multiple forms of disturbance and their potential interactive effects. The limited capacity for compensatory response to disturbance is likely to be important for understanding and managing the responses of other plant species to changing disturbance regimes and multiple forms of disturbance.

The multiple interactions I found highlights the importance of examining interactions among drivers – both natural and anthropogenic – in order to understand the dynamics of plant populations in general, not just harvested species. Plant populations of the same species have been found to exhibit substantial spatial and temporal demographic variation, but little is known about the causes of this variation (Jongejans & De Kroon 2005; Buckley *et al.* 2010). Results from my dissertation suggest that interactive effects among drivers are likely to play an important role in the dynamics of other plant species, and must be considered if we aim to conserve threatened plant populations and minimize the impacts of invasive species under future changes in disturbance regimes and environmental conditions.

Disturbances can affect plant demography, both from the direct removal of biomass and also through non-consumptive effects. For example, the non-consumptive effects of grazing are known to include trampling, soil compaction and changes to soil nutrient composition (e.g., Rooney & Waller 2003; Heckel *et al.* 2010). Few studies have attempted to distinguish between the consumptive and non-consumptive effects of grazing or NTFP harvest (Maron & Crone 2006; Schmidt *et al.* 2011). This poses a challenge for understanding the effects of grazing and harvest, as well as any mechanisms of resilience to these disturbances. A common approach to simulating the effects of ungulate herbivory in plant demographic studies has been to compare demographic rates across all individuals within a grazed population to demographic rates of the subset of individuals within the same population that have escaped herbivory (Knight 2004; McGraw & Furedi 2005; Farrington *et al.* 2009). Several studies of NTFP harvest have also modeled the effects of harvest by assuming identical demographic rates between unharvested individuals in harvested and unharvested populations, such as those plants too small for harvest (e.g., Baltzer *et al.* 2002; Guedje *et al.* 2007; Binh 2009). As discussed in Chapter 3, these approaches do not account for possible non-consumptive effects of grazing or harvest and can lead to inaccurate conclusions about their effects on plant demography if non-consumptive effects do exist. We found evidence of negative non-consumptive effects of both grazing and harvest on individual palm growth rates (Chapters 3 and 4). Simulation approaches are likely to underestimate the negative impacts of grazing if, as I found, ungrazed plants in populations with grazing are still affected by non-consumptive effects of grazing. In the case of harvest, the effects of harvest will be under- or overestimated depending on whether the unharvested individuals are modeled from harvested or unharvested populations.

Determining the compatibility between different forms of human land use and the maintenance of biodiversity is especially critical for conservation in face of growing human influence on tropical ecosystems (Chazdon *et al.* 2009; Gardner *et al.* 2009). Most studies of changes in plant functional diversity with human land use have focused on forms of substantial land use change (Flynn *et al.* 2009; Laliberté *et al.* 2010; Lin *et al.* 2011). My dissertation is one of few studies to examine the effects of moderate forms of land use on plant functional diversity. In the savanna woodland ecosystems I studied, I found little difference in diversity – both in terms of species and functional diversity – between areas with different histories of livestock grazing and NTFP harvest. I hypothesize that the maintenance of plant diversity under these conditions is related to two factors: 1) These forms of land use leave much of the native vegetation structure intact, and 2) With a long history of human land use in the Western Ghats, species sensitive to these forms of disturbance may already have been eliminated (Balmford 1996). However, I also find evidence that *Lantana camara*, a non-native invasive species, contributes to increased functional diversity. My finding points to the need for caution if increased functional diversity is used as a specific management target, as has recently been suggested (Cadotte 2011). Otherwise, management aimed at increasing functional diversity could promote non-native invasive species that would increase functional diversity over the short term, but might reduce functional diversity over the long term if their abundance within communities becomes too great. Overall, my findings suggest that conservation policy and resources in India, and elsewhere in the tropics, might be more productively directed towards managing the more extreme forms of land use change and restoring degraded land rather than restricting more moderate land use activities such as those considered here.

Understanding the linkages among human land use, biodiversity conservation, ecosystem processes and ecosystem services is necessary in order to maintain biodiversity while meeting human needs both currently and over the long term. Studies aimed at determining trade-offs among multiple management objectives have been focused primarily at regional and landscape scales (Naidoo *et al.* 2008; Anderson *et al.* 2009). Determining the most effective way to meet these multiple management objectives will require untangling the mechanisms that underlie the observed spatial patterns in biodiversity and ecosystem services across multiple ecological scales (Luck *et al.* 2009). My dissertation contributes to this new direction in ecology and conservation biology by examining both the population-level and community-level effects of human management activities in order to determine the trade-offs between managing for palm leaf harvest and overall plant diversity within a densely populated biodiversity hotspot.

Future directions

As a two-year study case study on the population dynamics of one species within a diverse plant community within a complex socio-ecological system, my dissertation necessarily has limitations and my findings have suggested further avenues of study.

Ecology of mountain date palm

A better understanding of several aspects of mountain date palm ecology would allow me to make improved and more precise management recommendations. Over the duration of the study, there was a high degree of inter-annual variation in grazing intensity. In addition, both wild ungulates and livestock grazed on mountain date palm, but their effects could not be differentiated due to similarities in dentition. Given the substantial effects of grazing on palm demography, understanding the source of the variation between years and determining if wild and domestic ungulates vary in their effects would be useful to managing palm populations.

I found evidence of density dependence and effects of fire, grazing and harvest on mountain date palm population dynamics. Models of the transient dynamics of mountain date palm populations are therefore likely to provide a better understanding of the effects of the land use activities on mountain date palm demography, compared to long-term projected population dynamics (Ezard *et al.* 2010; Stott *et al.* 2011). The capacity to assess transient dynamics with integral projection models is currently being developed (Eager *et al.* 2011; Rebarber *et al.* 2011), and I plan to apply these tools to exploring the effects of fire, grazing and harvest on mountain date palm populations to develop more relevant management results. Specifically, I intend to assess under what frequency of fire, and what intensities of grazing and harvest can mountain date palm populations be expected to persist.

Effects of human land use on plant diversity

The variation in conditions among my study sites was beneficial to my ability to draw robust conclusions about the effects of disturbance on palm population dynamics across gradients of disturbance and abiotic conditions. However it limited my ability to ascertain the source of differences in plant community composition. The diversity and structure of a plant community is determined by a number of factors, including but certainly not limited to climate, soil, disturbance history and current land use. A greater number of study sites, or reduced variation in abiotic conditions among sites would have been helpful for isolating the effects of recent land use differences on plant community composition. In general, there have been few studies of the effects of human land use on tropical dry ecosystems compared to moist ecosystems. This is especially the case in Asia and Africa. With longer histories of human land use compared to the neotropics, the effects of human land use may be different in these areas. As these areas are centers of future land use change and home to the majority of the world's population, understanding what forms of human land use are compatible with conservation in these systems is especially important.

Linking biodiversity to ecosystem processes and ecosystem services

My study of plant community composition was not originally designed to test for differences in functional diversity or composition. Because of this, I relied on species-level measures of functional traits and was limited to traits for which published data was available. Intraspecific differences in functional traits between sites, and even among individuals within sites, can be substantial, though there is debate over when it is important to consider (De Bello *et al.* 2011; Albert *et al.* 2012; Cianciaruso *et al.* 2012). Of the 12 functional traits included in my study, only three (maximum height, wood density and seed mass) have the potential to exhibit substantial variation between sites. My ability to translate the results of my functional diversity study into ecological and conservation implications was limited by the state of the field, in which theory about functional diversity outpaces empirical tests of its application. While increased functional diversity is expected to increase ecosystem stability and resilience, this has rarely been tested under realistic scenarios of species losses or outside of grassland ecosystems (Balvanera *et al.* 2006).

In addition, an ecological understanding of the relationships among functional diversity and composition, ecosystem processes and ecosystem services is lacking (Laliberté *et al.* 2010; Mace *et al.* 2011). I found no overall reduction in functional diversity with land management activities, suggesting managed ecosystems retain a high degree of resilience. However, it is unclear whether the functional traits that I measured capture the aspects of functional diversity most important to resilience. I found several shifts in functional composition, including changes in pollination and dispersal mechanisms and reductions in seed mass with NTFP harvest and livestock grazing. These changes could have implications for ecosystem processes and resulting ecosystem services in the savanna woodlands of the Western Ghats, but a better understanding of the relationship between functional traits, ecosystem processes and ecosystem services is needed to draw more specific conclusions.

Managing for multiple ecosystem services

Finally this dissertation focused on the ecology of a single provisioning service (mountain date palm leaves) and a limited measure of biodiversity (plant diversity). Like other seasonally dry tropical ecosystems, these savanna woodlands provide numerous provisioning, regulating and cultural ecosystem services (Balvanera *et al.* 2010). While mountain date palm leaves are an important source of income to many local communities, savanna woodlands provide many other important services, the provision of which must also be considered when making management decisions. In addition, the biodiversity of savanna woodlands is not limited to its plant species. Many in the conservation community may in fact place greater value on the conservation of the megafauna and bird species of these ecosystems, though these animal species certainly depend on the underlying vegetation. A more holistic picture of the services provided by savanna woodlands – at a range of spatial scales – and their ability to maintain a diversity of lifeforms with human land use would be useful to informing management decisions in the Western Ghats.

Applications to management decisions

The decision about how to balance local benefits from biodiversity with conservation is ultimately a choice to be made by societies, not just ecologists or conservation biologists (DeFries *et al.* 2004). Ecological studies such as this one can provide a valuable source of information about the nature of trade-offs between land use and biodiversity conservation, information that is lacking throughout much of the tropics (Chazdon *et al.* 2009).

By using a case-study approach, my results have direct relevance to management decisions being made by local communities in the study area. My dissertation research coincided with the passage and implementation of India's Forest Rights Act (details in Bawa *et al.* 2011). The Forest Rights Act recognizes local communities' rights to manage natural resources and biodiversity and provides for joint management of these resources with the state. The Forest Rights Act provides an opportunity for information about the effects of human land use on biodiversity to be incorporated into management decisions at a local level. It also provides an opportunity for decisions about how to balance human needs with biodiversity conservation to be made in a more participatory manner than it traditionally has been in India. As of October 2011, 25 of approximately 62 *gram sabhas* (village assemblies) in the Biligiri Rangaswamy Temple Wildlife Sanctuary, one of my study sites, have obtained NTFP harvest rights under the community forest rights provision of the Forest Rights Act. It is the first case in the country that NTFP collection and conservation rights have been awarded in a protected area, and the Ashoka Trust for Research in Ecology and the Environment (ATREE), one of the NGOs with which I have collaborated, has been supporting the local communities in this process.

In this context, I have taken several steps to ensure that the results of my study can contribute to management decisions. This research was designed and carried out in collaboration with two Indian environmental NGOs, Keystone Foundation and ATREE, both of which have longstanding relationships with local communities. My decision to focus on mountain date palm was based on the high levels of harvest of this species and the lack of ecological information. I have shared my results broadly with the members of Keystone and ATREE, as well as an additional Indian NGO, the Foundation for the Revitalisation of Local Health Traditions, interested in aligning conservation with sustainable use of medicinal plants. I met with harvester groups in two areas to share my findings with them and discuss how my results compared with their knowledge about mountain date palms and the ecosystems in which they occurred. I created materials so that members of Keystone could continue to share these results in future meetings with harvesters and local communities. Also in collaboration with Keystone, I am in the process of developing posters and print material in local languages that will illustrate the ecological role of mountain date palms. It is my intention that the results of my dissertation, in addition to informing ecological theory, will in these ways facilitate decision making about the management of these important, multiuse ecosystems.

APPENDIX A. DETAILS OF POPULATION PROJECTION MATRICES FOR MOUNTAIN DATE PALM (*PHOENIX LOUREIRI*) BASED ON OBSERVED VITAL RATES

Figure A.1. Life cycle diagram for mountain date palm (*Phoenix loureiri*) ramets. The life cycle is modeled with four stages, based on the petiole width of the longest leaf and the origin of the ramet: seedling (0.1-0.3 cm, from seed), sprout (0.1-0.3 cm, produced by vegetative reproduction), juvenile (0.4-0.6 cm, from seed or vegetative reproduction), adult (>0.7 cm, from seed or vegetative reproduction).

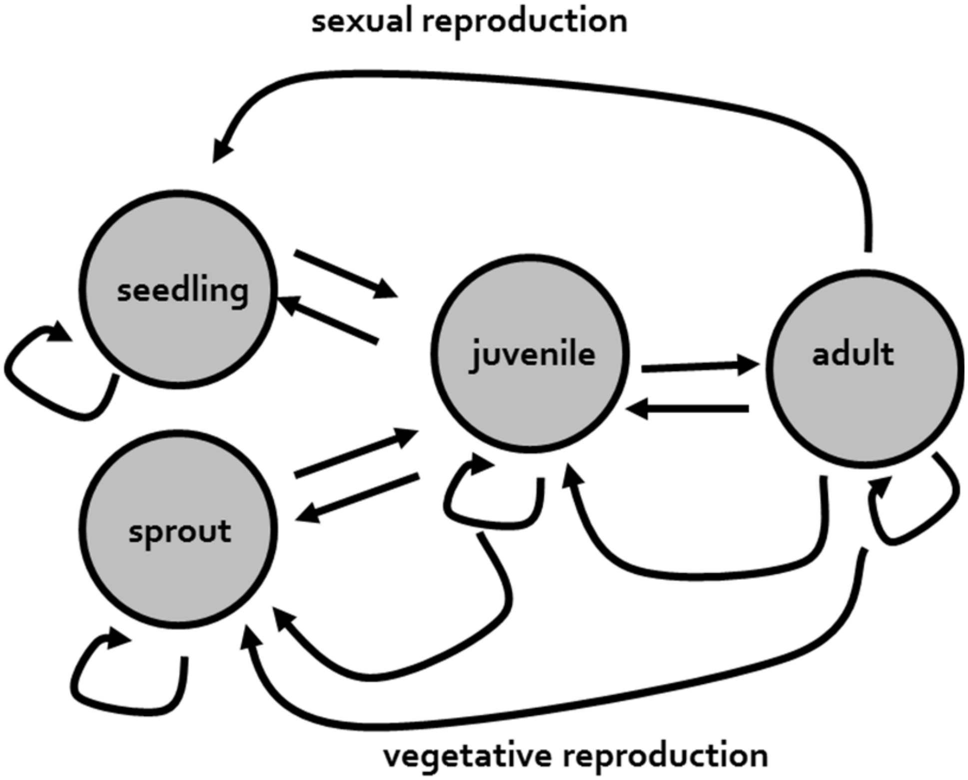


Table A.1. Generalized population projection matrix for mountain date palm (*Phoenix loureiri*) based on vital rates. Sprouts cannot produce seedlings, but all other transitions are possible. Survival rates are indicated with “s,” growth rates are indicated with “g,” rates of retrogression are indicated with “r,” rates of vegetative reproduction through the production of sprouts are indicated with “v,” and rates of sexual reproduction (fecundity) are indicated with “f.” Numbers following survival and fecundity indicate the size class to which that rate applies. Numbers following growth and retrogression indicate the final stage of the ramet and the starting stage of the ramet. Numbers following vegetative reproduction indicate the stage of the new sprout and the stage of the mother ramet that produced the sprout.

	seedling (1)	**sprout (2)**	**juvenile (3)**	**adult (4)**
seedling (1)	s1*(1-g21-g31-g41)	0	s3*r13+f3	s4*r14+f4
sprout (2)	s1*g21	s2*(1-g32-g42)+s2*v22	s3*r23+s3*v23	s4*r24+s4*v24
juvenile (3)	s1*g31	s2*g32+s2*v32	s3*(1-r13-r23-g43)+s3*v33	s4*r34+s4*v34
adult (4)	s1*g41	s2*g42+s2*v42	s3*g43+s3*v43	s4*(1-r14-r24-r34)+s4*v44

Table A.2. Projected population growth rates (λ + 95% bias-corrected bootstrapped confidence intervals) and vital rates calculated for 14 mountain date palm populations from five sites over two years based on annual censuses of approximately 150 individual ramets per population from 2009-2011. See Table A.1 for a description of vital rates. See Table 4.1 for additional information about the study populations. Harvest categories include high harvest (commercial harvest of mountain date palm leaves) and low harvest (no commercial harvest). Fire categories include F0 (fire during the year), F12 (1-2 years post-fire) and NF (>2 years post-fire).

Site	*Pillur Reserve Forest*							
Population	KK1		KK2		KSM1		KSM2	
Year	2009/2010	2010/2011	2009/2010	2010/2011	2009/2010	2010/2011	2009/2010	2010/2011
Harvest category	High harvest							
Fire category	F12	F12	F12	F0	F12	F0	F12	F0
λ (95% confidence interaval)	1.048 (1.003-1.162)	1.000 (0.972-1.034)	1.001 (1.000-1.004)	0.936 (0.882-0.974)	1.036 (0.996-1.102)	0.997 (0.912-1.041)	0.997 (0.979-0.1005)	0.959 (0.908-1.004)
Vital rates								
s1	0.458	0.267	0.458	0.556	0.458	0.556	0.458	0.556
s2	1.000	0.897	1.000	0.878	1.000	0.909	0.826	0.923
s3	0.991	0.992	0.984	0.980	0.972	0.986	0.989	0.910
s4	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
g21	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
g31	0.333	0.333	0.333	0.010	0.333	0.010	0.333	0.010
g41	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
g32	0.441	0.269	0.238	0.186	0.652	0.300	0.368	0.417
g42	0.017	0.019	0.024	0.000	0.130	0.000	0.000	0.000
g43	0.065	0.127	0.130	0.041	0.271	0.129	0.244	0.183
r13	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000
r23	0.074	0.103	0.130	0.194	0.029	0.129	0.011	0.042
r14	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Table A.2. continued Projected population growth rates and vital rates.

Site	*Pillur Reserve Forest*							
Population	KK1		KK2		KSM1		KSM2	
Year	2009/2010	2010/2011	2009/2010	2010/2011	2009/2010	2010/2011	2009/2010	2010/2011
Harvest category	High harvest							
Fire category	F12	F12	F12	F0	F12	F0	F12	F0
Vital rates								
r24	0.067	0.000	0.000	0.000	0.000	0.060	0.000	0.000
r34	0.400	0.313	0.417	0.609	0.100	0.280	0.227	0.282
f3	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
f4	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010
v22	0.186	0.019	0.000	0.000	0.087	0.000	0.000	0.000
v32	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
v42	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
v23	0.019	0.024	0.017	0.000	0.014	0.000	0.000	0.000
v33	0.009	0.016	0.000	0.000	0.029	0.000	0.000	0.000
v43	0.000	0.000	0.000	0.000	0.014	0.014	0.000	0.000
v24	0.000	0.000	0.000	0.010	0.033	0.080	0.010	0.000
v34	0.000	0.000	0.000	0.000	0.000	0.020	0.000	0.000
v44	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.026

Table A.2. continued Projected population growth rates and vital rates.

Site	*Palaniappa Estate Forest Fragment*			
Population	PE1		PE2	
Year	2009/2010	2010/2011	2009/2010	2010/2011
Harvest category	Low harvest			
Fire category	F12	F12	NF	NF
λ (95% confidence interaval)	1.009 (0.983-1.035)	0.968 (0.907-1.011)	0.998 (0.997-1.007)	0.994 (0.972-1.024)
Vital rates				
s1	1.000	1.000	0.750	0.742
s2	1.000	0.500	1.000	0.918
s3	0.939	0.975	0.969	0.921
s4	1.000	1.000	1.000	1.000
g21	0.000	0.000	0.000	0.000
g31	0.036	0.167	0.250	0.010
g41	0.000	0.000	0.000	0.000
g32	0.296	0.500	0.375	0.352
g42	0.197	0.000	0.024	0.025
g43	0.239	0.154	0.207	0.293
r13	0.000	0.026	0.000	0.000
r23	0.022	0.128	0.069	0.069
r14	0.000	0.000	0.000	0.000
r24	0.000	0.021	0.000	0.000
r34	0.079	0.160	0.240	0.072
f3	0.000	0.000	0.000	0.000
f4	0.034	0.032	0.010	0.014

Table A.2. continued Projected population growth rates and vital rates.

Site	*Palaniappa Estate Forest Fragment*			
Population	PE1		PE2	
Year	2009/2010	2010/2011	2009/2010	2010/2011
Harvest category	Low harvest			
Fire category	F12	F12	NF	NF
Vital rates				
v22	0.000	0.000	0.032	0.000
v32	0.000	0.000	0.000	0.000
v42	0.000	0.000	0.000	0.000
v23	0.022	0.000	0.017	0.000
v33	0.000	0.000	0.000	0.000
v43	0.000	0.000	0.000	0.000
v24	0.000	0.000	0.000	0.000
v34	0.000	0.011	0.000	0.014
v44	0.000	0.000	0.000	0.000

Table A.2. continued Projected population growth rates and vital rates.

Site	*Sathyamangalam Reserve Forest*				*Male Mahadeshwara Hills Reserve Forest*			
Population	OGF		OGF		MBL		MBU	
Year	2009/2010	2009/2010	2010/2011	2009/2010	2010/2011	2010/2011	2009/2010	2010/2011
Harvest category	High harvest				High harvest			
Fire category	NF	NF	NF	F12	F12	F12	NF	NF
λ (95% confidence interaval)	0.996 (0.969-1.017)	0.996 (0.969-1.017)	1.000 (0.958-1.048)	0.967 (0.932-0.990)	0.967 (0.950-0.981)	0.862 (0.783-0.925)	1.030 (0.978-1.155)	0.956 (0.905-1.012)
Vital rates								
s1	0.010	0.458	0.267	0.010	0.010	0.010	0.458	0.267
s2	1.000	0.903	0.731	0.929	0.784	0.945	0.943	0.871
s3	0.987	0.912	0.875	0.976	0.957	0.961	0.945	0.969
s4	1.000	0.976	0.895	1.000	0.977	1.000	1.000	1.000
g21	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
g31	0.010	0.333	0.333	0.010	0.010	0.010	0.333	0.333
g41	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
g32	0.319	0.429	0.474	0.308	0.207	0.558	0.364	0.370
g42	0.000	0.161	0.000	0.026	0.069	0.077	0.000	0.074
g43	0.158	0.735	0.143	0.346	0.224	0.137	0.155	0.138
r13	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
r23	0.224	0.012	0.214	0.062	0.090	0.288	0.078	0.128
r14	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
r24	0.103	0.011	0.000	0.136	0.023	0.033	0.000	0.031
r34	0.310	0.236	0.324	0.318	0.535	0.433	0.273	0.219
f3	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
f4	0.010	0.010	0.013	0.010	0.045	0.010	0.010	0.010

Table A.2. continued Projected population growth rates and vital rates.

Site	*Sathyamangalam Reserve Forest*				*Male Mahadeshwara Hills Reserve Forest*			
Population	OGF		OGF		MBL		MBU	
Year	2009/2010	2009/2010	2010/2011	2009/2010	2010/2011	2010/2011	2009/2010	2010/2011
Harvest category	High harvest				High harvest			
Fire category	NF	NF	NF	F12	F12	F12	NF	NF
Vital rates								
v22	0.000	0.018	0.000	0.000	0.000	0.000	0.030	0.037
v32	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
v42	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
v23	0.000	0.012	0.000	0.012	0.000	0.027	0.000	0.011
v33	0.000	0.000	0.000	0.012	0.000	0.027	0.000	0.000
v43	0.000	0.000	0.000	0.025	0.000	0.014	0.000	0.000
v24	0.010	0.006	0.029	0.000	0.047	0.000	0.000	0.000
v34	0.000	0.000	0.029	0.045	0.047	0.000	0.000	0.000
v44	0.000	0.000	0.000	0.045	0.000	0.000	0.000	0.000

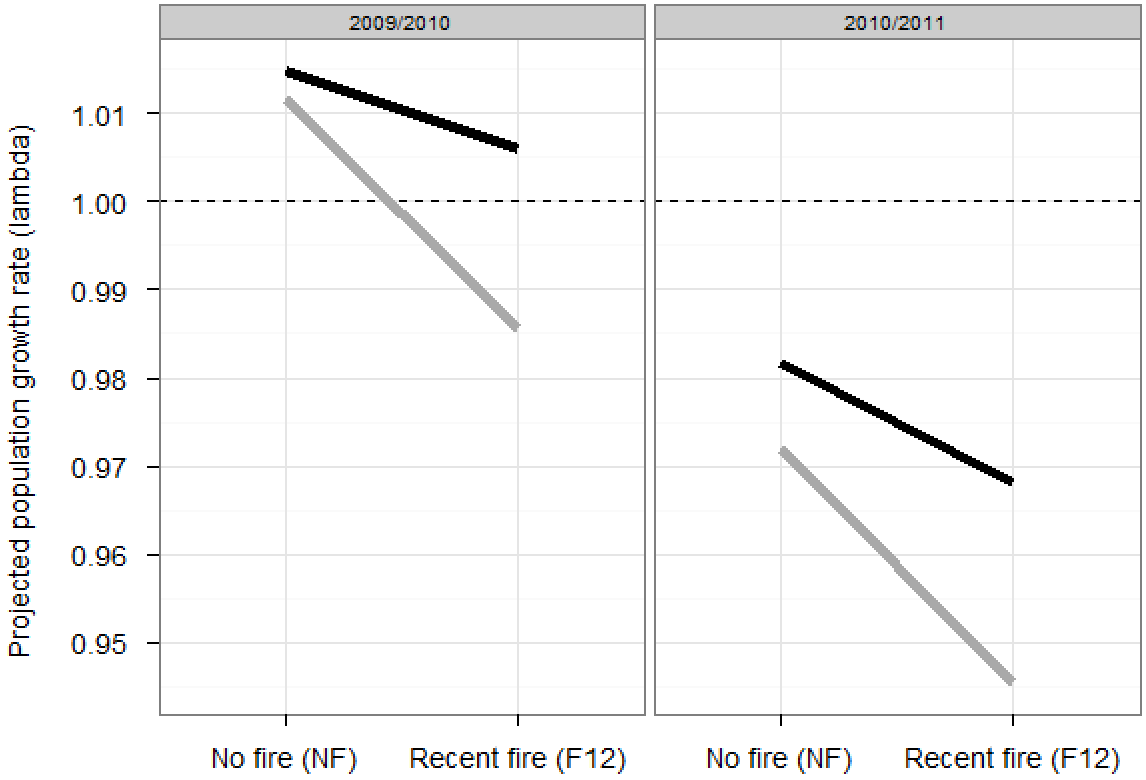
Table A.2. continued Projected population growth rates and vital rates.

Site	*BRT Wildlife Sanctuary*							
Population	BDB		IBK		NKF		NKN	
Year	2009/2010	2010/2011	2009/2010	2010/2011	2009/2010	2010/2011	2009/2010	2010/2011
Harvest category	Low harvest							
Fire category	NF	NF	F12	NF	NF	NF	NF	NF
λ (95% confidence interaval)	1.041 (0.990-1.114)	1.039 (0.980-1.190)	1.115 (1.000-1.258)	0.966 (0.915-0.998)	1.021 (1.001-1.063)	1.003 (0.992-1.018)	1.026 (0.974-1.081)	0.965 (0.886-1.007)
Vital rates								
s1	0.750	0.742	1.000	0.833	0.750	0.742	0.750	0.742
s2	1.000	0.957	1.000	0.840	1.000	1.000	1.000	0.918
s3	0.966	0.948	0.987	1.000	0.978	1.000	0.969	0.921
s4	0.974	1.000	1.000	1.000	1.000	0.974	1.000	1.000
g21	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
g31	0.250	0.010	0.071	0.010	0.250	0.010	0.250	0.010
g41	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
g32	0.195	0.318	0.592	0.429	0.222	0.111	0.375	0.352
g42	0.000	0.023	0.061	0.048	0.000	0.022	0.024	0.025
g43	0.175	0.255	0.243	0.064	0.345	0.127	0.207	0.293
r13	0.000	0.000	0.000	0.000	0.012	0.000	0.000	0.000
r23	0.105	0.145	0.108	0.192	0.119	0.236	0.069	0.069
r14	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
r24	0.026	0.000	0.000	0.000	0.000	0.053	0.000	0.000
r34	0.263	0.057	0.039	0.458	0.091	0.395	0.240	0.072
f3	0.000	0.000	0.000	0.000	0.027	0.000	0.000	0.000
f4	0.026	0.010	0.517	0.010	0.068	0.010	0.010	0.014

Table A.2. continued Projected population growth rates and vital rates.

Site	*BRT Wildlife Sanctuary*							
Population	BDB		IBK		NKF		NKN	
Year	2009/2010	2010/2011	2009/2010	2010/2011	2009/2010	2010/2011	2009/2010	2010/2011
Harvest category	Low harvest							
Fire category	NF	NF	F12	NF	NF	NF	NF	NF
Vital rates								
v22	0.098	0.000	0.000	0.000	0.000	0.000	0.032	0.000
v32	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
v42	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
v23	0.018	0.000	0.014	0.000	0.000	0.018	0.017	0.000
v33	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
v43	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
v24	0.026	0.000	0.000	0.042	0.010	0.000	0.000	0.000
v34	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.014
v44	0.026	0.057	0.000	0.000	0.000	0.000	0.000	0.000

Figure A.2. Mean projected population growth rates (λ) by harvest and fire categories across two years from population projection matrices. Black lines represent low harvest populations and gray lines represent high harvest populations. Projected population growth rates are calculated from matrices based on the mean vital rates for all populations in each fire and harvest combination in each year. The IBK population was omitted because of high observed deviation from the predicted stable stage distribution. Populations that burned in the 2010-2011 interval (F0) were also omitted because these fires occurred at single site in a single year.



APPENDIX B. DETAILS OF METHODS AND RESULTS FROM THE MANIPULATIVE EXPERIMENT OF THE EFFECTS OF FIRE, GRAZING AND HARVEST ON MOUNTAIN DATE PALM INDIVIDUALS

Abiotic conditions and correlations with disturbance

Canopy openness ranged from 21 to 84%, (mean = 56%). Plot measures of soil moisture ranged from 0.08 to 0.37 m^3 water/m^3 soil. Mean soil moisture in 2009 was 0.19 m^3/m^3. This increased to 0.24 m^3/m^3 in 2010 and then declined to 0.14 m^3/m^3 in 2011. Canopy openness and soil moisture were negatively correlated ($r = -0.335$, $p = 0.002$). Canopy openness did not differ significantly with fire history ($t = 0.0565$, $df = 35.019$, $p = 0.9553$), harvest ($t = -0.4505$, $df = 37.837$, $p = 0.6549$) or grazing treatment ($t = 0.4349$, $df = 37.404$, $p = 0.666$). Soil moisture at the start of the study also did not differ significantly with fire history ($t = 0.8941$, $df = 37.58$, $p = 0.377$), harvest ($t = -0.5076$, $df = 37.056$, $p = 0.6148$) or grazing treatment ($t = 0.9511$, $df = 37.949$, $p = 0.3476$).

Table B.1. Specifications of full linear and generalized linear mixed-effects models (LMM and GLMM) used to analyze effects of disturbance and abiotic factors on palm vital rates from manipulative experiment in Chapter 3.

Model	**Form**	**Response variable**	**Random effects**	**Fixed effects**		
				Main effects	***Covariates***	***Interactions***
Grazing intensity	Binomial GLMM	Grazed or not (1,0), by ramet	Block/split plot (fire)/genet (plot)	Fire	Canopy openness Soil moisture Ramet stem height Ramet starting size (largest petiole width) Ramets per genet Total leaves per genet	Two-way interactions between fire and covariates
Harvest intensity	Binomial GLMM	Number of leaves harvested (out of total number of leaves per ramet)	Block/split plot (fire)/genet (plot)/ramet	Fire Year Proportion leaves grazed (ramet)	Canopy openness Soil moisture Ramet stem height Ramet starting size (largest petiole width) Total leaves per genet	Two- and three-way interactions among main effects; two-way interactions between main effects and covariates
Mortality	Binomial GLMM	Ramet died or survived (1,0), by genet	Block/split plot (fire)/genet (plot)	Fire Proportion leaves grazed (genet) Proportion leaves harvested (genet) Year	Canopy openness Soil moisture Ramets per genet Total leaves per genet	Two-way interactions among main effects
Growth	LMM	Change in ramet size (petiole width)	Block/split plot (fire)/genet (plot)/ramet	Fire Proportion leaves grazed (ramet) Proportion leaves harvested (ramet) Year	Canopy openness Soil moisture Stem height Starting size (petiole width) Starting size^2	Two- and three-way interactions among main effects; two-way interactions between main effects and covariates
Flowering	Binomial GLMM	Genet flowered or did not (1,0)	Block/split plot (fire)/genet (plot)	Fire Proportion leaves grazed (genet) Proportion leaves harvested (genet) Year	Canopy openness Soil moisture Ramets per genet Total leaves per genet	Two-way interactions among main effects

Table B.1. continued Specifications of full linear and generalized linear mixed-effects models used in Chapter 3.

Model	Form	Response variable	Random effects	Fixed effects		
Vegetative reproduction	Binomial GLMM	Genet produced a vegetative sprout or did not (1,0)	Block/split plot (fire)/genet (plot)	Fire Proportion leaves grazed (genet) Proportion leaves harvested (genet) Year	Canopy openness Soil moisture Ramets per genet Total leaves per genet	None

Table B.2. Estimates and standard errors for main effects and covariates that were non-significant ($p > 0.05$) by likelihood ratio test during model reduction in Chapter 3.

Model	Main effect or covariate	Estimate	SE
Grazing intensity (2010)	Canopy openness	-0.011	0.023
	Ramet starting size (petiole width)	0.571	1.167
Grazing intensity (2011)	Fire	1.067	0.555
	Canopy openness	0.020	0.016
	Soil moisture	-13.915	6.878
	Ramet stem height	0.075	0.048
	Total leaves per genet	0.001	0.0219
Harvest intensity	Canopy openness	0.008	0.006
	Ramet stem height	0.020	0.016
Mortality	Proportion leaves harvested(genet)	-5.027	3.260
	Canopy openness	-0.002	0.027
	Soil moisture	1.554	10.465
Growth	Canopy openness	-0.002	0.027
	Soil moisture	1.554	10.465
Flowering	Proportion leaves harvested (genet)	1.432	2.136
	Soil moisture	-10.586	12.411
	Ramets per genet	-0.156	0.125
	Total leaves per genet	0.048	0.027
Vegetative reproduction	Fire	2.114	1.258
	Proportion leaves grazed (genet)	-0.615	3.397
	Proportion leaves harvested (genet)	-4.775	4.430
	Year	-0.344	0.993
	Canopy openness	0.001	0.041
	Soil moisture	-20.364	12.278
	Ramets per genet	0.150	0.106
	Total leaves per genet	-0.084	0.054

Figure B.1. Schematic of an experimental block used in the manipulative experiment in Chapter 3. Each of five blocks was located in a patch that had partially burned prior to the start of the experiment. Within the burned (dashed line) and unburned portions of the block, four focal palm genets were selected and each was randomly assigned to harvest (circle) and grazing (square) treatment combinations.

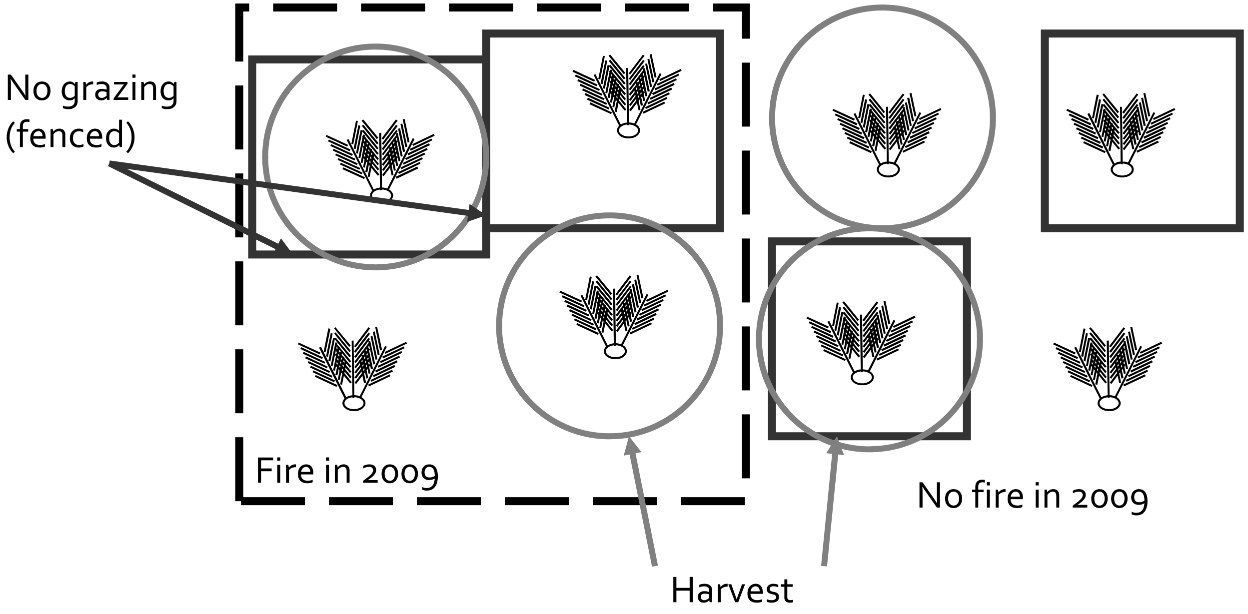
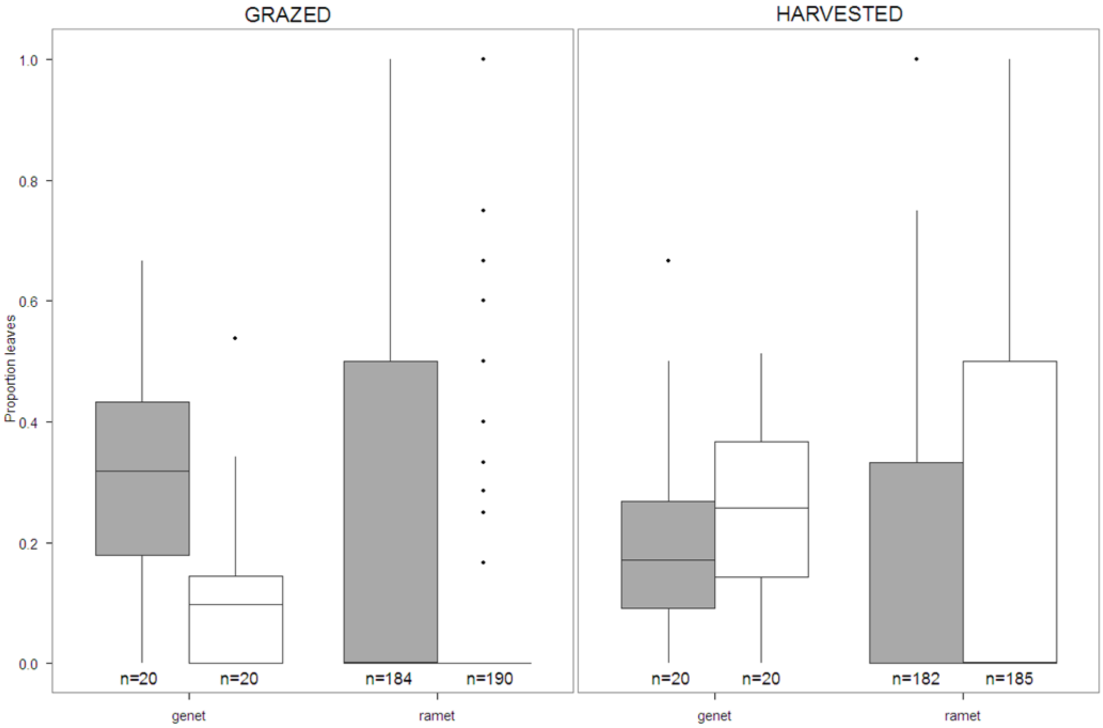


Figure B.2. Boxplots of proportions of mountain date palm leaves grazed and harvested per genet and ramet. Results from 2010 are shown in gray and 2011 in white.



APPENDIX C. DETAILS OF METHODS AND RESULTS FROM INTEGRAL PROJECTION MODELS OF MOUNTAIN DATE PALM (*PHOENIX LOUREIRI*)

Table C.1. Specifications of variables tested with linear and generalized linear mixed effects models (LMM and GLMM) for their effects on mountain date palm vital rates for integral projection model construction in Chapter 4

Model	**Form (R package)**	**Response variable**	**Random effects**[a]	**Fixed effects**		
				Main effects	*Covariates*	*Interactions*
Survival	Binomial GLMM (lme4)	Ramet survived from time *t* to *t*+1	Area/population/genet Year	Fire category Harvest intensity (genet-level) Grazing intensity (genet-level)	Ramet size at start[b] Ramets per genet Canopy openness Seedling (vs. vegetative sprout)	Two-way interactions between main effects and between main effects and covariates (except seedling)
Size at *t* + 1 of surviving ramets	LMM (lme4)	Ramet size at *t* + 1[b]	Population/genet/ramet Population*Ramet size at start[b] Year	Fire category Harvest intensity (ramet- and genet-level) Harvest intensity (ramet-level)^2 Grazing intensity (ramet- and genet-level) Grazing intensity (ramet-level)^2	Ramet size at start[b] Ramets per genet Canopy openness Seedling (vs. vegetative sprout)	Two-way interactions between main effects and between main effects and covariates, (except seedling, genet-level ramet and grazing intensities and quadratic terms)
Probability of flowering at time *t*	Binomial GLMM (lme4)	Ramet flowered at time *t*	Area/population/genet Year	Fire category Harvest intensity (ramet-level) Grazing intensity (ramet-level)	Ramet size at start[b] Ramets per genet Canopy openness	Two-way interactions between main effects and between main effects and covariates
Probability of producing a sprout	Binomial GLMM (lme4)	Ramet produced sprout	Area/population/genet Year	Fire category Harvest intensity (genet-level) Grazing intensity (genet-level)	Ramet size at start[b] Ramets per genet Canopy openness	Two-way interactions between main effects and between main effects and covariates

Table C.1. continued Specifications of models.

Model	Form (R package)	Response variable	Random effects[a]	Fixed effects		
				Main effects	*Covariates*	*Interactions*
Mean sprout size at $t + 1$	LMM (nlme)	Sprout size	Area/population/genet	Fire category Harvest intensity (genet-level) Grazing intensity (genet-level)	Mother ramet size at start[b] Ramets per genet Canopy openness	None

[a] Some random effects were omitted from some models because of problems with convergence with many nested random effects with estimated variances close to 0.

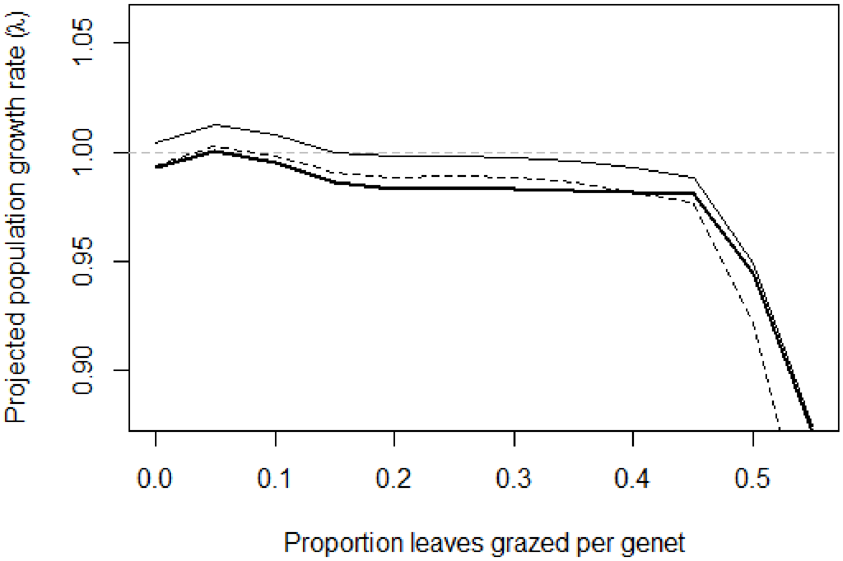
[b] Measured as the petiole width of the longest leaf.

Table C.2. A model predicting ramet-level grazing and harvest intensities from ramet size and genet-level grazing and harvest intensities. Because palm vital rates were affected by grazing and harvest at both the genet and ramet levels, we used a multinomial model to determine the relationship between the two. Our response variables were the number of grazed, harvested and intact leaves per ramet. Predictor variables included the intensity of grazing and harvest at the genet level, ramet size, and grazing-by-size and harvest-by-size interactions. The multinomial model was fitted with the multinom function in the nnet package in R (Venables & Ripley 2002). The model was reduced using AIC as the criteria for deciding whether to drop or retain individual terms. Our multinomial model showed that grazing and harvest at the ramet level increased with the corresponding level of grazing and harvest at the genet level. For a given genet-level intensity of harvest or grazing, ramet-level intensities of harvest and grazing were greater for larger ramets. Harvest especially had a greater effect on larger ramets.

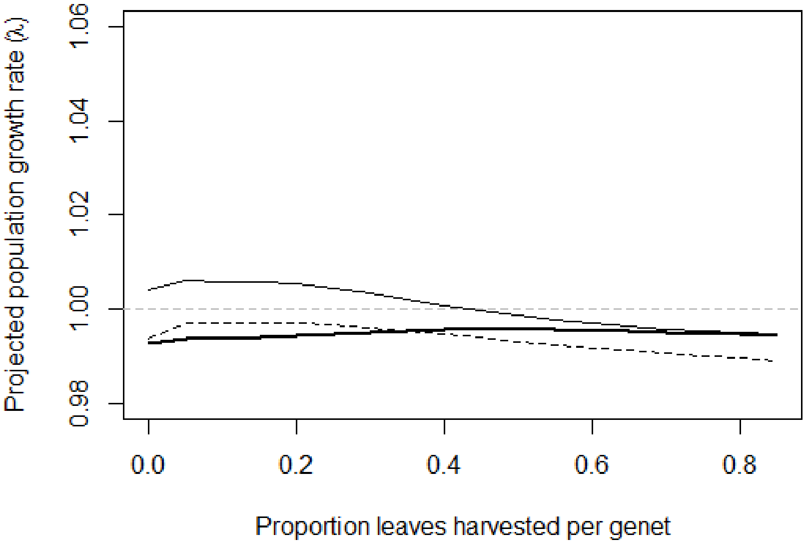
Factor	**Coefficient**	**SE**
Proportion of leaves grazed per ramet		
Intercept	-4.32	0.200
Grazing intensity (genet)	8.88	0.468
Harvest intensity (genet)	0.551	0.788
Starting size	1.61	0.288
Harvest intensity (genet) x starting size	0.00676	1.33
Proportion of leaves harvested per ramet		
Intercept	-4.27	0.197
Grazing intensity (genet)	-0.664	0.749
Harvest intensity (genet)	4.99	0.425
Starting size	2.07	0.290
Harvest intensity (genet) x starting size	2.62	0.689

Figure C.1. Effects of a) grazing; b) harvest; and their combination (c – no fire, d – fire within the past 1-2 years and e – fire within the past year) on projected population growth rates (λ), assuming that true fruiting rates were 1/3 those parameterized from ramets known to be female and averaging seedlings/stalk across all populations.

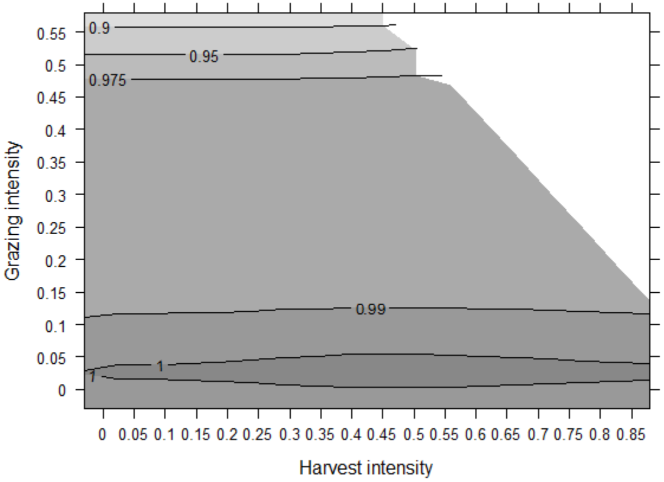
a)



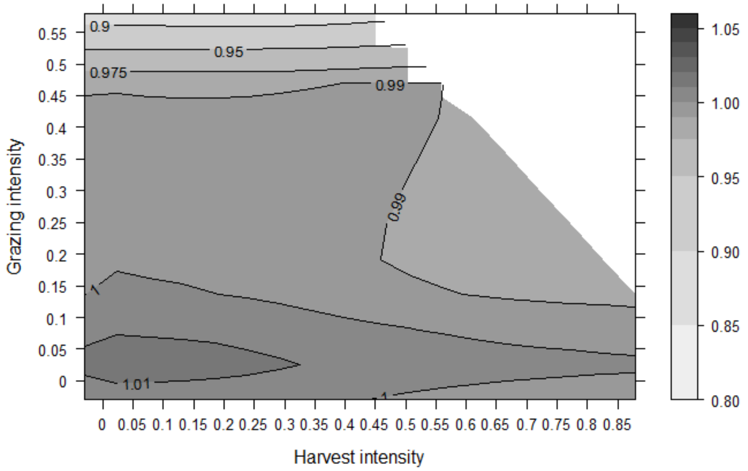
b)



c)


Grazing intensity
0.55
0.5
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Harvest intensity
0 0.05 0.1 0.15 0.2 0.25 0.3 0.35 0.4 0.45 0.5 0.55 0.6 0.65 0.7 0.75 0.8 0.85
0.9
0.95
0.975
0.99
1
1

d)


Grazing intensity
0.55
0.5
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Harvest intensity
0 0.05 0.1 0.15 0.2 0.25 0.3 0.35 0.4 0.45 0.5 0.55 0.6 0.65 0.7 0.75 0.8 0.85
0.9
0.95
0.975
0.99
0.99
1
1.01
1
1.05
1.00
0.95
0.90
0.85
0.80

e)

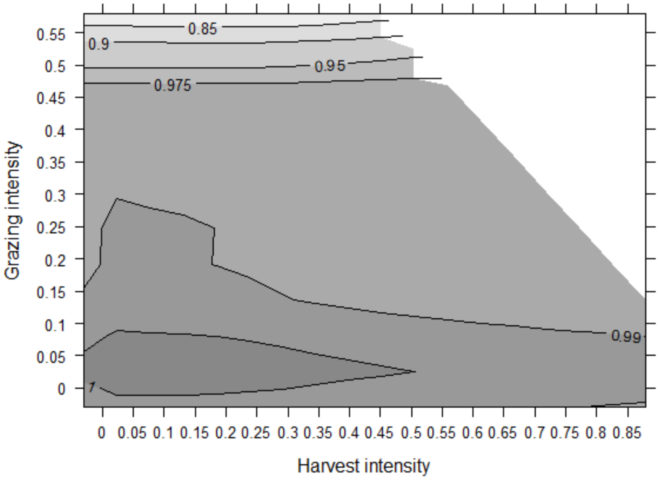
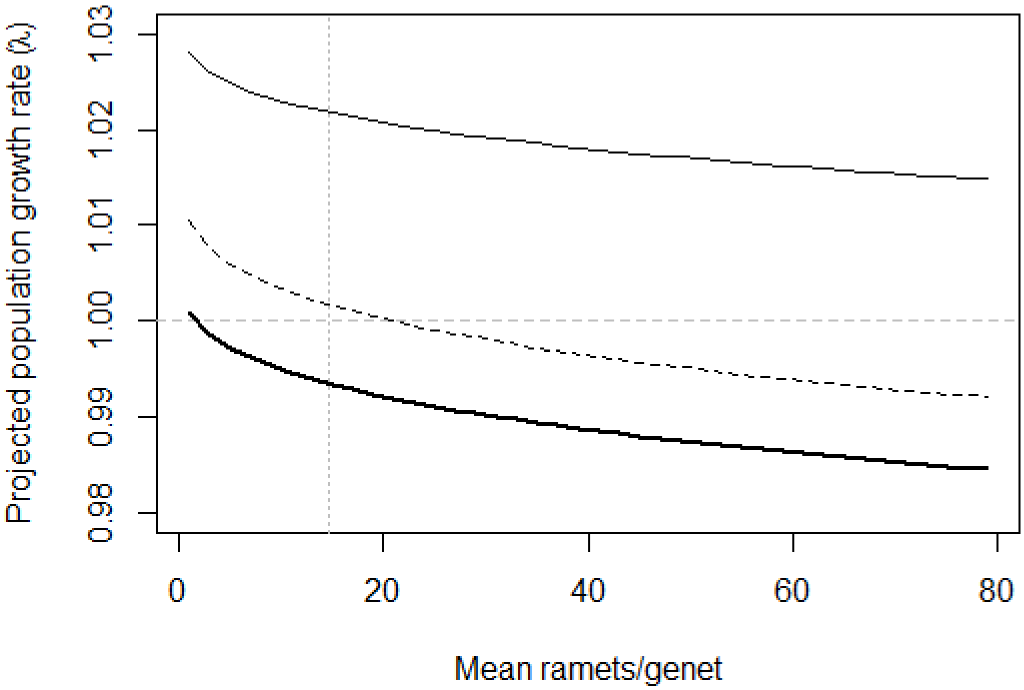

Grazing intensity
0.55
0.5
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Harvest intensity
0 0.05 0.1 0.15 0.2 0.25 0.3 0.35 0.4 0.45 0.5 0.55 0.6 0.65 0.7 0.75 0.8 0.85
0.85
0.9
0.95
0.975
0.99
1

Figure C.2. Projected population growth rates (λ) as a function of density (ramets/genet) by fire category (dashed – burned during the year, thin solid – 1-2 years post-fire, thick solid – >2 years post-fire). The vertical dashed line indicates the mean number of ramets per genet observed across our study populations.



APPENDIX D. DETAILS OF LAND USE CATEGORIES AND INTENSITY RANKINGS, AND METHODS USED TO ASSESS LIVESTOCK GRAZING AND BIOMASS EXTRACTION AT STUDY SITES

We assigned sites to ordinal land use intensity rankings. The protected area and forest fragment were ranked 1 because commercial biomass extraction did not occur there (though low levels of extraction may occur), nor did livestock grazing. Pillur Reserve Forest was ranked 2 because biomass extraction but not livestock grazing occurred there. Sathyamangalam and Male Mahadeshwara Hills reserve forests were ranked 3 because both commercial biomass extraction and livestock grazing were present. The protected area was managed as a reserve forest until it was declared a wildlife sanctuary in 1973. Collection of wood from standing trees has been banned since 1987 (Shankar *et al.* 1998a), while commercial non-timber forest product (NTFP) extraction was banned in 2004.

We assessed the presence of livestock and other herbivores by recording the presence of dung along transects within study plots. Dung transects (four 2 x 20m transects per plot) were sampled two to five times at each plot between May 2010 and May 2011. Results from camera traps at one site over the same time period were consistent with the dung transects. At the four plots with livestock grazing, domestic cow and buffalo dung was present at a density of 130-830 piles/ha (mean: 350), making up 25-50% (mean: 40%) of dung from ungulate herbivores in those plots. Wild ungulates were present at all sites, including sambar deer (*Rusa unicolor*) and gaur (*Bos gaurus*). Asian elephant (*Elephas maximus*) was present at all sites except the forest fragment.

We assessed the intensity of biomass extraction by measuring the intensity of mountain date palm (*Phoenix loureiri*) leaf harvest within each plot. Mountain date palm leaves are harvested commercially from the reserve forests in the study for broom production. The cut petioles of harvested mountain date palm leaves stay on the plant after harvest and provide a measure of harvest over the past year. Based on interviews with local harvesters at our study sites as well as previous studies in the area, collection of fuelwood and other non-timber forest products (NTFPs) co-occur along with palm leaf harvest (Chapter 2; Shankar *et al.* 1998b). Therefore, the intensity of palm leaf harvest provides a very good proxy for estimating overall levels of biomass extraction in the area.

We counted the number of cut mountain date palm petioles within a subplot of ~150 palm individuals in 2010 and 2011. An average of 5.9 leaves/m^2 (range: 0.2-14) were harvested from six of eight reserve forest plots, equivalent to an average of ~900 kg/ha. The other two reserve forest plots had low levels of palm leaf harvest during the study period, but were harvested at comparable intensities in the past five years. The latter was confirmed by interviews with local harvesters and the plots' location within currently harvested areas. In addition, the quantities of leaves harvested based on records from Village Forest Councils and Large Scale Adivasi Multi-Purpose Societies, which manage the sale of harvested palm leaves and other NTFPs from particular forest areas, provide evidence of intensive NTFP harvest in all the study areas (Chapter 2). The low levels of harvest in the two plots during the observed period were due either to the lack of recent fire (harvesters prefer to collect leaves from areas with fire in the past year), or to fire just prior to monitoring, which burned off old petioles and meant that regrowing leaves were too small to have been harvested.

Ground fires are often set by local people to manage for fodder and harvested plant species and improve visibility through the understory. Within reserve forests, it was rare to find areas that had not burned within the past three years; fires occurred less often in the protected area, though anthropogenic fire also occurred there. The fire return interval in all areas has likely increased over the past century (Kodandapani *et al.* 2004).

APPENDIX E. SCIENTIFIC NAMES AND GROWTH FORMS OF SPECIES PRESENT IN SAVANNA WOODLAND SITES

	Family	***Genus***	***Species***	***Growth form***
1	Acanthaceae	*Andrographis*	*Andrographis alata* Nees	Shrub
2	Acanthaceae	*Barleria*	*Barleria* sp.	Shrub
3	Acanthaceae	*Justicia*	*Justicia simplex* D. Don	Herb
4	Acanthaceae	*Meyenia*	*Meyenia hawtayneana* (Wall.) Nees	Climber
5	Acanthaceae	*Strobilanthes*	*Strobilanthes kunthiana* (Nees) T. Anderson ex Benth	Shrub
6	Acanthaceae	*Thunbergia*	*Thunbergia fragrans* Roxb.	Climber
7	Acanthaceae	*Thunbergia*	*Thunbergia* sp.	Climber
8	Anacardiaceae	*Buchanania*	*Buchanania axillaris* (Desr.) Ramamoorthy	Tree
9	Anacardiaceae	*Buchanania*	*Buchanania lanzan* Spreng.	Tree
10	Anacardiaceae	*Semecarpus*	*Semecarpus anacardium* L. f.	Tree
11	Annonaceae	*Miliusa*	*Miliusa tomentosa* (Roxb.) J. Sinclair	Tree
12	Apiaceae	*Bupleurum*	*Bupleurum ramosissimum* Wight & Arn. var. *wightii* (P.K.Mukh.) Bennet	Herb
13	Apiaceae	*Centella*	*Centella asiatica* (L.) Urb.	Herb
14	Apiaceae		Unidentified Apiaceae	Herb
15	Apocynaceae	*Asclepias*	*Asclepias curassavica* L.*	Herb
16	Apocynaceae	*Hemidesmus*	*Hemidesmus indicus* (L.) W. T. Aiton	Climber
17	Arecaceae	*Phoenix*	*Phoenix loureiri* Kunth	Palmoid
18	Asparagaceae	*Asparagus*	*Asparagus racemosus* Willd.	Climber
19	Asteraceae	*Ageratina*	*Ageratina adenophora* (Spreng.) R. M. King & H. Rob.*	Herb
20	Asteraceae	*Ageratum*	*Ageratum conyzoides* L.*	Herb
21	Asteraceae	*Anaphalis*	*Anaphalis* sp.	Herb
22	Asteraceae	*Bidens*	*Bidens pilosa* L.*	Herb
23	Asteraceae	*Blumea*	*Blumea* sp.	Herb
24	Asteraceae	*Chromolaena*	*Chromolaena odorata* (L.) R. M. King & H. Rob.*	Shrub
25	Asteraceae	*Vernonia*	*Vernonia cinerea* (L.) Less.	Herb

	Family	***Genus***	***Species***	***Growth form***
26	Asteraceae	*Vicoa*	*Vicoa indica* (L.) DC.	Herb
27	Asteraceae		Unidentified Asteraceae	Herb
28	Boraginaceae	*Cordia*	*Cordia* sp.	Shrub
29	Caprifoliaceae	*Viburnum*	*Viburnum punctatum* Buch.-Ham. ex D. Don	Tree
30	Celastraceae	*Celastrus*	*Celastrus paniculatus* Willd.	Climber
31	Celastraceae		Unidentified Celastraceae	Tree
32	Clusiaceae	*Hypericum*	*Hypericum mysorense* Heyne	Shrub
33	Combretaceae	*Anogeissus*	*Anogeissus latifolia* (Roxb. ex DC.) Wall. ex Guill. & Perr.	Tree
34	Combretaceae	*Terminalia*	*Terminalia bellerica* (Gaertn.) Roxb.	Tree
35	Combretaceae	*Terminalia*	*Terminalia chebula* Retz.	Tree
36	Combretaceae	*Terminalia*	*Terminalia crenulata* (Roth.)	Tree
37	Commelinaceae	*Cyanotis*	*Cyanotis tuberosa* Schult.	Herb
38	Commelinaceae	*Cyanotis*	*Cyanotis villosa* Schultes f.	Herb
39	Convolvulaceae	*Argyreia*	*Argyreia* sp.	Climber
40	Convolvulaceae	*Argyreia*	*Argyreia cuneata* (Willd.) Ker Gawl.	Shrub
41	Convolvulaceae	*Evolvulus*	*Evolvulus alsinoides* (L.) L.	Herb
42	Dipterocarpaceae	*Shorea*	*Shorea roxburghii* G. Don	Tree
43	Ebenaceae	*Diospyros*	*Diospyros montana* Roxb.	Tree
44	Euphorbiaceae	*Acalypha*	*Acalypha alnifolia* Klein ex Willd.	Shrub
45	Euphorbiaceae	*Mallotus*	*Mallotus tetracoccus* (Roxb.) Kurz	Tree
46	Fabaceae	*Albizia*	*Albizia odoratissima* (L. f.) Benth.	Tree
47	Fabaceae	*Albizia*	*Albizia* sp.	Tree
48	Fabaceae	*Alysicarpus*	*Alysicarpus* sp.	Herb
49	Fabaceae	*Cassia*	*Cassia fistula* L.	Tree
50	Fabaceae	*Cassia*	*Cassia* sp. 1	Shrub
51	Fabaceae	*Cassia*	*Cassia* sp. 2	Shrub
52	Fabaceae	*Chamaecrista*	*Chamaecrista mimosoides* L.	Herb

	Family	***Genus***	***Species***	***Growth form***
53	Fabaceae	*Crotalaria*	*Crotalaria scabrella* Wright & Arn.	Shrub
54	Fabaceae	*Dalbergia*	*Dalbergia latifolia* Roxb.	Tree
55	Fabaceae	*Dalbergia*	*Dalbergia* sp.	Tree
56	Fabaceae	*Desmodium*	*Desmodium* sp. 1	Shrub
57	Fabaceae	*Desmodium*	*Desmodium* sp. 2	Shrub
58	Fabaceae	*Desmodium*	*Desmodium triflorum* (L.) DC.	Herb
59	Fabaceae	*Galactia*	*Galactia tenuiflora* (J. G. Klein ex Willd.) Wight & Arn.	Climber
60	Fabaceae	*Indigofera*	*Indigofera* sp.	Shrub
61	Fabaceae	*Indigofera*	*Indigofera tinctoria* L.	Shrub
62	Fabaceae	*Peltophorum*	*Peltophorum pterocarpum* (DC.) Backer ex K. Heyne	Tree
63	Fabaceae	*Pterocarpus*	*Pterocarpus marsupium* Roxb.	Tree
64	Fabaceae	*Pycnospora*	*Pycnospora lutescens* (Poiret) Schindler	Shrub
65	Fabaceae	*Rhynchosia*	*Rhynchosia filipes* Benth.	Climber
66	Fabaceae	*Rhynchosia*	*Rhynchosia* sp.	Herb
67	Fabaceae	*Tephrosia*	*Tephrosia pulcherrima* (Baker) Gamble	Shrub
68	Fabaceae	*Vigna*	*Vigna* sp.	Climber
69	Fabaceae		Unidentified Fabaceae 1	Herb
70	Fabaceae		Unidentified Fabaceae 2	Tree
71	Hypoxidaceae	*Curculigo*	*Curculigo orchioides* Gaertn.	Herb
72	Lamiaceae	*Anisomeles*	*Anisomeles indica* (L.) Kuntze	Herb
73	Lamiaceae	*Anisomeles*	*Anisomeles malabarica* (L.) R. Br. ex Sims	Herb
74	Lamiaceae	*Leucas*	*Leucas aspera* (Willd.) Link	Herb
75	Lamiaceae	*Leucas*	*Leucas biflora* (Vahl) R. Br.	Herb
76	Lamiaceae	*Leucas*	*Leucas chinensis* (Retz.) Sm.	Herb
77	Lamiaceae	*Leucas*	*Leucas* sp. 1	Herb
78	Lamiaceae	*Leucas*	*Leucas* sp. 2	Herb
79	Lamiaceae	*Orthosiphon*	*Orthosiphon rubicundus* (D. Don) Benth. In Wall.	Herb

	Family	***Genus***	***Species***	***Growth form***
80	Lamiaceae	*Orthosiphon*	*Orthosiphon* sp.	Herb
81	Lamiaceae	*Tectona*	*Tectona grandis* L. f.	Tree
82	Lauraceae	*Persea*	*Persea macrantha* (Nees) Kosterm	Tree
83	Lecythidaceae	*Careya*	*Careya arborea* Roxb.	Tree
84	Loranthaceae	*Taxillus*	*Taxillus tomentosus* (Roth.) Var. Tiegh	Hemi-parasite
85	Lythraceae	*Lagerstroemia*	*Lagerstroemia parviflora* Roxb.	Tree
86	Malvaceae	*Abelmoschus*	*Abelmoschus* sp.	Herb
87	Malvaceae	*Byttneria*	*Byttneria herbacea* Roxb.	Herb
88	Malvaceae	*Decaschista*	*Decaschistia crotonifolia* Wight & Arn.	Shrub
89	Malvaceae	*Grewia*	*Grewia hirsuta* Vahl	Shrub
90	Malvaceae	*Grewia*	*Grewia tiliaefolia* Vahl	Tree
91	Malvaceae	*Kydia*	*Kydia calycina* Roxb.	Tree
92	Malvaceae	*Pavonia*	*Pavonia odorata* Willd.	Herb
93	Malvaceae	*Thespesia*	*Thespesia lampas* (Cav.) Dalzell	Shrub
94	Meliaceae	*Chukrasia*	*Chukrasia tabularis* A. Juss.	Tree
95	Meliaceae	*Cipadessa*	*Cipadessa baccifera* (Roth) Miq.	Shrub
96	Meliaceae	*Melia*	*Melia dubia* Cav.	Tree
97	Menispermaceae	*Cissampelos*	*Cissampelos pareira* L.	Climber
98	Myrtaceae	*Syzygium*	*Syzygium cumini* (L.) Skeels	Tree
99	Oleaceae	*Jasminum*	*Jasminum calophyllum* Wall. ex A. DC.	Climber
100	Oleaceae	*Jasminum*	*Jasminum* sp.	Climber
101	Oleaceae	*Olea*	*Olea glandulifera* Wall.	Tree
102	Oleaceae	*Schrebera*	*Schrebera swietenioides* Roxb.	Tree
103	Orchidaceae	*Habenaria*	*Habenaria* sp.	Herb
104	Orchidaceae	*Nervilia*	*Nervilia* sp.	Herb
105	Oxalidaceae	*Biophytum*	*Biophytum candolleanum* Wight	Herb
106	Oxalidaceae	*Biophytum*	*Biophytum sensitivum* (L.) DC.	Herb

	Family	*Genus*	*Species*	*Growth form*
107	Oxalidaceae	*Oxalis*	*Oxalis corniculata* L.*	Herb
108	Phyllanthaceae	*Breynia*	*Breynia vitis-idaea* (Burm. f.) C. E. C. Fisch.	Shrub
109	Phyllanthaceae	*Bridelia*	*Bridelia retusa* (L.) A. Juss.	Tree
110	Phyllanthaceae	*Glochidion*	*Glochidion heyneanum* (Wight & Arn.) Wight	Tree
111	Phyllanthaceae	*Phyllanthus*	*Phyllanthus emblica* L.	Tree
112	Phyllanthaceae	*Phyllanthus*	*Phyllanthus indofischeri* Bennet	Tree
113	Phyllanthaceae	*Phyllanthus*	*Phyllanthus reticulatus* Poir.	Shrub
114	Phyllanthaceae	*Phyllanthus*	*Phyllanthus* sp.	Herb
115	Phyllanthaceae	*Phyllanthus*	*Phyllanthus urinaria* L.	Herb
116	Phyllanthaceae	*Phyllanthus*	*Phyllanthus virgatus* var. *gardnerianus* (Wight) Govaerts & Radcl.-Sm.	Herb
117	Phyllanthaceae	*Glochidion*	*Glochidion zeylanicum* A. Juss.	Tree
118	Polygalaceae	*Polygala*	*Polygala chinensis* L.	Herb
119	Primulaceae	*Maesa*	*Maesa indica* (Roxb.) A. DC.	Tree
120	Rhamnaceae	*Scutia*	*Scutia myrtina* (Burm.f.) Kurz	Shrub
121	Rhamnaceae	*Ziziphus*	*Ziziphus nummularia* (Burm. f.) Wight & Arn.	Shrub
122	Rhamnaceae	*Ziziphus*	*Ziziphus xylopyrus* (Retz.) Willd.	Tree
123	Rosaceae	*Rubus*	*Rubus niveus* Thunb.	Shrub
124	Rubiaceae	*Benkara*	*Benkara malabarica* (Lam.) Tirveng.	Shrub
125	Rubiaceae	*Hedyotis*	*Hedyotis* sp.	Shrub
126	Rubiaceae	*Ixora*	*Ixora pavetta* Andrews	Tree
127	Rubiaceae	*Knoxia*	*Knoxia sumatrensis* (Retz.) DC.	Herb
128	Rubiaceae	*Oldenlandia*	*Oldenlandia* sp.	Herb
129	Rubiaceae	*Randia*	*Randia dumetorum* (Retz.) Poir.	Shrub
130	Rubiaceae	*Rubia*	*Rubia cordifolia* L.	Climber
131	Rubiaceae	*Spermacoce*	*Spermacoce exilis* (L. O. Williams) C. D. Adams	Herb
132	Rubiaceae	*Wendlandia*	*Wendlandia thyrsoidea* (Schult.) Steud.	Tree
133	Rubiaceae		Unidentified Rubiaceae 1	Shrub

	Family	***Genus***	***Species***	***Growth form***
134	Rubiaceae		Unidentified Rubiaceae 2	Tree
135	Rutaceae	*Chloroxylon*	*Chloroxylon swietiana* DC.	Tree
136	Rutaceae	*Toddalia*	*Toddalia asiatica* var. *gracilis* Gamble	Climber
137	Solanaceae	*Solanum*	*Solanum* sp.	Herb
138	Verbenaceae	*Lantana*	*Lantana camara* L.*	Shrub
139	Verbenaceae	*Lantana*	*Lantana indica* Roxb.	Shrub
140	Vitaceae		Unidentified Vitaceae	Climber
141	Zingiberaceae	*Curcuma*	*Curcuma neilgherrensis* Wight	Herb
142			Unidentified herb 1	Herb
143			Unidentified herb 2	Herb
144			Unidentified herb 3	Herb
145			Unidentified herb 4	Herb
146			Unidentified herb 5	Herb
147			Unidentified herb 6	Herb

* Non-native invasive species

APPENDIX F. RANKING OF CANDIDATE MODELS FOR PREDICTORS OF SPECIES RICHNESS AND DIVERSITY

Models with ΔAICc ≤ 2 are shown in bold, along with the sign of the estimated effects for the model terms. All models include site as a random effect in the model. The "site only" model serves as a null model on which all other models are based, with the addition of environmental and management factors.

a) Overstory

Richness

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Canopy openness (-)	**4**	**75.62**	**0**	**0.41**	**0.41**	**-31.59**
Elevation	4	78.03	2.41	0.12	0.53	-32.8
Grass cover	4	78.74	3.12	0.09	0.61	-33.15
Canopy openness & LUI	5	78.97	3.35	0.08	0.69	-30.74
Site only	3	79.2	3.58	0.07	0.76	-35.4
Canopy openness & Livestock	5	79.21	3.59	0.07	0.83	-30.85
Canopy openness & Biomass extraction	5	79.61	3.99	0.06	0.88	-31.06
PC1	4	80.17	4.55	0.04	0.92	-33.87
Fire	4	81.54	5.92	0.02	0.94	-34.55
Biomass extraction	4	82.25	6.63	0.01	0.96	-34.9
PC2	4	82.92	7.3	0.01	0.97	-35.24
LUI	4	83.08	7.46	0.01	0.98	-35.32
Livestock	4	83.21	7.59	0.01	0.99	-35.38
PC1 & PC2	5	84.12	8.5	0.01	0.99	-33.31
Canopy openness & Biomass extraction & Livestock	6	85.4	9.78	0	1	-30.7
Biomass extraction & Livestock	5	85.77	10.15	0	1	-34.13

Diversity

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Fire (-)	**4**	**21.82**	**0**	**0.68**	**0.68**	**-4.69**
Fire & Biomass extraction	5	26.39	4.57	0.07	0.75	-4.45
Fire & Livestock	5	26.77	4.95	0.06	0.81	-4.64
Fire & LUI	5	26.84	5.02	0.06	0.86	-4.67
Canopy openness	4	27.27	5.45	0.04	0.91	-7.41
Site only	3	28.26	6.44	0.03	0.94	-9.93
Elevation	4	28.9	7.08	0.02	0.96	-8.23
PC1	4	29.91	8.09	0.01	0.97	-8.73
Grass cover	4	30.47	8.65	0.01	0.98	-9.01
Fire & Biomass extraction & Livestock	6	31.57	9.75	0.01	0.98	-3.79

Livestock	4	31.96	10.14	0	0.99	-9.76
LUI	4	32.23	10.41	0	0.99	-9.89
PC2	4	32.26	10.44	0	0.99	-9.91
Biomass extraction	4	32.27	10.45	0	1	-9.91
PC1 & PC2	5	34.41	12.59	0	1	-8.46
Biomass extraction & Livestock	5	36	14.18	0	1	-9.25

b) Seedlings

Richness

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Fire (-)	**4**	**72.35**	**0**	**0.44**	**0.44**	**-29.96**
Site only	3	74.4	2.04	0.16	0.59	-33
PC2	4	75.54	3.18	0.09	0.68	-31.55
Fire & Livestock	5	76.86	4.51	0.05	0.73	-29.68
Fire & LUI	5	77	4.64	0.04	0.77	-29.75
Fire & Biomass extraction	5	77.22	4.86	0.04	0.81	-29.86
Biomass extraction	4	77.31	4.96	0.04	0.85	-32.44
Canopy openness	4	77.87	5.52	0.03	0.87	-32.71
LUI	4	77.94	5.59	0.03	0.9	-32.75
Grass cover	4	78.36	6.01	0.02	0.92	-32.96
PC1	4	78.36	6.01	0.02	0.94	-32.96
Livestock	4	78.41	6.06	0.02	0.97	-32.98
Elevation	4	78.43	6.08	0.02	0.99	-32.99
PC1 & PC2	5	80.5	8.14	0.01	0.99	-31.5
Biomass extraction & Livestock	5	81.6	9.25	0	1	-32.05
Fire & Biomass extraction & Livestock	6	83.33	10.98	0	1	-29.67

Diversity

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Fire (-)	**4**	**20.8**	**0**	**0.49**	**0.49**	**-4.18**
Site only	3	23.18	2.39	0.15	0.63	-7.39
PC2	4	24.85	4.06	0.06	0.7	-6.2
Fire & Biomass extraction	5	25.29	4.5	0.05	0.75	-3.9
Fire & LUI	5	25.67	4.87	0.04	0.79	-4.08
Fire & Livestock	5	25.84	5.05	0.04	0.83	-4.17
Biomass extraction	4	26.49	5.69	0.03	0.86	-7.02
Grass cover	4	26.73	5.94	0.02	0.88	-7.14
Canopy openness	4	26.83	6.03	0.02	0.91	-7.19
Elevation	4	27.09	6.3	0.02	0.93	-7.32
LUI	4	27.11	6.31	0.02	0.95	-7.33

Livestock	4	27.14	6.35	0.02	0.97	-7.35
PC1	4	27.2	6.4	0.02	0.99	-7.38
PC1 & PC2	5	29.87	9.08	0.01	0.99	-6.19
Biomass extraction & Livestock	5	30.65	9.86	0	1	-6.58
Fire & Biomass extraction & Livestock	6	31.3	10.5	0	1	-3.65

c) Understory, all species included

Richness

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Canopy openness (+)	**4**	**90.94**	**0**	**0.23**	**0.23**	**-39.25**
Livestock (+)	**4**	**91.49**	**0.55**	**0.18**	**0.41**	**-39.52**
Canopy openness (+) & Livestock (+)	**5**	**92.18**	**1.24**	**0.13**	**0.54**	**-37.34**
Site only	**3**	**92.4**	**1.46**	**0.11**	**0.65**	**-42**
Canopy openness & LUI	5	93.63	2.69	0.06	0.71	-38.06
Elevation	4	93.77	2.83	0.06	0.77	-40.66
LUI	4	94.16	3.23	0.05	0.81	-40.86
PC1	4	94.3	3.37	0.04	0.86	-40.93
Canopy openness & Biomass extraction	5	95.1	4.16	0.03	0.88	-38.8
Biomass extraction & Livestock	5	95.38	4.44	0.03	0.91	-38.94
PC2	4	95.71	4.77	0.02	0.93	-41.63
Fire	4	95.84	4.9	0.02	0.95	-41.7
Biomass extraction	4	95.91	4.97	0.02	0.97	-41.73
Grass cover	4	96.03	5.1	0.02	0.99	-41.79
PC1 & PC2	5	98.36	7.43	0.01	0.99	-40.43
Canopy openness & Biomass extraction & Livestock	6	98.49	7.56	0.01	1	-37.25

Diversity

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Grass cover (+) & Livestock (+)	**5**	**12.47**	**0**	**0.25**	**0.25**	**2.51**
Livestock (+)	**4**	**12.81**	**0.34**	**0.21**	**0.46**	**-0.18**
Site only	**3**	**13.43**	**0.96**	**0.15**	**0.61**	**-2.52**
LUI	4	14.91	2.44	0.07	0.69	-1.23
Grass cover	4	15.44	2.97	0.06	0.74	-1.5
PC2	4	15.83	3.36	0.05	0.79	-1.69
Canopy openness	4	16.1	3.63	0.04	0.83	-1.83
Biomass extraction	4	16.51	4.04	0.03	0.86	-2.03
Grass cover & LUI	5	16.69	4.22	0.03	0.89	0.41
Elevation	4	17.25	4.78	0.02	0.91	-2.4
Fire	4	17.28	4.81	0.02	0.94	-2.42

PC1	4	17.4	4.93	0.02	0.96	-2.48
Biomass extraction & Livestock	5	17.74	5.27	0.02	0.98	-0.12
Grass cover & Biomass extraction & Livestock	6	18.48	6.01	0.01	0.99	2.76
Gras cover & Biomass extraction	5	19.37	6.9	0.01	1	-0.93
PC1 & PC2	5	20.85	8.38	0	1	-1.68

d) Understory, excluding non-native invasive species

Richness

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Canopy openness (+)	**4**	**88.73**	**0**	**0.32**	**0.32**	**-38.14**
Site only	**3**	**90.59**	**1.86**	**0.13**	**0.45**	**-41.09**
Livestock (+)	4	90.88	2.15	0.11	0.56	-39.22
Canopy openness & Livestock	5	91.47	2.74	0.08	0.64	-36.98
Elevation	4	91.75	3.02	0.07	0.71	-39.65
Canopy openness & LUI	5	92.14	3.41	0.06	0.77	-37.32
PC1	4	92.36	3.63	0.05	0.82	-39.96
LUI	4	92.84	4.11	0.04	0.86	-40.2
Canopy openness & Biomass extraction	5	93.04	4.31	0.04	0.9	-37.77
Grass cover	4	94.16	5.43	0.02	0.92	-40.86
Fire	4	94.18	5.45	0.02	0.94	-40.87
Biomass extraction	4	94.21	5.48	0.02	0.96	-40.88
PC2	4	94.29	5.56	0.02	0.98	-40.92
Biomass extraction & Livestock	5	95.38	6.65	0.01	0.99	-38.94
PC1 & PC2	5	96.77	8.04	0.01	1	-39.64
Canopy openness & Biomass extraction & Livestock	6	97.94	9.21	0	1	-36.97

Diversity

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Livestock (+)	**4**	**13.11**	**0**	**0.55**	**0.55**	**-0.33**
LUI	4	16.23	3.12	0.12	0.66	-1.89
Canopy openness & Livestock	5	17.51	4.4	0.06	0.72	-0.01
Site only	3	17.84	4.73	0.05	0.78	-4.72
Canopy openness & LUI	5	17.85	4.74	0.05	0.83	-0.18
Biomass extraction & Livestock	5	18.16	5.05	0.04	0.87	-0.33
Canopy openness	4	18.95	5.84	0.03	0.9	-3.25
Grass cover	4	19.47	6.36	0.02	0.92	-3.51
Biomass extraction	4	19.75	6.64	0.02	0.94	-3.65
Canopy openness & Biomass extraction	5	19.95	6.84	0.02	0.96	-1.22
PC2	4	20.64	7.53	0.01	0.97	-4.1

Elevation	4	21.37	8.26	0.01	0.98	-4.46
Fire	4	21.8	8.69	0.01	0.99	-4.68
PC1	4	21.85	8.74	0.01	1	-4.7
Canopy openness & Biomass extraction & Livestock	6	23.71	10.6	0	1	0.15
PC1 & PC2	5	25.69	12.58	0	1	-4.1

APPENDIX G. DETAILS OF METHODS USED TO ASSESS FUNCTIONAL COMPOSITION AND DIVERSITY

1. Community sampling methods

We measured the overstory and understory in 2010 and seedlings only in 2011. For the overstory, we counted the number of stems > 1 cm diameter breast height (dbh) within the full 20x20 m plot and recorded dbh. The understory community was measured in eight 1 x 1 m subplots with a stratified-random placement (two plots within each quadrant of the full plot). We recorded the percent cover category by species for all shrubs and forbs whose maximum size was < 1 cm dbh based on visual estimation. The total percent cover of grasses and sedges was also recorded, but without identification to species. Non-vascular plants were omitted. All estimates were carried out by the same observer. Percent cover categories included ≤ 1%, 1-5%, 5-10%, 10-20% and subsequent 10% ranges. Individuals < 1 cm dbh of tree species were not included in the understory community, but were instead measured as part of the seedling community. The seedling community was defined as individuals < 1 cm dbh or without a dbh (technically seedlings and saplings) of tree species reaching a maximum size of > 1 cm dbh and was measured in 25 randomly placed1 x 1 m subplots. The number of seedlings per species was recorded per subplot. Individuals with multiple stems were counted as a single seedling. Seedlings < 1 cm dbh arising from root suckers or resprouting from the base of coppiced trees were not included. Trees, shrubs and forbs were identified taxonomically by botanists R. Ganesan, S. Rehel and R. Laden, and with the assistance of local floras. Of 147 morphospecies, 141 were identified to family, 133 to genus and 106 to species.

2. Functional trait data sources

Trait data were compiled from regional floras (Gamble *et al.* 1967; Matthew 1983, 1995), trait databases (Royal Botanic Gardens Kew 2008; Chave *et al.* 2009; Zanne *et al.* 2009), literature searches and the expert assessment of botanist R. Ganesan. When wood density was not available for a species, we used the mean wood density for the genus, as most species-level variation in wood density can be accounted for at the genus level (Chave *et al.* 2006). When seed mass was unavailable for a species, but varied by less than an order of magnitude within its genus within the database from the Royal Botanic Garden Kew (2008), we used the midpoint of the genus range. Because pollination syndrome and dispersal mode were nominal traits with multiple values allowed per species, these traits were broken into multiple (nine and six, respectively) binary traits.

3. Environmental conditions

We determined the elevation of each plot with a barometric altimeter on a Garmin e-Trex Vista H handheld GPS unit. We measured canopy openness using the average of five hemispherical photos taken 1 m off the ground, analyzed with Gap Light Analyzer version 2 (Frazer *et al.* 1999). For each plot, we extracted 19 bioclimatic variables from WorldClim 1.4 representing mean climate conditions between 1950-2000 with measures of temperature, precipitation and their seasonality (Hijmans *et al.* 2005).

To reduce the number of inter-correlated environmental variables, we used principal components analysis (PCA) to summarize the variation across the 19 bioclimatic variables and elevation. The first two PCA axes accounted for 95% of the variation in the data. We extracted the plot scores on these axes to create the variables PC1 and PC2. Plots with positive scores for PC1 tended to be cooler, at higher elevations and with more precipitation. Plots with positive scores for PC2 had more precipitation and less seasonal variation in precipitation and temperature.

Canopy openness, elevation and PC1 were all significantly positively correlated (canopy-elevation: $r = 0.749$, $p = 0.002$, $df = 12$; canopy-PC1: $r = 0.546$, $p = 0.043$, $df = 12$; elevation-PC1: $r = 0.843$, $p < 0.001$, $df = 12$). Plots with livestock grazing had substantially more open canopies (mean = 62 vs. 45% open; $p = 0.012$, $df = 11.006$), and negative PC2 scores (mean = -0.197 vs. 0.079; $p = 0.018$, $df = 11.356$). All other correlations among environmental variables and between environmental and land use variables were not significant at the $p = 0.05$ level.

4. Specifications of candidate model sets

We included four groups of candidate models: 1) site alone (one model), 2) site + environmental conditions (seven models: elevation, PC1, PC2, PC1 + PC2, canopy openness, grass cover, years since fire), 3) site + land use (four models: harvest, livestock, harvest + livestock, ranked LUI) and 4) site + environmental conditions + land use (four models: harvest, livestock, harvest+livestock and ranked LUI each added to the site + environmental conditions model with the lowest AICc). The number of candidate models included for each functional trait depended on the number of management-related variables (fire, biomass extraction, livestock grazing and/or LUI) for which we had hypotheses. For example, if we did not have an *a priori* prediction about the effect of time since fire on a particular trait, models including time since fire were omitted from the candidate model set.

5. Similarity matrices

Distances between species were calculated with the Gower dissimilarity index to accommodate the mix of continuous, nominal and ordinal functional traits. Because pollination syndrome and dispersal mode were composed of multiple binary variables, each binary variable was proportionally down-weighted in the calculation of the Gower dissimilarity matrix so that these traits were weighted equally relative to the other functional traits (Laliberté & Legendre 2011).

6. Post-hoc tests for effects of land use on variance and mean of functional traits

We calculated abundance-weighted plot variances for each trait, breaking categorical traits into sets of binary variables. These variances were then analyzed as response variables in models using the same explanatory variables as the focal model of trait dispersion, in which the statistical significance of each explanatory variable (for a given trait variance) was tested by a likelihood ratio test (comparing the full model and the model with that explanatory variable omitted). Because the mean and variance are interdependent for binary traits, we also tested for shifts in the abundance-weighted means of binary traits.

APPENDIX H. RANKING OF CANDIDATE MODELS FOR CHANGES IN FUNCTIONAL COMPOSITION WITH LAND USE

Models with ΔAICc ≤ 2 are shown in bold, along with the sign of the estimated effects for the model terms. All models include site as a random effect in the model. The "site only" model serves as a null model on which all other models are based, with the addition of environmental and management factors.

a) Overstory

Maximum height:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Grass cover (-)	**4**	**84.03**	**0**	**0.21**	**0.21**	**-35.79**
Site only	**3**	**84.23**	**0.2**	**0.19**	**0.4**	**-37.92**
PC2 (+)	**4**	**84.65**	**0.62**	**0.15**	**0.55**	**-36.1**
Grass cover (-) & Livestock (-)	**5**	**85.36**	**1.33**	**0.11**	**0.66**	**-33.93**
Livestock	4	87.14	3.11	0.04	0.7	-37.35
PC1	4	87.18	3.15	0.04	0.74	-37.37
Fire	4	87.29	3.26	0.04	0.78	-37.42
Canopy openness	4	87.55	3.52	0.04	0.82	-37.55
Grass cover & LUI	5	87.59	3.56	0.04	0.85	-35.04
LUI	4	87.64	3.61	0.03	0.89	-37.6
PC1 & PC2	5	87.96	3.93	0.03	0.92	-35.23
Biomass extraction	4	88.12	4.09	0.03	0.94	-37.84
Elevation	4	88.27	4.24	0.02	0.97	-37.91
Grass cover & Biomass extraction	5	88.84	4.81	0.02	0.99	-35.67
Grass cover & Biomass extraction & Livestock	6	90.36	6.33	0.01	1	-33.18
Biomass extraction & Livestock	5	92.31	8.28	0	1	-37.4

Physical defense:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Elevation (-)	**4**	**-18.68**	**0**	**0.25**	**0.25**	**15.56**
Site only	**3**	**-18.67**	**0.01**	**0.24**	**0.49**	**13.54**
PC1 (-)	**4**	**-17.44**	**1.25**	**0.13**	**0.62**	**14.94**
PC2 (+)	**4**	**-17.09**	**1.59**	**0.11**	**0.73**	**14.77**
Canopy openness	4	-16.64	2.04	0.09	0.82	14.54
PC1 & PC2	5	-15.46	3.22	0.05	0.87	16.48
Fire	4	-15.18	3.5	0.04	0.91	13.81
Livestock	4	-14.84	3.84	0.04	0.95	13.64
Grass cover	4	-14.63	4.06	0.03	0.98	13.54

Wood density:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Site only	**3**	**-29.72**	**0**	**0.41**	**0.41**	**19.06**
Fire	4	-26.41	3.31	0.08	0.49	19.43
PC2	4	-26.26	3.46	0.07	0.56	19.35
Biomass extraction	4	-25.98	3.75	0.06	0.63	19.21
Grass cover	4	-25.84	3.88	0.06	0.69	19.14
Elevation	4	-25.79	3.93	0.06	0.75	19.12
Livestock	4	-25.76	3.96	0.06	0.8	19.1
LUI	4	-25.71	4.02	0.06	0.86	19.08
Canopy openness	4	-25.69	4.03	0.05	0.91	19.07
PC1	4	-25.68	4.04	0.05	0.97	19.06
Fire & Livestock	5	-21.53	8.2	0.01	0.97	19.51
Biomass extraction & Livestock	5	-21.42	8.3	0.01	0.98	19.46
Fire & Biomass extraction	5	-21.39	8.34	0.01	0.99	19.44
Fire & LUI	5	-21.37	8.35	0.01	0.99	19.44
PC1 & PC2	5	-21.21	8.51	0.01	1	19.36
Fire & Biomass extraction & Livestock	6	-15.26	14.46	0	1	19.63

Clonality: Too few plots with clonally reproducing trees, so not tested.

Resprouting capacity:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Site only	**3**	**1.16**	**0**	**0.4**	**0.4**	**3.62**
PC2	4	4.18	3.02	0.09	0.48	4.13
Grass cover	4	4.68	3.51	0.07	0.55	3.88
PC1	4	4.71	3.55	0.07	0.62	3.87
Fire	4	4.72	3.56	0.07	0.69	3.86
Biomass extraction	4	4.92	3.76	0.06	0.75	3.76
LUI	4	5.05	3.88	0.06	0.8	3.7
Livestock	4	5.18	4.02	0.05	0.86	3.63
Elevation	4	5.19	4.03	0.05	0.91	3.63
Canopy openness	4	5.21	4.04	0.05	0.96	3.62
PC2 & Livestock	5	8.7	7.54	0.01	0.97	4.4
PC1 & PC2	5	8.7	7.54	0.01	0.98	4.4
PC2 & LUI	5	9.01	7.84	0.01	0.99	4.25
PC2 & Biomass extraction	5	9.18	8.02	0.01	0.99	4.16

Biomass extraction & Livestock	5	9.95	8.79	0	1	3.78
PC2 & Biomass extraction & Livestock	6	14.71	13.55	0	1	4.65

Seed mass:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
PC1 (+)	**4**	**208.21**	**0**	**0.31**	**0.31**	**-97.88**
Site only	**3**	**209.57**	**1.36**	**0.16**	**0.47**	**-100.58**
Elevation (+)	**4**	**210.21**	**2**	**0.11**	**0.58**	**-98.88**
Canopy openness	4	210.57	2.36	0.1	0.68	-99.06
Grass cover	4	211.81	3.6	0.05	0.73	-99.68
PC1 & Biomass extraction	5	211.81	3.61	0.05	0.78	-97.16
PC1 & LUI	5	212	3.8	0.05	0.83	-97.25
PC1 & Livestock	5	212.58	4.37	0.03	0.86	-97.54
Livestock	4	213.18	4.98	0.03	0.89	-100.37
PC1 & PC2	5	213.24	5.03	0.03	0.91	-97.87
Biomass extraction	4	213.55	5.34	0.02	0.93	-100.55
LUI	4	213.57	5.36	0.02	0.95	-100.56
PC2	4	213.6	5.39	0.02	0.97	-100.58
Fire	4	213.61	5.4	0.02	1	-100.58
Biomass extraction & Livestock	5	217.69	9.48	0	1	-100.09
PC1 & Biomass extraction & Livestock	6	218.3	10.1	0	1	-97.15

Wind dispersal:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Elevation (-) & Biomass extraction (-)	**5**	**3.99**	**0**	**0.23**	**0.23**	**6.75**
Elevation (-)	**4**	**4.15**	**0.15**	**0.21**	**0.43**	**4.15**
Site only	**3**	**5.18**	**1.19**	**0.12**	**0.56**	**1.61**
Elevation (-) & LUI (-)	**5**	**5.73**	**1.74**	**0.09**	**0.65**	**5.89**
Canopy openness	4	6.16	2.17	0.08	0.73	3.14
PC1	4	6.52	2.53	0.06	0.79	2.96
Elevation & Livestock	5	7.33	3.34	0.04	0.84	5.08
Livestock	4	7.61	3.62	0.04	0.87	2.42
Fire	4	8.1	4.11	0.03	0.9	2.17
LUI	4	8.75	4.76	0.02	0.92	1.85
PC2	4	9.1	5.11	0.02	0.94	1.67
Grass cover	4	9.22	5.22	0.02	0.96	1.61
Biomass extraction	4	9.22	5.23	0.02	0.97	1.61

Elevation & Biomass extraction & Livestock	6	9.39	5.4	0.02	0.99	7.31
PC1 & PC2	5	11.07	7.08	0.01	0.99	3.21
Biomass extraction & Livestock	5	11.41	7.42	0.01	1	3.05

Endozoochory:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Elevation (+) & Biomass extraction (+)	**5**	**-0.07**	**0**	**0.4**	**0.4**	**8.79**
Elevation (+)	**4**	**1.53**	**1.6**	**0.18**	**0.59**	**5.46**
Elevation & LUI (+)	**5**	**1.76**	**1.83**	**0.16**	**0.75**	**7.87**
Canopy openness	4	3.04	3.11	0.09	0.83	4.7
Elevation & Livestock	5	3.89	3.96	0.06	0.89	6.81
Site only	3	5.2	5.27	0.03	0.92	1.6
Elevation & Biomass extraction & Livestock	6	5.52	5.59	0.02	0.94	9.24
PC1	4	5.79	5.87	0.02	0.96	3.32
Livestock	4	7.27	7.34	0.01	0.97	2.59
LUI	4	8.73	8.8	0	0.98	1.86
Fire	4	8.78	8.85	0	0.98	1.83
PC2	4	8.99	9.06	0	0.99	1.73
Grass cover	4	9.1	9.18	0	0.99	1.67
Biomass extraction	4	9.25	9.32	0	0.99	1.6
PC1 & PC2	5	9.77	9.84	0	1	3.86
Biomass extraction & Livestock	5	10.38	10.45	0	1	3.56

Exozoochory: Not tested because no exozoochorous overstory species

b) Understory, all species included
Maximum height:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
PC2 (+)	**4**	**79.36**	**0**	**0.23**	**0.23**	**-33.46**
Site only	**3**	**79.73**	**0.37**	**0.19**	**0.43**	**-35.67**
Elevation (-)	**4**	**80.52**	**1.16**	**0.13**	**0.56**	**-34.04**
Biomass extraction	4	81.66	2.3	0.07	0.63	-34.61
Grass cover	4	81.93	2.57	0.06	0.7	-34.74
PC1	4	83.04	3.68	0.04	0.74	-35.3
Fire	4	83.21	3.85	0.03	0.77	-35.38
Canopy openness	4	83.25	3.89	0.03	0.8	-35.4
PC1 & PC2	5	83.4	4.04	0.03	0.84	-32.95

LUI	4	83.47	4.11	0.03	0.87	-35.51
PC2 & Biomass extraction	5	83.48	4.12	0.03	0.9	-32.99
Livestock	4	83.51	4.15	0.03	0.92	-35.53
Biomass extraction & Livestock	5	83.69	4.33	0.03	0.95	-33.09
PC2 & LUI	5	83.78	4.42	0.03	0.98	-33.14
PC2 & Livestock	5	84.14	4.78	0.02	1	-33.32
PC2 & Biomass extraction & Livestock	6	89.71	10.35	0	1	-32.86

Physical defense:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Livestock (+)	**4**	**-13.02**	**0**	**0.25**	**0.25**	**12.73**
PC2 (-)	**4**	**-12.49**	**0.54**	**0.19**	**0.44**	**12.47**
Grass cover (-)	**4**	**-11.76**	**1.26**	**0.13**	**0.57**	**12.1**
Site only	**3**	**-11.48**	**1.54**	**0.11**	**0.68**	**9.94**
Canopy openness (+)	**4**	**-11.38**	**1.64**	**0.11**	**0.79**	**11.91**
PC2 (-) & Livestock (+)	**5**	**-11.04**	**1.99**	**0.09**	**0.88**	**14.27**
Elevation	4	-10.23	2.79	0.06	0.94	11.34
PC1 & PC2	5	-9.03	3.99	0.03	0.98	13.27
PC1	4	-8.2	4.82	0.02	1	10.32

Clonality:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Grass cover (+)	**4**	**-3.4**	**0**	**0.21**	**0.21**	**7.92**
Grass cover (+) & Livestock (-)	**5**	**-3.13**	**0.27**	**0.19**	**0.4**	**10.32**
Site only	**3**	**-3.12**	**0.28**	**0.18**	**0.58**	**5.76**
Livestock (-)	**4**	**-1.5**	**1.9**	**0.08**	**0.66**	**6.97**
Grass cover & LUI	5	-1.18	2.23	0.07	0.73	9.34
LUI	4	-0.37	3.03	0.05	0.78	6.41
Elevation	4	0.1	3.5	0.04	0.82	6.17
Fire	4	0.36	3.76	0.03	0.85	6.04
PC1	4	0.37	3.78	0.03	0.88	6.04
Biomass extraction	4	0.6	4	0.03	0.91	5.92
Canopy openness	4	0.91	4.32	0.02	0.93	5.77
PC2	4	0.92	4.32	0.02	0.96	5.76
Grass cover & Biomass extraction	5	0.93	4.34	0.02	0.98	8.28
Biomass extraction & Livestock	5	3.29	6.69	0.01	0.99	7.11

Grass cover & Biomass extraction & Livestock	6	3.34	6.75	0.01	1	10.33
PC1 & PC2	5	5.41	8.82	0	1	6.04

Resprouting capacity:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
PC1 (-)	**4**	**-11.93**	**0**	**0.34**	**0.34**	**12.19**
Grass cover (+)	**4**	**-10.98**	**0.95**	**0.21**	**0.56**	**11.71**
Site only	3	-9.55	2.39	0.1	0.66	8.97
PC1 & Biomass extraction	5	-8.47	3.46	0.06	0.72	12.99
PC1 & LUI	5	-8.19	3.74	0.05	0.77	12.85
Elevation	4	-8.16	3.78	0.05	0.82	10.3
PC1 & PC2	5	-7.55	4.39	0.04	0.86	12.52
PC1 & Livestock	5	-7.54	4.39	0.04	0.9	12.52
PC2	4	-6.29	5.65	0.02	0.92	9.37
Biomass extraction	4	-5.98	5.96	0.02	0.94	9.21
Canopy openness	4	-5.72	6.22	0.02	0.95	9.08
LUI	4	-5.61	6.33	0.01	0.97	9.03
Livestock	4	-5.51	6.42	0.01	0.98	8.98
Fire	4	-5.5	6.43	0.01	1	8.97
PC1 & Biomass extraction & Livestock	6	-1.98	9.96	0	1	12.99
Biomass extraction & Livestock	5	-1.47	10.46	0	1	9.49

Seed mass:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
LUI (-)	**4**	**135.03**	**0**	**0.24**	**0.24**	**-61.29**
Biomass extraction (-)	**4**	**135.52**	**0.48**	**0.19**	**0.42**	**-61.54**
Site only	**3**	**135.8**	**0.76**	**0.16**	**0.59**	**-63.7**
Livestock (-)	**4**	**136.99**	**1.95**	**0.09**	**0.68**	**-62.27**
PC1	4	137.21	2.18	0.08	0.76	-62.38
PC1 & LUI	5	138.69	3.66	0.04	0.79	-60.6
PC1 & Livestock	5	138.84	3.8	0.04	0.83	-60.67
Elevation	4	139.07	4.04	0.03	0.86	-63.32
Grass cover	4	139.54	4.51	0.02	0.89	-63.55
Canopy openness	4	139.65	4.62	0.02	0.91	-63.6
Fire	4	139.82	4.79	0.02	0.93	-63.69
PC2	4	139.84	4.81	0.02	0.95	-63.7
Biomass extraction & Livestock	5	139.97	4.94	0.02	0.97	-61.24
PC1 & Biomass extraction	5	139.98	4.94	0.02	0.99	-61.24

PC1 & PC2	5	142.26	7.23	0.01	1	-62.38
PC1 & Biomass extraction & Livestock	6	145.07	10.03	0	1	-60.53

Wind dispersal:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Grass cover (+)	**4**	**-5.98**	**0**	**0.64**	**0.64**	**9.21**
Grass cover & Livestock	5	-2.71	3.27	0.13	0.77	10.11
Grass cover & Biomass extraction	5	-1.67	4.31	0.07	0.84	9.58
Grass cover & LUI	5	-1.18	4.8	0.06	0.9	9.34
Grass cover & Biomass extraction & Livestock	6	-0.95	5.03	0.05	0.95	12.48
PC1	4	1.83	7.8	0.01	0.96	5.31
Elevation	4	1.94	7.92	0.01	0.98	5.25
Site only	3	2.21	8.19	0.01	0.99	3.09
Canopy openness	4	4.96	10.93	0	0.99	3.74
Livestock	4	4.99	10.97	0	0.99	3.73
PC1 & PC2	5	5.72	11.7	0	0.99	5.89
PC2	4	5.99	11.97	0	0.99	3.23
LUI	4	6.08	12.06	0	1	3.18
Biomass extraction	4	6.19	12.17	0	1	3.13
Fire	4	6.24	12.22	0	1	3.1
Biomass extraction & Livestock	5	7.91	13.89	0	1	4.79

Endozoochory:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Livestock (+)	**4**	**-9.16**	**0**	**0.21**	**0.21**	**10.8**
Grass cover (-) & Livestock (+)	**5**	**-8.25**	**0.91**	**0.13**	**0.34**	**12.87**
Grass cover (-)	**4**	**-8.08**	**1.08**	**0.12**	**0.46**	**10.26**
Canopy openness (+)	**4**	**-7.79**	**1.37**	**0.11**	**0.57**	**10.12**
Site only	**3**	**-7.48**	**1.68**	**0.09**	**0.66**	**7.94**
Elevation	4	-6.92	2.24	0.07	0.73	9.68
Biomass extraction & Livestock	5	-6.9	2.26	0.07	0.79	12.2
PC2	4	-6.75	2.41	0.06	0.86	9.6
LUI	4	-5.12	4.03	0.03	0.88	8.78
Grass cover & Biomass extraction & Livestock	6	-4.67	4.48	0.02	0.91	14.34
PC1	4	-4.63	4.53	0.02	0.93	8.54

Grass cover & LUI	5	-4.61	4.55	0.02	0.95	11.05
PC1 & PC2	5	-3.91	5.25	0.02	0.96	10.71
Biomass extraction	4	-3.55	5.61	0.01	0.98	8
Fire	4	-3.48	5.68	0.01	0.99	7.96
Grass cover & Biomass extraction	5	-3.13	6.03	0.01	1	10.31

Exozoochory:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Grass cover (+)	**4**	**-3.89**	**0**	**0.45**	**0.45**	**8.17**
PC1 (-)	**4**	**-2.49**	**1.4**	**0.22**	**0.67**	**7.47**
Elevation	4	0.01	3.9	0.06	0.73	6.22
Site only	3	0.27	4.16	0.06	0.79	4.07
Grass cover & Livestock	5	0.6	4.49	0.05	0.83	8.45
Grass cover & Biomass extraction	5	0.74	4.64	0.04	0.88	8.38
Grass cover & LUI	5	1.15	5.05	0.04	0.91	8.17
PC1 & PC2	5	2.16	6.05	0.02	0.93	7.67
Canopy openness	4	3.41	7.3	0.01	0.95	4.52
Grass cover & Biomass extraction & Livestock	6	3.47	7.36	0.01	0.96	10.26
Livestock	4	3.65	7.54	0.01	0.97	4.4
Biomass extraction	4	4.17	8.06	0.01	0.98	4.14
LUI	4	4.27	8.16	0.01	0.98	4.09
Fire	4	4.28	8.18	0.01	0.99	4.08
PC2	4	4.31	8.2	0.01	1	4.07
Biomass extraction & Livestock	5	6.98	10.87	0	1	5.26

c) Understory, excluding non-native invasive species

Maximum height:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
PC2 (+)	**4**	**85.27**	**0**	**0.26**	**0.26**	**-36.41**
Site only	**3**	**86.01**	**0.74**	**0.18**	**0.43**	**-38.8**
Elevation (-)	**4**	**86.62**	**1.35**	**0.13**	**0.56**	**-37.09**
Biomass extraction	4	87.96	2.69	0.07	0.63	-37.76
Grass cover	4	88.16	2.89	0.06	0.69	-37.86
PC1 & PC2	5	89.1	3.83	0.04	0.73	-35.8
PC2 & Biomass extraction	5	89.1	3.83	0.04	0.77	-35.8
Biomass extraction & Livestock	5	89.12	3.85	0.04	0.8	-35.81
Fire	4	89.41	4.14	0.03	0.84	-38.48

PC2 & LUI	5	89.54	4.27	0.03	0.87	-36.02
PC1	4	89.68	4.41	0.03	0.89	-38.62
Canopy openness	4	89.78	4.51	0.03	0.92	-38.67
Livestock	4	89.79	4.53	0.03	0.95	-38.68
LUI	4	89.87	4.6	0.03	0.97	-38.71
PC2 & Livestock	5	90.02	4.75	0.02	1	-36.26
PC2 & Biomass extraction & Livestock	6	95.14	9.87	0	1	-35.57

Physical defense:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Site only	**3**	**-15.89**	**0**	**0.36**	**0.36**	**12.15**
PC1 (+)	**4**	**-14.54**	**1.36**	**0.18**	**0.54**	**13.49**
Elevation	4	-13.78	2.11	0.12	0.66	13.11
Grass cover	4	-13.22	2.67	0.09	0.76	12.83
PC2	4	-13.03	2.87	0.09	0.84	12.74
Canopy openness	4	-12.22	3.67	0.06	0.9	12.33
Livestock	4	-12.05	3.85	0.05	0.95	12.25
PC1 & PC2	5	-10.92	4.97	0.03	0.98	14.21
PC1 & Livestock	5	-9.7	6.19	0.02	1	13.6

Clonality:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Grass cover (+)	**4**	**-7.67**	**0**	**0.47**	**0.47**	**10.06**
Site only	3	-5.17	2.5	0.13	0.6	6.79
Grass cover & Livestock	5	-4.13	3.54	0.08	0.68	10.81
Grass cover & LUI	5	-3.83	3.84	0.07	0.75	10.67
Grass cover & Biomass extraction	5	-3.17	4.5	0.05	0.8	10.33
PC1	4	-2.49	5.18	0.03	0.83	7.47
Elevation	4	-2.1	5.57	0.03	0.86	7.27
Livestock	4	-2.07	5.6	0.03	0.89	7.26
Fire	4	-1.64	6.03	0.02	0.91	7.04
LUI	4	-1.59	6.08	0.02	0.94	7.02
PC2	4	-1.38	6.29	0.02	0.96	6.91
Biomass extraction	4	-1.21	6.46	0.02	0.97	6.83
Canopy openness	4	-1.13	6.54	0.02	0.99	6.79
Grass cover & Biomass extraction & Livestock	6	2.37	10.03	0	0.99	10.82
PC1 & PC2	5	2.47	10.14	0	1	7.52
Biomass extraction & Livestock	5	2.82	10.49	0	1	7.34

Resprouting capacity:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Grass cover (+)	**4**	**-10.03**	**0**	**0.4**	**0.4**	**11.24**
Site only	**3**	**-8.38**	**1.65**	**0.17**	**0.57**	**8.39**
Grass cover & Livestock	5	-6.4	3.63	0.06	0.64	11.95
Elevation	4	-6.24	3.79	0.06	0.7	9.34
PC1	4	-6.2	3.83	0.06	0.75	9.32
Grass cover & LUI	5	-5.35	4.68	0.04	0.79	11.43
Livestock	4	-5.25	4.78	0.04	0.83	8.85
Grass cover & Biomass extraction	5	-4.98	5.05	0.03	0.86	11.24
Fire	4	-4.76	5.27	0.03	0.89	8.6
LUI	4	-4.59	5.44	0.03	0.91	8.52
PC2	4	-4.5	5.53	0.03	0.94	8.47
Canopy openness	4	-4.47	5.56	0.02	0.96	8.46
Biomass extraction	4	-4.33	5.7	0.02	0.99	8.39
PC1 & PC2	5	-1.14	8.89	0	0.99	9.32
Biomass extraction & Livestock	5	-0.91	9.12	0	1	9.2
Grass cover & Biomass extraction & Livestock	6	-0.59	9.44	0	1	12.29

Seed mass:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
LUI (-)	**4**	**138**	**0**	**0.24**	**0.24**	**-62.78**
Biomass extraction (-)	**4**	**138.38**	**0.39**	**0.2**	**0.43**	**-62.97**
Site only	**3**	**138.56**	**0.56**	**0.18**	**0.61**	**-65.08**
Livestock (-)	**4**	**139.92**	**1.92**	**0.09**	**0.71**	**-63.74**
PC1	4	140.61	2.61	0.06	0.77	-64.08
Elevation	4	142.06	4.07	0.03	0.8	-64.81
PC1 & LUI	5	142.16	4.17	0.03	0.83	-62.33
Grass cover	4	142.22	4.22	0.03	0.86	-64.89
Canopy openness	4	142.58	4.58	0.02	0.88	-65.07
PC2	4	142.58	4.59	0.02	0.91	-65.07
PC1 & Livestock	5	142.6	4.6	0.02	0.93	-62.55
Fire	4	142.6	4.61	0.02	0.96	-65.08
Biomass extraction & Livestock	5	142.91	4.92	0.02	0.98	-62.71
PC1 & Biomass extraction	5	143.16	5.16	0.02	0.99	-62.83

PC1 & PC2	5	145.64	7.64	0.01	1	-64.07
PC1 & Biomass extraction & Livestock	6	148.64	10.64	0	1	-62.32

Wind dispersal:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Grass cover (+)	**4**	**-8.74**	**0**	**0.6**	**0.6**	**10.59**
Grass cover (+) & Biomass extraction (+)	**5**	**-6.76**	**1.97**	**0.22**	**0.82**	**12.13**
Grass cover & LUI	5	-4.78	3.96	0.08	0.91	11.14
Grass cover & Livestock	5	-3.68	5.05	0.05	0.95	10.59
Grass cover & Biomass extraction & Livestock	6	-1.7	7.04	0.02	0.97	12.85
PC1	4	-1.49	7.25	0.02	0.99	6.97
Elevation	4	1.03	9.76	0	0.99	5.71
Site only	3	1.43	10.17	0	0.99	3.48
PC1 & PC2	5	3.22	11.95	0	1	7.14
Canopy openness	4	4.47	13.21	0	1	3.99
Biomass extraction	4	4.93	13.66	0	1	3.76
Livestock	4	5.35	14.08	0	1	3.55
PC2	4	5.41	14.15	0	1	3.52
Fire	4	5.46	14.2	0	1	3.49
LUI	4	5.46	14.2	0	1	3.49
Biomass extraction & Livestock	5	7.98	16.72	0	1	4.76

Endozoochory:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Site only	**3**	**-11.86**	**0**	**0.22**	**0.22**	**10.13**
PC1 (+)	**4**	**-11.38**	**0.48**	**0.18**	**0.4**	**11.91**
Elevation (+)	**4**	**-10.76**	**1.1**	**0.13**	**0.53**	**11.6**
Grass cover (-)	**4**	**-10.7**	**1.16**	**0.13**	**0.66**	**11.57**
Biomass extraction	4	-9.21	2.66	0.06	0.71	10.83
Canopy openness	4	-9	2.86	0.05	0.77	10.72
PC2	4	-8.92	2.94	0.05	0.82	10.68
LUI	4	-8.09	3.77	0.03	0.85	10.27
Fire	4	-7.98	3.88	0.03	0.89	10.21
Livestock	4	-7.91	3.95	0.03	0.92	10.18
PC1 & PC2	5	-7.77	4.09	0.03	0.95	12.63
PC1 & Livestock	5	-6.46	5.4	0.02	0.96	11.98
PC1 & Biomass extraction	5	-6.43	5.43	0.01	0.98	11.96
PC1 & LUI	5	-6.32	5.54	0.01	0.99	11.91

Biomass extraction & Livestock	5	-5.6	6.26	0.01	1	11.55
PC1 & Biomass extraction & Livestock	6	-0.49	11.37	0	1	12.24

Exozoochory:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
PC1 (-)	**4**	**-7**	**0**	**0.51**	**0.51**	**9.72**
Grass cover	4	-4.52	2.48	0.15	0.66	8.48
PC1 & LUI	5	-3.41	3.59	0.09	0.75	10.46
PC1 & Biomass extraction	5	-3.39	3.61	0.08	0.83	10.45
PC1 & Livestock	5	-2.91	4.09	0.07	0.9	10.2
PC1 & PC2	5	-1.99	5.02	0.04	0.94	9.74
Elevation	4	-0.63	6.37	0.02	0.96	6.54
Site only	3	-0.44	6.56	0.02	0.98	4.42
Biomass extraction	4	2.95	9.95	0	0.98	4.75
PC1 & Biomass extraction & Livestock	6	3.01	10.01	0	0.99	10.49
Canopy openness	4	3.24	10.24	0	0.99	4.6
PC2	4	3.44	10.44	0	0.99	4.5
LUI	4	3.48	10.48	0	0.99	4.48
Fire	4	3.51	10.51	0	1	4.47
Livestock	4	3.57	10.57	0	1	4.44
Biomass extraction & Livestock	5	7.06	14.07	0	1	5.22

d) Seedlings

Maximum height:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Site only	**3**	**82.24**	**0**	**0.27**	**0.27**	**-36.92**
Grass cover (-)	**4**	**82.62**	**0.37**	**0.22**	**0.49**	**-35.09**
PC2	4	84.75	2.51	0.08	0.57	-36.15
Biomass extraction	4	84.87	2.63	0.07	0.64	-36.21
Grass cover & Biomass extraction	5	85.22	2.98	0.06	0.7	-33.86
LUI	4	85.67	3.43	0.05	0.75	-36.61
PC1	4	86.1	3.86	0.04	0.79	-36.83
Livestock	4	86.13	3.88	0.04	0.83	-36.84
Fire	4	86.16	3.92	0.04	0.86	-36.86
Canopy openness	4	86.21	3.97	0.04	0.9	-36.88
Elevation	4	86.24	4	0.04	0.94	-36.9
Grass cover & LUI	5	86.8	4.56	0.03	0.97	-34.65

Grass cover & Livestock	5	87.67	5.43	0.02	0.98	-35.08
PC1 & PC2	5	89.57	7.32	0.01	0.99	-36.03
Biomass extraction & Livestock	5	89.83	7.59	0.01	1	-36.17
Grass cover & Biomass extraction & Livestock	6	90.57	8.33	0	1	-33.29

Physical defense:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
PC2 (-)	**4**	**2.69**	**0**	**0.46**	**0.46**	**4.88**
Site only	**3**	**4.64**	**1.96**	**0.17**	**0.63**	**1.88**
Canopy openness	4	5.08	2.39	0.14	0.77	3.68
Elevation	4	7.53	4.85	0.04	0.81	2.46
PC2 & Livestock	5	7.67	4.98	0.04	0.85	4.92
Grass cover	4	7.69	5	0.04	0.89	2.38
PC1 & PC2	5	7.74	5.05	0.04	0.92	4.88
Livestock	4	7.97	5.29	0.03	0.96	2.24
PC1	4	8.69	6	0.02	0.98	1.88
Fire	4	8.92	6.24	0.02	1	1.76

Wood density:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
PC1 (+)	**4**	**-24.57**	**0**	**0.26**	**0.26**	**18.51**
PC1 (+) & PC2 (+)	**5**	**-23.64**	**0.93**	**0.16**	**0.43**	**20.57**
Canopy openness (+)	**4**	**-23.15**	**1.41**	**0.13**	**0.55**	**17.8**
Site only	**3**	**-22.77**	**1.8**	**0.11**	**0.66**	**15.59**
PC1 & Biomass extraction	5	-22.3	2.27	0.08	0.75	19.9
PC2	4	-21.18	3.39	0.05	0.79	16.81
Fire	4	-20.77	3.8	0.04	0.83	16.61
Elevation	4	-20.48	4.09	0.03	0.87	16.46
PC1 & Biomass extraction & Livestock	6	-20.13	4.44	0.03	0.89	22.06
PC1 & LUI	5	-19.77	4.8	0.02	0.92	18.63
PC1 & Livestock	5	-19.59	4.98	0.02	0.94	18.55
Livestock	4	-18.85	5.72	0.02	0.96	15.65
LUI	4	-18.82	5.75	0.01	0.97	15.63
Grass cover	4	-18.77	5.8	0.01	0.98	15.61
Biomass extraction	4	-18.77	5.8	0.01	1	15.61
Biomass extraction & Livestock	5	-13.8	10.77	0	1	15.65

Clonality:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Site only	**3**	**-1.83**	**0**	**0.25**	**0.25**	**5.12**
PC2 (+)	**4**	**-1.3**	**0.53**	**0.19**	**0.44**	**6.87**
Elevation (-)	**4**	**0.07**	**1.9**	**0.1**	**0.54**	**6.19**
Biomass extraction	4	0.19	2.02	0.09	0.63	6.13
Canopy openness	4	1.41	3.24	0.05	0.68	5.52
PC1	4	1.61	3.44	0.04	0.72	5.42
Grass cover	4	1.77	3.6	0.04	0.76	5.34
Fire	4	1.93	3.76	0.04	0.8	5.26
Livestock	4	2.06	3.89	0.04	0.84	5.19
LUI	4	2.11	3.95	0.03	0.87	5.17
Biomass extraction & Livestock	5	2.26	4.09	0.03	0.9	7.62
PC1 & PC2	5	2.58	4.41	0.03	0.93	7.46
PC2 & Biomass extraction	5	2.61	4.44	0.03	0.96	7.45
PC2 & LUI	5	3.04	4.87	0.02	0.98	7.23
PC2 & Livestock	5	3.5	5.33	0.02	1	7
PC2 & Biomass extraction & Livestock	6	8.59	10.42	0	1	7.71

Resprouting capacity:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
PC1 (-)	**4**	**-4.79**	**0**	**0.33**	**0.33**	**8.62**
Grass cover (+)	**4**	**-4.22**	**0.57**	**0.25**	**0.57**	**8.33**
Site only	**3**	**-2.82**	**1.97**	**0.12**	**0.69**	**5.61**
Fire	4	-1.05	3.74	0.05	0.74	6.75
Elevation	4	-0.24	4.55	0.03	0.78	6.34
Biomass extraction	4	-0.2	4.59	0.03	0.81	6.32
PC2 & Livestock	5	0.14	4.93	0.03	0.84	8.68
PC2 & LUI	5	0.21	5	0.03	0.87	8.65
PC1 & PC2	5	0.22	5.01	0.03	0.89	8.64
PC2 & Biomass extraction	5	0.26	5.05	0.03	0.92	8.62
LUI	4	0.36	5.15	0.02	0.94	6.04
Livestock	4	0.97	5.76	0.02	0.96	5.74
PC2	4	0.98	5.77	0.02	0.98	5.73
Canopy openness	4	1.22	6.01	0.02	1	5.61
Biomass extraction & Livestock	5	4.75	9.54	0	1	6.37
PC2 & Biomass extraction & Livestock	6	6.6	11.39	0	1	8.7

Seed mass:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
PC1 (+)	**4**	**215.31**	**0**	**0.42**	**0.42**	**-101.43**
Site only	3	217.35	2.04	0.15	0.57	-104.48
Elevation	4	219.06	3.75	0.06	0.63	-103.31
PC1 & PC2	5	219.23	3.92	0.06	0.69	-100.87
PC1 & Biomass extraction	5	219.3	3.99	0.06	0.75	-100.9
PC1 & LUI	5	220.11	4.8	0.04	0.78	-101.31
Grass cover	4	220.18	4.86	0.04	0.82	-103.87
PC1 & Livestock	5	220.36	5.05	0.03	0.85	-101.43
Canopy openness	4	220.67	5.36	0.03	0.88	-104.11
PC2	4	220.67	5.36	0.03	0.91	-104.11
Biomass extraction	4	221.21	5.9	0.02	0.93	-104.38
LUI	4	221.31	5.99	0.02	0.95	-104.43
Fire	4	221.35	6.04	0.02	0.97	-104.45
Livestock	4	221.39	6.08	0.02	0.99	-104.47
PC1 & Biomass extraction & Livestock	6	224.87	9.56	0	1	-100.43
Biomass extraction & Livestock	5	226.23	10.92	0	1	-104.37

Wind dispersal:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Elevation (-)	**4**	**4.7**	**0**	**0.47**	**0.47**	**3.87**
PC1 & PC2	5	7.75	3.05	0.1	0.57	4.87
Canopy openness	4	8.59	3.9	0.07	0.63	1.93
Elevation & Livestock	5	9.02	4.33	0.05	0.69	4.24
PC2	4	9.03	4.33	0.05	0.74	1.71
Biomass extraction & Livestock	5	9.22	4.53	0.05	0.79	4.14
Elevation & LUI	5	9.4	4.71	0.04	0.83	4.05
Site only	3	9.6	4.9	0.04	0.87	-0.6
Elevation & Biomass extraction	5	9.66	4.97	0.04	0.91	3.92
Fire	4	10.25	5.56	0.03	0.94	1.1
PC1	4	11.09	6.4	0.02	0.96	0.68
Grass cover	4	12.1	7.4	0.01	0.97	0.17
Livestock	4	12.12	7.42	0.01	0.98	0.16
Biomass extraction	4	13.13	8.43	0.01	0.99	-0.34

LUI	4	13.58	8.89	0.01	1	-0.57
Elevation & Biomass extraction & Livestock	6	14.64	9.95	0	1	4.68

Endozoochory:

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
PC2 (-)	**4**	**0.92**	**0**	**0.34**	**0.34**	**5.76**
PC2 (-) & Livestock (+)	**5**	**2.78**	**1.86**	**0.13**	**0.47**	**7.36**
Biomass extraction & Livestock	5	2.93	2.01	0.12	0.59	7.29
PC2 & LUI	5	4.06	3.14	0.07	0.66	6.72
PC1 & PC2	5	4.39	3.47	0.06	0.72	6.55
Livestock	4	4.47	3.55	0.06	0.78	3.99
Site only	3	4.51	3.58	0.06	0.84	1.95
Elevation	4	4.79	3.87	0.05	0.89	3.83
PC2 & Biomass extraction	5	5.39	4.47	0.04	0.92	6.06
Canopy openness	4	6.91	5.99	0.02	0.94	2.77
PC2 & Biomass extraction & Livestock	6	7.36	6.44	0.01	0.95	8.32
LUI	4	7.39	6.47	0.01	0.97	2.53
Fire	4	8.17	7.25	0.01	0.98	2.14
PC1	4	8.18	7.26	0.01	0.98	2.13
Grass cover	4	8.37	7.45	0.01	0.99	2.04
Biomass extraction	4	8.52	7.6	0.01	1	1.96

Exozoochory: Too few plots with exozoochorous species to test.

APPENDIX I. RANKING OF CANDIDATE MODELS FOR CHANGES IN FUNCTIONAL DIVERSITY (DISPERSION, FDIS; AND EVENNESS, FEVE) WITH LAND USE

Models with ΔAICc ≤ 2 are shown in bold, along with the sign of the estimated effects for the model terms. All models include site as a random effect in the model. The "site only" model serves as a null model on which all other models are based, with the addition of environmental and management factors.

a) Overstory

Effect trait diversity

FDis

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Site only	**3**	**-28.39**	**0**	**0.4**	**0.4**	**18.39**
Livestock	4	-25.56	2.83	0.1	0.49	19
LUI	4	-25.09	3.29	0.08	0.57	18.77
Elevation	4	-24.86	3.53	0.07	0.64	18.65
Biomass extraction	4	-24.55	3.84	0.06	0.7	18.5
PC2	4	-24.48	3.91	0.06	0.75	18.46
Grass cover	4	-24.43	3.96	0.05	0.81	18.44
PC1	4	-24.42	3.97	0.05	0.86	18.43
Fire	4	-24.37	4.02	0.05	0.91	18.41
Canopy openness	4	-24.34	4.04	0.05	0.97	18.39
Grass cover & Livestock	5	-20.89	7.5	0.01	0.98	19.19
Biomass extraction & Livestock	5	-20.53	7.86	0.01	0.98	19.02
Grass cover & LUI	5	-20.25	8.13	0.01	0.99	18.88
Grass cover & Biomass extraction	5	-19.6	8.79	0	0.99	18.55
PC1 & PC2	5	-19.49	8.89	0	1	18.5
Grass cover & Biomass extraction & Livestock	6	-14.45	13.94	0	1	19.22

FEve

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Site only	**3**	**-4**	**0**	**0.37**	**0.37**	**6.71**
PC1	4	-1.94	2.06	0.13	0.5	8.3
Elevation	4	-1.58	2.42	0.11	0.61	8.12
Fire	4	-1.4	2.59	0.1	0.71	8.03
Biomass extraction	4	-1.05	2.95	0.08	0.8	7.86
Grass cover	4	-0.21	3.78	0.06	0.85	7.44
LUI	4	0.12	4.11	0.05	0.9	7.28
PC2	4	1.15	5.14	0.03	0.93	6.76

Livestock	4	1.16	5.15	0.03	0.95	6.75
Canopy openness	4	1.24	5.23	0.03	0.98	6.72
PC1 & Biomass extraction	5	4.8	8.8	0	0.99	8.6
PC1 & LUI	5	4.93	8.92	0	0.99	8.54
PC1 & Livestock	5	5.19	9.18	0	0.99	8.41
PC1 & PC2	5	5.38	9.38	0	1	8.31
Biomass extraction & Livestock	5	6.06	10.06	0	1	7.97
PC1 & Biomass extraction & Livestock	6	15.8	19.79	0	1	8.6

Response trait diversity

FDis

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Elevation (-)	**4**	**-41.87**	**0**	**0.39**	**0.39**	**27.16**
Elevation (-) & Biomass extraction (-)	**5**	**-40.14**	**1.73**	**0.17**	**0.56**	**28.82**
Elevation & LUI	5	-39.34	2.54	0.11	0.67	28.42
PC1	4	-38.91	2.96	0.09	0.76	25.68
Elevation & Livestock	5	-38.38	3.5	0.07	0.83	27.94
Canopy openness	4	-38.03	3.84	0.06	0.89	25.24
Site only	3	-37.33	4.54	0.04	0.93	22.87
PC1 & PC2	5	-35.51	6.36	0.02	0.94	26.51
Fire	4	-34.72	7.15	0.01	0.95	23.58
Livestock	4	-34.43	7.44	0.01	0.96	23.44
Elevation & Biomass extraction & Livestock	6	-34.1	7.78	0.01	0.97	29.05
Grass cover	4	-33.89	7.98	0.01	0.98	23.17
PC2	4	-33.52	8.36	0.01	0.99	22.98
LUI	4	-33.44	8.43	0.01	0.99	22.94
Biomass extraction	4	-33.37	8.5	0.01	1	22.91
Biomass extraction & Livestock	5	-31.88	9.99	0	1	24.69

FEve

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
PC2 (-)	**4**	**-4.29**	**0**	**0.51**	**0.51**	**9.48**
Site only	**3**	**-2.68**	**1.61**	**0.23**	**0.74**	**6.05**
Elevation	4	1.47	5.75	0.03	0.77	6.6
Fire	4	1.58	5.86	0.03	0.8	6.54
Biomass extraction	4	1.85	6.13	0.02	0.83	6.41
Canopy openness	4	1.89	6.17	0.02	0.85	6.39

Livestock	4	1.98	6.27	0.02	0.87	6.34
Grass cover	4	2.12	6.4	0.02	0.89	6.28
PC2 & LUI	5	2.33	6.62	0.02	0.91	9.83
PC2 & Biomass extraction	5	2.37	6.65	0.02	0.93	9.82
PC2 & Livestock	5	2.42	6.7	0.02	0.95	9.79
PC1	4	2.56	6.84	0.02	0.96	6.05
LUI	4	2.56	6.85	0.02	0.98	6.05
PC1 & PC2	5	2.91	7.2	0.01	1	9.54
Biomass extraction & Livestock	5	5.13	9.42	0	1	8.43
PC2 & Biomass extraction & Livestock	6	13.33	17.62	0	1	9.84

b) Understory, including all species

Effect trait diversity

FDis

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Grass cover (-)	4	-35.24	0	0.38	0.38	23.84
Grass cover (-) & Livestock (+)	5	-33.68	1.56	0.17	0.56	25.59
Elevation	4	-32.41	2.83	0.09	0.65	22.43
Grass cover & Biomass extraction & Livestock	6	-32.36	2.88	0.09	0.74	28.18
Grass cover & LUI	5	-31.02	4.21	0.05	0.78	24.26
Livestock	4	-30.94	4.3	0.04	0.83	21.69
Area only	3	-30.93	4.3	0.04	0.87	19.67
Grass cover & Biomass extraction	5	-30.18	5.06	0.03	0.9	23.84
Biomass extraction & Livestock	5	-29.67	5.57	0.02	0.93	23.58
PC1	4	-29.48	5.76	0.02	0.95	20.96
PC2	4	-28.15	7.08	0.01	0.96	20.3
Canopy openness	4	-28.07	7.17	0.01	0.97	20.26
LUI	4	-27.81	7.43	0.01	0.98	20.13
PC1 & PC2	5	-27.72	7.52	0.01	0.99	22.61
Fire	4	-26.93	8.3	0.01	0.99	19.69
Biomass extraction	4	-26.89	8.35	0.01	1	19.67

FEve

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Site only	**3**	**-32.38**	**0**	**0.24**	**0.24**	**20.39**
Biomass extraction (-)	**4**	**-31.39**	**0.99**	**0.15**	**0.39**	**21.92**

Fire (-)	**4**	**-30.9**	**1.48**	**0.11**	**0.5**	**21.67**
Grass cover (-)	**4**	**-30.56**	**1.83**	**0.1**	**0.6**	**21.5**
Elevation	4	-30.05	2.34	0.07	0.67	21.25
PC2	4	-29.69	2.69	0.06	0.73	21.07
LUI	4	-29.19	3.2	0.05	0.78	20.81
Biomass extraction & Livestock	5	-29.1	3.28	0.05	0.83	23.3
PC1	4	-29.01	3.37	0.04	0.87	20.73
Canopy openness	4	-28.39	3.99	0.03	0.91	20.42
Livestock	4	-28.35	4.03	0.03	0.94	20.4
Fire & Biomass extraction	5	-27.82	4.56	0.02	0.96	22.66
PC1 & PC2	5	-26.63	5.75	0.01	0.98	22.07
Fire & LUI	5	-26.33	6.06	0.01	0.99	21.91
Fire & Livestock	5	-25.85	6.53	0.01	1	21.67
Fire & Biomass extraction & Livestock	6	-23.74	8.65	0	1	23.87

Response trait diversity

FDis

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Grass cover (-) & Livestock (+)	**5**	**-43.75**	**0**	**0.49**	**0.49**	**30.62**
Grass cover (-)	**4**	**-42.53**	**1.21**	**0.26**	**0.75**	**27.49**
Grass cover & LUI	5	-39.76	3.99	0.07	0.82	28.63
Grass cover & Biomass extraction & Livestock	6	-39.16	4.58	0.05	0.87	31.58
Livestock	4	-38.91	4.84	0.04	0.91	25.68
Grass cover & Biomass extraction	5	-37.88	5.87	0.03	0.93	27.69
Site only	3	-37.07	6.68	0.02	0.95	22.74
Elevation	4	-36.47	7.28	0.01	0.96	24.46
Biomass extraction & Livestock	5	-35.41	8.34	0.01	0.97	26.45
LUI	4	-35.03	8.72	0.01	0.98	23.74
PC1	4	-34.95	8.8	0.01	0.98	23.7
Canopy openness	4	-34.63	9.12	0.01	0.99	23.54
PC2	4	-34.2	9.55	0	0.99	23.32
Biomass extraction	4	-33.28	10.47	0	1	22.86
Fire	4	-33.14	10.6	0	1	22.79
PC1 & PC2	5	-31.85	11.9	0	1	24.67

FEve

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Site only	**3**	**-30.21**	**0**	**0.2**	**0.2**	**19.31**
Elevation (+)	**4**	**-29.87**	**0.34**	**0.17**	**0.37**	**21.16**
PC2 (-)	**4**	**-29.61**	**0.6**	**0.15**	**0.51**	**21.03**
Canopy openness (+)	**4**	**-28.29**	**1.93**	**0.08**	**0.59**	**20.37**
Biomass extraction & Livestock	5	-28.16	2.05	0.07	0.66	22.83
Livestock	4	-28.05	2.16	0.07	0.73	20.25
Fire	4	-27.34	2.88	0.05	0.78	19.89
PC1	4	-26.82	3.39	0.04	0.81	19.63
PC1 & PC2	5	-26.8	3.41	0.04	0.85	22.15
Grass cover	4	-26.43	3.78	0.03	0.88	19.44
LUI	4	-26.41	3.8	0.03	0.91	19.43
Biomass extraction	4	-26.33	3.88	0.03	0.94	19.39
Elevation & Livestock	5	-26.21	4	0.03	0.96	21.86
Elevation & LUI	5	-25.45	4.76	0.02	0.98	21.47
Elevation & Biomass extraction	5	-24.96	5.25	0.01	1	21.23
Elevation & Biomass extraction & Livestock	6	-21.71	8.5	0	1	22.86

c) Understory, excluding non-native invasive species

Effect trait diversity

FDis

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Grass cover (-)	**4**	**-31.56**	**0**	**0.32**	**0.32**	**22**
Grass cover (-) & Livestock	**5**	**-30.61**	**0.95**	**0.2**	**0.51**	**24.05**
Grass cover (-) & Biomass extraction (-) & Livestock (+)	**6**	**-30.21**	**1.35**	**0.16**	**0.67**	**27.11**
Elevation	4	-28.72	2.85	0.08	0.75	20.58
Grass cover & LUI	5	-27.53	4.03	0.04	0.79	22.52
Site only	3	-27.47	4.09	0.04	0.83	17.94
Livestock	4	-27.37	4.19	0.04	0.87	19.91
Biomass extraction & Livestock	5	-26.52	5.04	0.03	0.9	22.01
Grass cover & Biomass extraction	5	-26.51	5.05	0.03	0.92	22.01
PC1	4	-26.03	5.54	0.02	0.94	19.24
Canopy openness	4	-25.93	5.63	0.02	0.96	19.19

PC2	4	-24.99	6.57	0.01	0.97	18.72
LUI	4	-24.39	7.17	0.01	0.98	18.42
PC1 & PC2	5	-24.09	7.47	0.01	0.99	20.79
Biomass extraction	4	-23.44	8.13	0.01	0.99	17.94
Fire	4	-23.43	8.13	0.01	1	17.94

FEve

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
PC2 (-)	**4**	**-34.44**	**0**	**0.2**	**0.2**	**23.44**
Site only	**3**	**-34**	**0.44**	**0.16**	**0.36**	**21.2**
Grass cover (-)	**4**	**-33.66**	**0.78**	**0.13**	**0.49**	**23.05**
Fire (-)	**4**	**-33.57**	**0.87**	**0.13**	**0.62**	**23.01**
Canopy openness (-)	**4**	**-32.87**	**1.57**	**0.09**	**0.71**	**22.66**
Elevation	4	-32.02	2.43	0.06	0.77	22.23
Biomass extraction & Livestock	5	-31.57	2.88	0.05	0.82	24.53
Livestock	4	-31.04	3.41	0.04	0.85	21.74
Biomass extraction	4	-30.4	4.04	0.03	0.88	21.42
PC1 & PC2	5	-30.25	4.19	0.02	0.9	23.88
LUI	4	-29.99	4.46	0.02	0.93	21.22
PC1	4	-29.96	4.48	0.02	0.95	21.2
PC2 & Biomass extraction	5	-29.64	4.8	0.02	0.97	23.57
PC2 & Livestock	5	-29.5	4.95	0.02	0.98	23.5
PC2 & LUI	5	-29.4	5.04	0.02	1	23.45
PC2 & Biomass extraction & Livestock	6	-25.19	9.26	0	1	24.59

Response trait diversity

FDis

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Grass cover (-)	**4**	**-46.42**	**0**	**0.53**	**0.53**	**29.43**
Grass cover (-) & Livestock (+)	**5**	**-44.96**	**1.46**	**0.26**	**0.79**	**31.23**
Grass cover & LUI	5	-42.55	3.87	0.08	0.87	30.02
Grass cover & Biomass extraction	5	-41.4	5.02	0.04	0.91	29.45
Grass cover & Biomass extraction & Livestock	6	-39.67	6.75	0.02	0.93	31.84
Site only	3	-39.05	7.37	0.01	0.94	23.73
Livestock	4	-39.02	7.4	0.01	0.96	25.73
Elevation	4	-39.02	7.41	0.01	0.97	25.73
PC1	4	-38.78	7.65	0.01	0.98	25.61

Canopy openness	4	-36.93	9.49	0	0.99	24.69
LUI	4	-36.49	9.93	0	0.99	24.47
PC2	4	-35.65	10.77	0	0.99	24.05
Fire	4	-35.12	11.3	0	0.99	23.78
Biomass extraction	4	-35.09	11.33	0	1	23.77
Biomass extraction & Livestock	5	-35.03	11.4	0	1	26.26
PC1 & PC2	5	-34.58	11.85	0	1	26.04

FEve

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Livestock (+)	**4**	**-35.21**	**0**	**0.24**	**0.24**	**23.83**
Site only	**3**	**-34.83**	**0.39**	**0.2**	**0.44**	**21.61**
Biomass extraction (-) & Livestock (+)	**5**	**-33.6**	**1.61**	**0.11**	**0.55**	**25.55**
PC2	4	-32.63	2.58	0.07	0.61	22.54
Grass cover	4	-32.63	2.59	0.07	0.68	22.53
LUI	4	-32.19	3.02	0.05	0.73	22.32
Elevation	4	-32.09	3.13	0.05	0.78	22.27
Canopy openness	4	-31.89	3.32	0.05	0.83	22.17
PC1	4	-31.26	3.96	0.03	0.86	21.85
PC2 & Livestock	5	-31.22	4	0.03	0.9	24.36
Fire	4	-30.92	4.29	0.03	0.92	21.68
Biomass extraction	4	-30.89	4.32	0.03	0.95	21.67
PC2 & LUI	5	-30.75	4.47	0.03	0.98	24.12
PC1 & PC2	5	-28.78	6.43	0.01	0.99	23.14
PC2 & Biomass extraction	5	-28	7.21	0.01	0.99	22.75
PC2 & Biomass extraction & Livestock	6	-27.54	7.67	0.01	1	25.77

d) Seedlings

Effect trait diversity

FDis

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Fire (+)	**4**	**-42.77**	**0**	**0.76**	**0.76**	**27.61**
Fire & Biomass extraction	5	-38.65	4.12	0.1	0.85	28.08
Fire & Livestock	5	-37.88	4.89	0.07	0.92	27.69
Fire & LUI	5	-37.8	4.97	0.06	0.98	27.65
Fire & Biomass extraction & Livestock	6	-35.16	7.61	0.02	1	29.58
Grass cover	4	-28.98	13.79	0	1	20.71
Site only	3	-28.79	13.98	0	1	18.59

Canopy openness	4	-26.63	16.14	0	1	19.53
PC1	4	-25.24	17.53	0	1	18.84
Elevation	4	-25.14	17.63	0	1	18.79
LUI	4	-24.83	17.94	0	1	18.64
Livestock	4	-24.82	17.95	0	1	18.63
Biomass extraction	4	-24.8	17.97	0	1	18.62
PC2	4	-24.76	18.01	0	1	18.6
PC1 & PC2	5	-20.21	22.56	0	1	18.85
Biomass extraction & Livestock	5	-19.77	22.99	0	1	18.64

FEve

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Biomass extraction (+)	**4**	**-28.76**	**0**	**0.32**	**0.32**	**21.24**
LUI (+)	**4**	**-27.55**	**1.21**	**0.17**	**0.49**	**20.63**
Site only	**3**	**-27.46**	**1.3**	**0.16**	**0.65**	**18.23**
PC1	4	-26.16	2.6	0.09	0.74	19.93
Livestock	4	-24.76	4	0.04	0.78	19.24
Fire & LUI	5	-24.66	4.1	0.04	0.82	22.33
Fire	4	-24.34	4.42	0.03	0.86	19.03
Fire & Biomass extraction	5	-24.16	4.6	0.03	0.89	22.08
Elevation	4	-23.69	5.07	0.03	0.91	18.7
Fire & Livestock	5	-23.39	5.37	0.02	0.93	21.7
Grass cover	4	-22.8	5.96	0.02	0.95	18.26
Canopy openness	4	-22.79	5.97	0.02	0.97	18.25
PC2	4	-22.76	6	0.02	0.98	18.24
Biomass extraction & Livestock	5	-22.48	6.28	0.01	1	21.24
PC1 & PC2	5	-19.88	8.88	0	1	19.94
Fire & Biomass extraction & Livestock	6	-15.92	12.84	0	1	22.36

Response trait diversity

FDis

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
PC1 (+)	**4**	**-48.18**	**0**	**0.38**	**0.38**	**30.31**
Elevation	4	-45.63	2.55	0.1	0.48	29.04
PC1 & Biomass extraction	5	-45.31	2.87	0.09	0.57	31.41
Canopy openness	4	-45.28	2.9	0.09	0.66	28.86
Site only	3	-45.16	3.02	0.08	0.74	26.78
PC1 & LUI	5	-44.98	3.21	0.08	0.82	31.24
PC1 & Livestock	5	-44.09	4.09	0.05	0.86	30.8

Grass cover	4	-43.62	4.56	0.04	0.9	28.03
PC1 & PC2	5	-43.2	4.98	0.03	0.93	30.35
Livestock	4	-41.65	6.53	0.01	0.95	27.05
Fire	4	-41.31	6.87	0.01	0.96	26.88
Biomass extraction	4	-41.18	7	0.01	0.97	26.81
LUI	4	-41.18	7	0.01	0.98	26.81
PC2	4	-41.17	7.01	0.01	0.99	26.81
PC1 & Biomass extraction & Livestock	6	-38.82	9.36	0	1	31.41
Biomass extraction & Livestock	5	-37.23	10.95	0	1	27.37

FEve

	K	AICc	Δ AICc	AICc weight	Cumulative weight	Log likelihood
Site only	**3**	**-18.59**	**0**	**0.29**	**0.29**	**13.8**
Fire (+)	**4**	**-17.72**	**0.87**	**0.18**	**0.47**	**15.72**
Biomass extraction (+)	**4**	**-17.06**	**1.53**	**0.13**	**0.6**	**15.39**
PC2 (+)	**4**	**-16.94**	**1.66**	**0.12**	**0.73**	**15.33**
Elevation	4	-15.36	3.24	0.06	0.78	14.54
LUI	4	-14.85	3.74	0.04	0.83	14.28
PC1	4	-14.38	4.21	0.03	0.86	14.05
Grass cover	4	-14.2	4.39	0.03	0.89	13.96
Canopy openness	4	-14.01	4.58	0.03	0.92	13.86
Livestock	4	-13.9	4.7	0.03	0.95	13.81
Biomass extraction & Livestock	5	-12.42	6.17	0.01	0.96	16.21
Fire & Biomass extraction	5	-12.18	6.42	0.01	0.97	16.09
Fire & LUI	5	-11.71	6.88	0.01	0.98	15.86
Fire & Livestock	5	-11.48	7.12	0.01	0.99	15.74
PC1 & PC2	5	-11.33	7.26	0.01	1	15.66
Fire & Biomass extraction & Livestock	6	-3.91	14.68	0	1	16.35

APPENDIX J. DETAILS OF EFFECTS OF NON-NATIVE INVASIVE SPECIES ON UNDERSTORY FUNCTIONAL COMPOSITION

Increased physical defenses and endozoochory in the understory community with livestock grazing were due entirely to the non-native invasive species within these areas (Figures J.1 and J.2). Specifically, this trend was due to the presence of *Lantana camara*, the only non-native invasive understory species that is endozoochorous and has physical defenses. The increase in physical defenses due to non-native invasive species associated with livestock resulted in increased variance ($p = 0.040$, $\chi^2 = 4.207$, $df = 1$). When non-native invasive species were excluded from the analysis, there was no longer increased variance in physical defenses with livestock grazing ($p = 0.539$, $\chi^2 = 0.3768$, $df = 1$).

Understory communities with livestock grazing continued to show greater functional dispersion even with non-native invasive species omitted from the analysis, though the relative support for livestock was reduced within the candidate model sets (Appendix I). When non-native invasive species were excluded from the analysis, butterfly pollination and endozoochory were no longer significantly more prevalent or variable in areas with livestock grazing (butterfly: $p = 0.720$, $\chi^2 = 0.129$, $df = 1$; $p = 0.736$, $\chi^2 = 0.1131$, $df = 1$; endozoochory: $p = 0.896$, $\chi^2 = 0.017$, $df = 1$; $p = 0.790$, $\chi^2 = 0.071$, $df = 1$). Thrip pollination remained significantly more prevalent and variable ($p = 0.039$, $\chi^2 = 4.264$, $df = 1$; $p = 0.038$, $\chi^2 = 4.292$, $df = 1$), though the estimated effect of livestock grazing on the abundance-weighted variance decreased (0.165 vs. 0.047). *Lantana camara*, present in all four plots with livestock and in only one plot without livestock, is the only non-native invasive species that is pollinated by butterflies, is endozoochorous and has physical defenses. Lantana is also thrip pollinated.

Figure J.1 Percent cover-weighted proportion of understory species with physical defenses in plots with and without livestock, including all species (a) and omitting non-native invasive species (b).

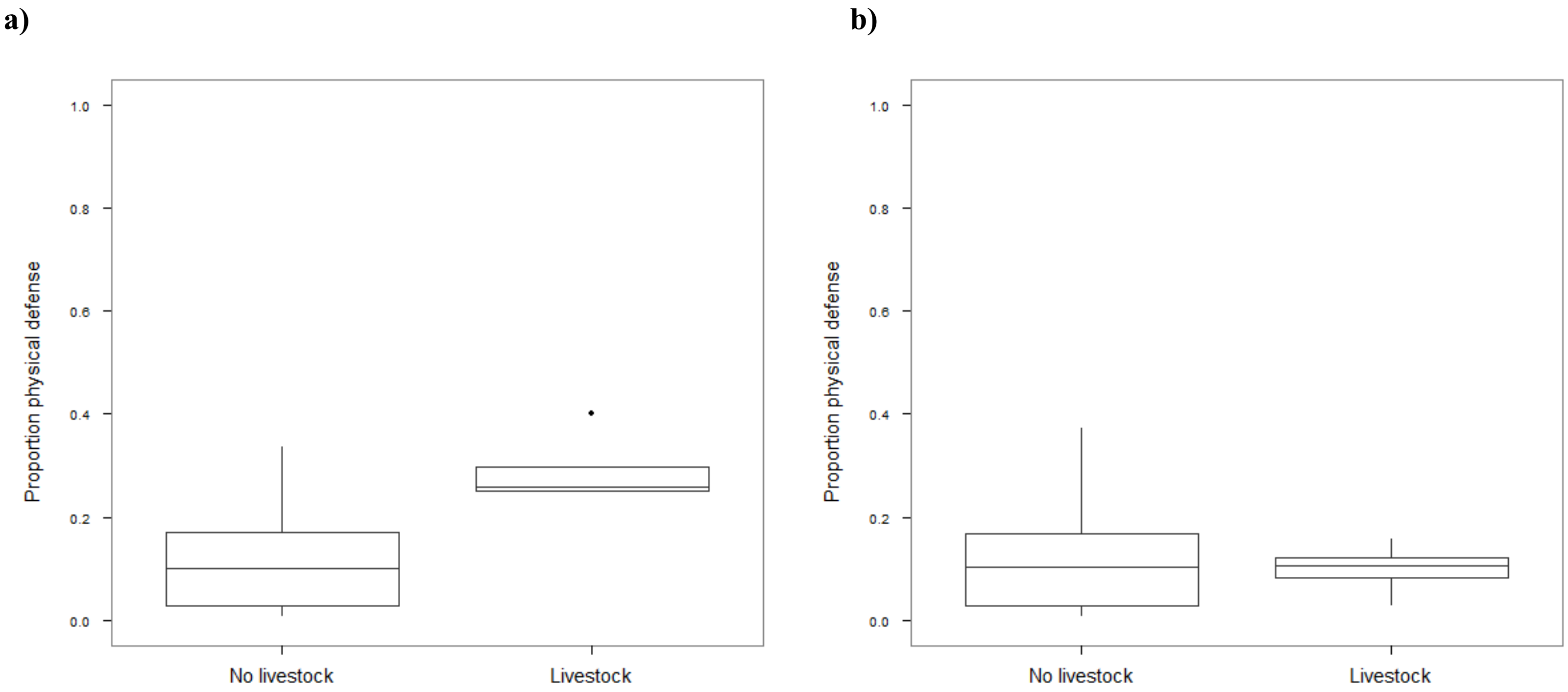
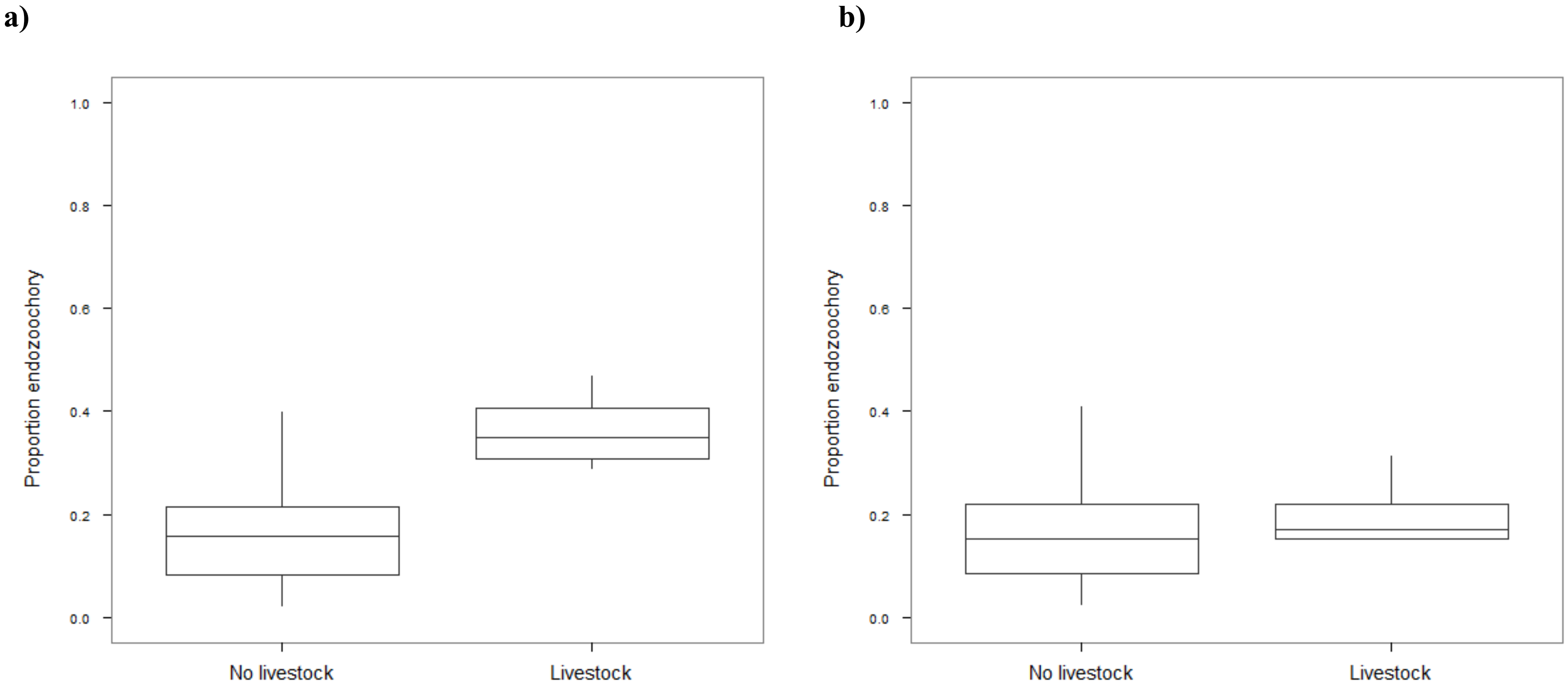
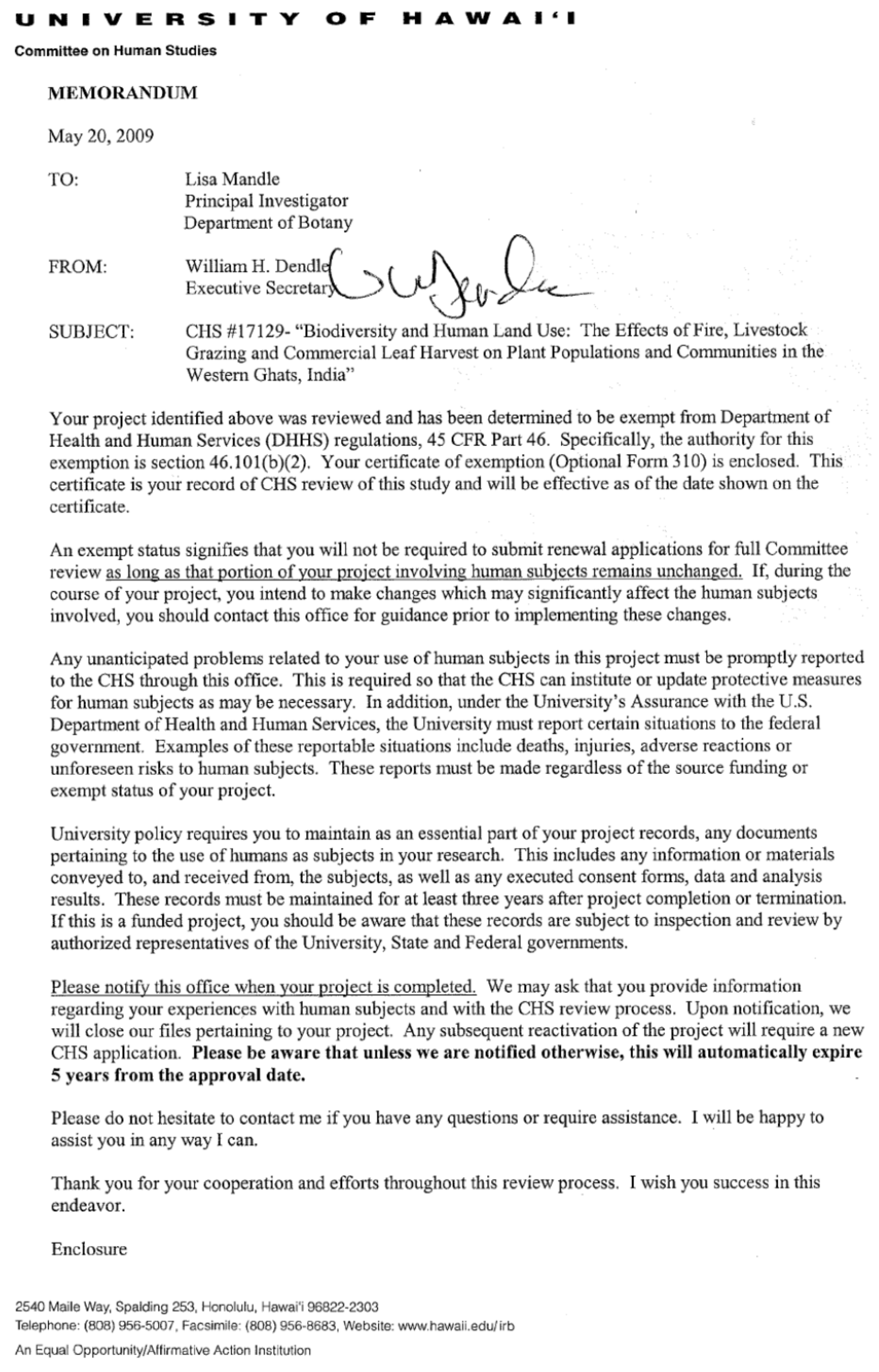


Figure J.2 Percent cover-weighted proportion of endozoochorous species within the understory community with and without livestock, including all species (a) and omitting non-native invasive species (b).



APPENDIX K. UNIVERSITY OF HAWAI‘I COMMITTEE ON HUMAN SUBJECTS RESEARCH EXEMPTION



UNIVERSITY OF HAWAI‘I
Committee on Human Studies

MEMORANDUM

May 20, 2009

TO: Lisa Mandle
Principal Investigator
Department of Botany

FROM: William H. Dendle
Executive Secretary

SUBJECT: CHS #17129- “Biodiversity and Human Land Use: The Effects of Fire, Livestock Grazing and Commercial Leaf Harvest on Plant Populations and Communities in the Western Ghats, India”

Your project identified above was reviewed and has been determined to be exempt from Department of Health and Human Services (DHHS) regulations, 45 CFR Part 46. Specifically, the authority for this exemption is section 46.101(b)(2). Your certificate of exemption (Optional Form 310) is enclosed. This certificate is your record of CHS review of this study and will be effective as of the date shown on the certificate.

An exempt status signifies that you will not be required to submit renewal applications for full Committee review as long as that portion of your project involving human subjects remains unchanged. If, during the course of your project, you intend to make changes which may significantly affect the human subjects involved, you should contact this office for guidance prior to implementing these changes.

Any unanticipated problems related to your use of human subjects in this project must be promptly reported to the CHS through this office. This is required so that the CHS can institute or update protective measures for human subjects as may be necessary. In addition, under the University’s Assurance with the U.S. Department of Health and Human Services, the University must report certain situations to the federal government. Examples of these reportable situations include deaths, injuries, adverse reactions or unforeseen risks to human subjects. These reports must be made regardless of the source funding or exempt status of your project.

University policy requires you to maintain as an essential part of your project records, any documents pertaining to the use of humans as subjects in your research. This includes any information or materials conveyed to, and received from, the subjects, as well as any executed consent forms, data and analysis results. These records must be maintained for at least three years after project completion or termination. If this is a funded project, you should be aware that these records are subject to inspection and review by authorized representatives of the University, State and Federal governments.

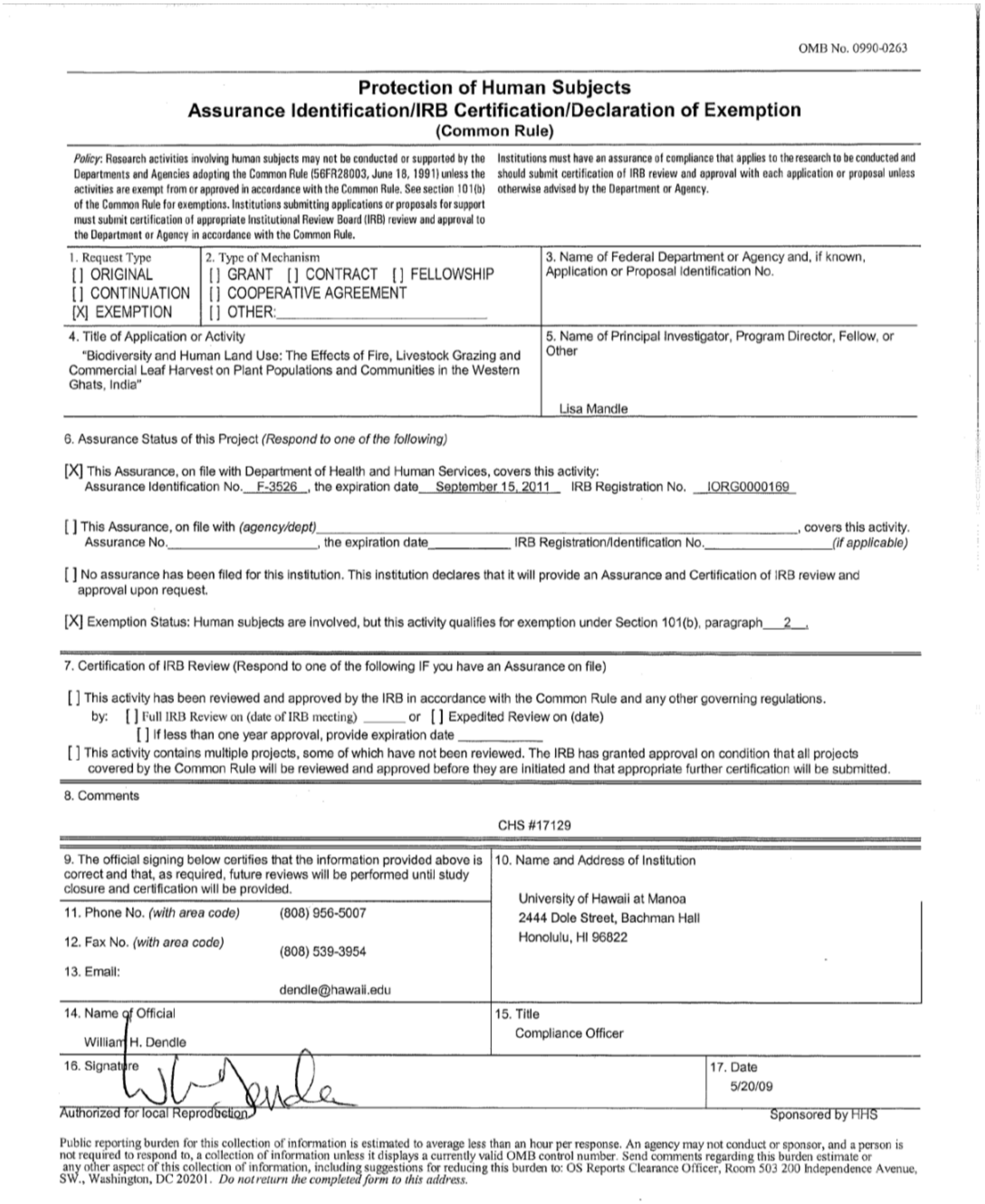
Please notify this office when your project is completed. We may ask that you provide information regarding your experiences with human subjects and with the CHS review process. Upon notification, we will close our files pertaining to your project. Any subsequent reactivation of the project will require a new CHS application. **Please be aware that unless we are notified otherwise, this will automatically expire 5 years from the approval date.**

Please do not hesitate to contact me if you have any questions or require assistance. I will be happy to assist you in any way I can.

Thank you for your cooperation and efforts throughout this review process. I wish you success in this endeavor.

Enclosure

2540 Maile Way, Spalding 253, Honolulu, Hawai‘i 96822-2303
Telephone: (808) 956-5007, Facsimile: (808) 956-8683, Website: www.hawaii.edu/irb
An Equal Opportunity/Affirmative Action Institution



OMB No. 0990-0263

Protection of Human Subjects
Assurance Identification/IRB Certification/Declaration of Exemption
(Common Rule)

Policy: Research activities involving human subjects may not be conducted or supported by the Departments and Agencies adopting the Common Rule (56FR28003, June 18, 1991) unless the activities are exempt from or approved in accordance with the Common Rule. See section 101(b) of the Common Rule for exemptions. Institutions submitting applications or proposals for support must submit certification of appropriate Institutional Review Board (IRB) review and approval to the Department or Agency in accordance with the Common Rule.

Institutions must have an assurance of compliance that applies to the research to be conducted and should submit certification of IRB review and approval with each application or proposal unless otherwise advised by the Department or Agency.

1. Request Type [] ORIGINAL [] CONTINUATION [X] EXEMPTION	2. Type of Mechanism [] GRANT [] CONTRACT [] FELLOWSHIP [] COOPERATIVE AGREEMENT [] OTHER:____________________	3. Name of Federal Department or Agency and, if known, Application or Proposal Identification No.

4. Title of Application or Activity "Biodiversity and Human Land Use: The Effects of Fire, Livestock Grazing and Commercial Leaf Harvest on Plant Populations and Communities in the Western Ghats, India"	5. Name of Principal Investigator, Program Director, Fellow, or Other Lisa Mandle

6. Assurance Status of this Project *(Respond to one of the following)*

[X] This Assurance, on file with Department of Health and Human Services, covers this activity:
Assurance Identification No.__F-3526__, the expiration date__September 15, 2011__ IRB Registration No. __IORG0000169__

[ ] This Assurance, on file with *(agency/dept)*______________________________, covers this activity.
Assurance No.________________, the expiration date__________ IRB Registration/Identification No.________________*(if applicable)*

[ ] No assurance has been filed for this institution. This institution declares that it will provide an Assurance and Certification of IRB review and approval upon request.

[X] Exemption Status: Human subjects are involved, but this activity qualifies for exemption under Section 101(b), paragraph__2__.

7. Certification of IRB Review (Respond to one of the following IF you have an Assurance on file)

[ ] This activity has been reviewed and approved by the IRB in accordance with the Common Rule and any other governing regulations.
by: [ ] Full IRB Review on (date of IRB meeting) ______ or [ ] Expedited Review on (date)
[ ] If less than one year approval, provide expiration date __________

[ ] This activity contains multiple projects, some of which have not been reviewed. The IRB has granted approval on condition that all projects covered by the Common Rule will be reviewed and approved before they are initiated and that appropriate further certification will be submitted.

8. Comments

CHS #17129

9. The official signing below certifies that the information provided above is correct and that, as required, future reviews will be performed until study closure and certification will be provided.	10. Name and Address of Institution University of Hawaii at Manoa 2444 Dole Street, Bachman Hall Honolulu, HI 96822
11. Phone No. *(with area code)* (808) 956-5007 12. Fax No. *(with area code)* (808) 539-3954 13. Email: dendle@hawaii.edu	
14. Name of Official William H. Dendle	15. Title Compliance Officer
16. Signature	17. Date 5/20/09

Authorized for local Reproduction

Sponsored by HHS

Public reporting burden for this collection of information is estimated to average less than an hour per response. An agency may not conduct or sponsor, and a person is not required to respond to, a collection of information unless it displays a currently valid OMB control number. Send comments regarding this burden estimate or any other aspect of this collection of information, including suggestions for reducing this burden to: OS Reports Clearance Officer, Room 503 200 Independence Avenue, SW., Washington, DC 20201. *Do not return the completed form to this address.*

LITERATURE CITED

Agrawal A.A., Ackerly D.D., Adler F., Arnold A.E., Cáceres C., Doak D.F., Post E., Hudson P.J., Maron J., Mooney K.A., Power M., Schemske D., Stachowicz J., Strauss S., Turner M.G. & Werner E. (2007). Filling key gaps in population and community ecology. *Frontiers in Ecology and the Environment*, 5, 145-152.

Albert C.H., de Bello F., Boulangeat I., Pellet G., Lavorel S. & Thuiller W. (2012). On the importance of intraspecific variability for the quantification of functional diversity. *Oikos*, 121, 116-126.

Anand M.O., Krishnaswamy J., Kumar A. & Bali A. (2010). Sustaining biodiversity conservation in human-modified landscapes in the Western Ghats: Remnant forests matter. *Biological Conservation*, 143, 2363-2374.

Anderson B.J., Armsworth P.R., Eigenbrod F., Thomas C.D., Gillings S., Heinemeyer A., Roy D.B. & Gaston K.J. (2009). Spatial covariance between biodiversity and other ecosystem service priorities. *Journal of Applied Ecology*, 46, 888-896.

Anderson D.R. (2008). *Model Based Inference in the Life Sciences*. Springer, New York.

Anten N.P.R., Ackerly D.D. & Martinez-Ramos M. (2003). Defoliation and growth in an understory palm: Quantifying the contributions of compensatory responses. *Ecology*, 84, 2905-2918.

Archibald S., Bond W., Stock W. & Fairbanks D. (2005). Shaping the landscape: Fire-grazer interactions in an African savanna. *Ecological Applications*, 15, 96-109.

Archibald S. & Bond W.J. (2004). Grazer movements: Spatial and temporal responses to burning in a tall-grass African savanna. *International Journal of Wildland Fire*, 13, 377-385.

Arjunan M., Puyravaud J.-P. & Davidar P. (2005). The impact of resource collection by local communities on the dry forests of the Kalakad-Mundanthurai Tiger Reserve. *Tropical Ecology*, 46.

Asner G.P., Elmore A.J., Olander L.P., Martin R.E. & Harris A.T. (2004). Grazing systems, ecosystem responses, and global change. *Annual Review of Environment and Resources*, 29, 261-299.

Balick M.J. & Beck H.T. (1990). *Useful Palms of the World: A Synoptic Bibliography*. Columbia University Press, New York.

Balmford A. (1996). Extinction filters and current resilience: The significance of past selection pressures for conservation biology. *Trends in Ecology and Evolution*, 11, 193-196.

Baltzer J.L., E. G. Reekie, H. L. Hewlin, Taylor P.D. & Boates J.S. (2002). Impact of flower harvesting on the salt marsh plant Limonium carolinianum. *Canadian Journal of Botany* 80.

Balvanera P., Castillo A. & Martínez-Harms M.J. (2010). Ecosystem services in seasonally dry tropical forests. In: *Seasonally Dry Tropical Forests: Ecology and Conservation* (eds. Dirzo R, Young HS, Mooney HA & Ceballos G). Island Press Washington, D.C., pp. 259-277.

Balvanera P., Pfisterer A.B., Buchmann N., He J.-S., Nakashizuka T., Raffaelli D. & Schmid B. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, 9, 1146-56.

Barrow S.C. (1998). A monograph of *Phoenix* L. (Palmae: Coryphoideae). *Kew Bulletin*, 53, 513-575.

Barve N., Kiran M., Vanaraj G., Aravind N.A., Rao D., Shaanker R.U., Ganeshaiah K. & Poulsen J. (2005). Measuring and mapping threats to a wildlife sanctuary in southern India. *Conservation Biology*, 19, 122-130.

Bates D., Maechler M. & Bolker B. (2011). lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-40.

Bawa K.S., Das A., Krishnaswamy J., Karanth K.U., Kumar N.S. & Rao M. (2007). *Ecosystem Profile: Western Ghats & Sri Lanka Biodiversity Hotspot, Western Ghats Region.* Conservation International, Arlington, Virginia.

Bawa K.S., Rai N.D. & Sodhi N.S. (2011). Rights, governance, and conservation of biological diversity. *Conservation Biology*, 25, 639-641.

Berry E.J., Gorchov D.L. & Endress B.A. (2011). Source-sink population dynamics and sustainable leaf harvesting of the understory palm *Chamaedorea radicalis*. In: *Sources, Sinks and Sustainability* (eds. Liu J, Hull V, Morzillo AT & Wiens JA). Cambridge University Press Cambridge, pp. 450-474.

Bezemer T.M., Lawson C.S., Hedlund K., Edwards A.R., Brook A.J., Igual J.M., Mortimer S.R. & Van Der Putten W.H. (2006). Plant species and functional group effects on abiotic and microbial soil properties and plant-soil feedback responses in two grasslands. *Journal of Ecology*, 94, 893-904.

Bhagwat S.A., Willis K.J., Birks H.J.B. & Whittaker R.J. (2008). Agroforestry: A refuge for tropical biodiversity? *Trends in Ecology & Evolution*, 23, 261-267.

Binh B.M. (2009). *Rattans of Vietnam: Ecology, Demography and Harvesting*. Ph.D. thesis. Utrecht University, Utrecht, p. 194.

Biswal R. (2009). *Exploring the Contribution of NTFPs to Rural Livelihoods: The Case of the Nilgiri Biosphere Reserve, India*. M.A. thesis. University of East Anglia, East Anglia, p. 63.

Blancas J., Casas A., Rangel-Landa S., Moreno-Calles A., Torres I., Pérez-Negrón E., Solís L., Delgado-Lemus A., Parra F., Yaaye A., Caballero J., Cortés L., Lira R. & Dávila P. (2010). Plant management in the Tehuacán-Cuicatlán Valley, Mexico. *Economic Botany*, 64, 287-302.

Bond W.J. & Keeley J.E. (2005). Fire as a global ‘herbivore’: The ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution*, 20, 387-394.

Bond W.J. & Midgley J.J. (2001). Ecology of sprouting in woody plants: The persistence niche. *Trends in Ecology and Evolution*, 16, 45-51.

Bond W.J., Woodward F.I. & Midgley G.F. (2005). The global distribution of ecosystems in a world without fire. *New Phytologist*, 165, 525-37.

Bradshaw C.J., Sodhi N.S. & Brook B.W. (2009). Tropical turmoil: A biodiversity tragedy in progress. *Frontiers in Ecology and the Environment*, 7, 79-87.

Brummit N. & Bachman S. (2010). P*lants Under Pressure – A Global Assessment: The First Report of the IUCN Sampled Red List Index for Plants*. Kew, UK, p. 16.

Buckley Y.M., Ramula S., Blomberg S.P., Burns J.H., Crone E.E., Ehrlén J., Knight T.M., Pichancourt J.-B., Quested H. & Wardle G.M. (2010). Causes and consequences of variation in plant population growth rate: A synthesis of matrix population models in a phylogenetic context. *Ecology Letters*, 13, 1182-1197.

Cadotte M.W. (2011). The new diversity: Management gains through insights into the functional diversity of communities. *Journal of Applied Ecology*, 48, 1067-1069.

Caswell H. (2001). *Matrix Population Models: Construction, Analysis and Interpretation*. 2nd edn. Sinauer Associates, Sunderland, Massachusetts.

Chandran M. (1997). On the ecological history of the Western Ghats. *Current Science*, 73, 146-155.

Chape S., Harrison J., Spalding M. & Lysenko I. (2005). Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360, 443-455.

Chapman D.F., Robson M.J. & Snaydon R.W. (1992). Physiological integration in the clonal perennial herb *Trifolium repens* L. *Oecologia*, 89, 338-347.

Chave J., Coomes D., Jansen S., Lewis S.L., Swenson N.G. & Zanne A.E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, 12, 351-66.

Chave J., Muller-Landau H.C., Baker T.R., Easdale T.A., ter Steege H. & Webb C.O. (2006). Regional and phylogenetic variation of wood density across 2456 neotropical tree species. *Ecological Applications*, 16, 2356-2367.

Chazdon R.L. (1991). Effects of leaf and ramet removal on growth and reproduction of *Geonoma congesta*, a clonal understorey palm. *Journal of Ecology*, 79, 1137-1146.

Chazdon R.L., Harvey C.A., Komar O., Griffith D.M., Ferguson B.G., Martínez-Ramos M., Morales H., Nigh R., Soto-Pinto L., van Breugel M. & Philpott S.M. (2009). Beyond reserves: A research agenda for conserving biodiversity in human-modified tropical landscapes. *Biotropica*, 41, 142-153.

Chien P.D. & Zuidema P.A. (2006). What dimensions to use for matrix models of trees? Recommendations based on a validation of age estimate by tree ring analysis. In: *Demography of threatened tree species in Vietnam*. Ph.D. thesis. Utrecht University, Utrecht, pp. 107-124.

Cianciaruso M.V., Silva I.a., Batalha M.a., Gaston K.J. & Petchey O.L. (2012). The influence of fire on phylogenetic and functional structure of woody savannas: Moving from species to individuals. *Perspectives in Plant Ecology, Evolution and Systematics*.

Cincotta R.P., Wisnewski J. & Engelman R. (2000). Human population in the biodiversity hotspots. *Nature*, 404, 990-992.

Clavel J., Julliard R. & Devictor V. (2011). Worldwide decline of specialist species: Toward a global functional homogenization? *Frontiers in Ecology and the Environment*, 9, 222-228.

Collins S.L. & Calabrese L.B. (2011). Effects of fire, grazing and topographic variation on vegetation structure in tallgrass prairie. *Journal of Vegetation Science*.

Collins S.L., Knapp A.K., Briggs J.M., Blair J.M. & Steinauer E.M. (1998). Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science*, 280, 745-747.

Connell J.H. & Slatyer R.O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist*, 111, 1119-1144.

Cornelissen J.H.C., Lavorel S., Garnier E., Díaz S., Buchmann N., Gurvich D.E., Reich P.B., Steege H.T., Morgan H.D., Heijden M.G.a.V.D., Pausas J.G. & Poorter H. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, 51, 335-380.

Crone E.E., Menges E.S., Ellis M.M., Bell T., Bierzychudek P., Ehrlén J., Kaye T.N., Knight T.M., Lesica P., Morris W.F., Oostermeijer G., Quintana-Ascencio P.F., Stanley A., Ticktin T., Valverde T. & Williams J.L. (2011). How do plant ecologists use matrix population models? *Ecology Letters*, 14, 1-8.

Cunningham A.B. (2001). *Applied Ethnobotany: People, Wild Plant Use, and Conservation*. Earthscan, London.

Cunningham S.A. (1997). The effect of light environment, leaf area, and stored carbohydrates on inflorescence production by a rain forest understory palm. *Oecologia*, 111, 36-44.

Dahlgren J.P. & Ehrlén J. (2011). Incorporating environmental change over succession in an integral projection model of population dynamics of a forest herb. *Oikos*, 120, 1183-1190.

Das A., Krishnaswamy J., Bawa K., Kiran M.C., Srinivas V., Kumar N.S. & Karanth K.U. (2006). Prioritisation of conservation areas in the Western Ghats, India. *Biological Conservation*, 133, 16-31.

Dave C. & Jhala Y. (2011). Is competition with livestock detrimental for native wild ungulates? A case study of chital (*Axis axis*) in Gir Forest, India. *Journal of Tropical Ecology*, 27, 239-247.

Davidar P., Sahoo S., Mammen P.C., Acharya P., Puyravaud J.-P., Arjunan M., Garrigues J.P. & Roessingh K. (2010). Assessing the extent and causes of forest degradation in India: Where do we stand? *Biological Conservation*, 143, 2937-2944.

De Bello F., Lavorel S., Albert C.H., Thuiller W., Grigulis K., Dolezal J., Janeček Š. & Lepš J. (2011). Quantifying the relevance of intraspecific trait variability for functional diversity. *Methods in Ecology and Evolution*, 2, 163-174.

de Steven D. (1989). Genet and ramet demography of *Oenocarpus mapora* ssp. *mapora*, a clonal palm of Panamanian tropical moist forest. *Journal of Ecology*, 77, 579-596.

DeFries R.S., Foley J.A. & Asner G.P. (2004). Land-use choices: Balancing human needs and ecosystem function. *Frontiers in Ecology and the Environment*, 2, 249-257.

Díaz S. & Cabido M. (2001). Vive la différence: Plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution*, 16, 646-655.

Díaz S., Fargione J., Chapin F.S. & Tilman D. (2006). Biodiversity loss threatens human well-being. *PLoS biology*, 4, 1300-1305.

Díaz S., Lavorel S., McIntyre S., Falczuk V., Casanoves F., Milchunas D.G., Skarpe C., Rusch G., Sternberg M., Noy-Meir I., Landsberg J., Zhang W., Clark H. & Campbell B.D. (2007). Plant trait responses to grazing – A global synthesis. *Global Change Biology*, 13, 313-341.

Didham R.K., Tylianakis J.M., Gemmell N.J., Rand T.A. & Ewers R.M. (2007). Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology and Evolution*, 22, 489-96.

Eager E.A., Rebarber R. & Tenhumberg B. (2011). Choice of density-dependent seedling recruitment function affects predicted transient dynamics: A case study with Platte thistle. *Theoretical Ecology*, 1-15.

Easterling M.R., Ellner S.P. & Dixon P.M. (2000). Size-specific sensitivity: Applying a new structured population model. *Ecology*, 81, 694-708.

Elderd B.D. & Doak D.F. (2006). Comparing the direct and community-mediated effects of disturbance on plant population dynamics: Flooding, herbivory and *Mimulus guttatus*. *Journal of Ecology*, 94, 656-669.

Ellis E.C. & Ramankutty N. (2008). Putting people in the map: Anthropogenic biomes of the world. *Frontiers in Ecology and the Environment*, 6, 439-447.

Ellner S.P. & Rees M. (2006). Integral projection models for species with complex demography. *American Naturalist*, 167, 410-28.

Elmqvist T., Folke C., Nyström M., Peterson G., Bengtsson J., Walker B. & Norberg J. (2003). Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, 1, 488-494.

Endress B.A., Gorchov D.L. & Berry E.J. (2006). Sustainability of a non-timber forest product: Effects of alternative leaf harvest practices over 6 years on yield and demography of the palm *Chamaedorea radicalis*. *Forest Ecology and Management*, 234, 181-191.

Endress B.A., Gorchov D.L. & Noble R.B. (2004). Non-timber forest product extraction: Effects of harvest and browsing on an understory palm. *Ecological Applications*, 14, 1139-1153.

Estrada A. & Coates-Estrada R. (1997). Anthropogenic landscape changes and avian diversity at Los Tuxtlas, Mexico. *Biodiversity and Conservation*, 43, 19-43.

Ezard T.H.G., Bullock J.M., Dalgleish H.J., Millon A., Pelletier F., Ozgul A. & Koons D.N. (2010). Matrix models for a changeable world: The importance of transient dynamics in population management. *Journal of Applied Ecology*, 47, 515-523.

FAO (2010). *Global Forest Resources Assessment 2010: Main Report*. Food and Agriculture Organization of the United Nations, Rome, Italy, p. 378.

Farrington S.J., Muzika R.-M., Drees D. & Knight T.M. (2009). Interactive effects of harvest and deer herbivory on the population dynamics of American ginseng. *Conservation Biology*, 23, 719-728.

Flynn D.F.B., Gogol-Prokurat M., Nogeire T., Molinari N., Richers B.T., Lin B.B., Simpson N., Mayfield M.M. & DeClerck F. (2009). Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters*, 12, 22-33.

Foley J.A., Defries R., Asner G.P., Barford C., Bonan G., Carpenter S.R., Chapin F.S., Coe M.T., Daily G.C., Gibbs H.K., Helkowski J.H., Holloway T., Howard E.A., Kucharik C.J., Monfreda C., Patz J.A., Prentice I.C., Ramankutty N. & Snyder P.K. (2005). Global consequences of land use. *Science*, 309, 570-574.

Franco M. & Silvertown J. (2004). A comparative demography of plants based upon elasticities of vital rates. *Ecology*, 85, 531-538.

Frazer G.W., Canham C.D., Sallaway P. & Marinakis D. (1999). Gap Light Analyzer. In. Simon Fraser University and Institute of Ecosystem Studies, Burnaby, Canada and Millbook, New York.

Fuhlendorf S.D., Engle D.M., Kerby J.A.Y. & Hamilton R. (2009). Pyric herbivory: Rewilding landscapes through the recoupling of fire and grazing. *Conservation Biology*, 23, 588-598.

Fulé P.Z., Ramos-Gómez M., Cortés-Montaño C. & Miller A.M. (2011). Fire regime in a Mexican forest under indigenous resource management. *Ecological Applications*, 21, 764-775.

Gadgil M. (1992). Conserving biodiversity as if people matter: A case study from India. *Ambio*, 21, 266-270.

Gadgil M. & Vartak V. (1976). The sacred groves of Western Ghats in India. *Economic Botany*, 30, 152-160.

Gamble J.S., Dunn S.T. & Fischer C.E.C. (1967). *Flora of the Presidency of Madras*. 2 edn. Botanical Survey of India, Calcutta.

Gaoue O.G. & Ticktin T. (2007). Patterns of harvesting foliage and bark from the multipurpose tree *Khaya senegalensis* in Benin: Variation across ecological regions and its impacts on population structure. *Biological Conservation*, 137, 424-436.

Gardner T.A., Barlow J., Chazdon R., Ewers R.M., Harvey C.A., Peres C.A. & Sodhi N.S. (2009). Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters*, 12.

Garnier E., Cortez J., Billès G., Navas M.-L., Roumet C., Debussche M., Laurent G., Blanchard A., Aubry D., Bellmann A., Neill C. & Toussaint J.-P. (2004). Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, 85, 2630-2637.

Gascon C., Lovejoy T.E., Bierregaard Jr. R.O., Malcolm J.R., Stouffer P.C., Vasconcelos H.L., Laurance W.F., Zimmerman B., Tocher M. & Borges S. (1999). Matrix habitat and species richness in tropical forest remnants. *Biological Conservation*, 91, 223-229.

Gaston K.J. (2010). Valuing common species. *Science*, 327, 154-155.

Gaston K.J. & Fuller R.A. (2008). Commonness, population depletion and conservation biology. *Trends in Ecology and Evolution*, 23, 14-19.

Girish M.R. & Girish M. (2009). Non-timber forest products and tribal livelihoods – An economic study in the Western Ghats region of Karnataka, India. In: *Non-timber Forest Products: Conservation, Management and Policy in the Tropics* (eds. Uma Shaanker R, Hiremath AJ, Joseph GC & Rai ND). Ashoka Trust for Research In Ecology and the Environment, Bangalore, India, pp. 211-223.

Grace J.B. (1999). The factors controlling species density in herbaceous plant communities: An assessment. *Perspectives in Plant Ecology, Evolution and Systematics*, 2, 1-28.

Guedje N., P. A. Zuidema, H. During, B. Foahom, J. Lejoly & Marie N. (2007). Tree bark as a non-timber forest product: The effect of bark collection on population structure and dynamics of *Garcinia lucida* Vesque. *Forest Ecology and Management*, 240, 1-12.

Gurvich D.E., Enrico L. & Cingolani A.M. (2005). Linking plant functional traits with post-fire sprouting vigour in woody species in central Argentina. *Austral Ecology*, 30, 789-796.

Hartnett D.C., Steuter A.A. & Hickman K.R. (1997). Comparative ecology of native and introduced ungulates. In: *Ecology and Conservation of Great Plains Vertebrates* (eds. Knopf FL & Samson FB). Springer-Verlag, New York, pp. 72-104.

Hawkes C.V. & Sullivan J.J. (2001). The impact of herbivory on plants in different resource conditions: A meta-analysis. *Ecology*, 82, 2045-2058.

Heckel C.D., Bourg N.A., McShea W.J. & Kalisz S. (2010). Non-consumptive effects of a generalist ungulate herbivore drive decline of unpalatable forest herbs. *Ecology*, 91, 319-326.

Hector A. & Bagchi R. (2007). Biodiversity and ecosystem multifunctionality. *Nature*, 448, 188-90.

Hegde R., Suryaprakash S., Achoth L. & Bawa K.S. (1996). Extraction of non-timber forest products in the forests of Biligiri Rangan Hills, India. 1. Contribution to rural income. *Economic Botany*, 50, 243-251.

Hegland S.J., Jongejans E., Rydgren K., Joar S. & Eelke H. (2010). Investigating the interaction between ungulate grazing and resource effects on *Vaccinium myrtillus* populations with integral projection models. *Oecologia*, 163, 695-706.

Henry H.A.L., Chiariello N.R., Vitousek P.M., Mooney H.A. & Field C.B. (2006). Interactive effects of fire, elevated carbon dioxide, nitrogen deposition, and precipitation on a California annual grassland. *Ecosystems*, 9, 1066-1075.

Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G. & Jarvis A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25, 1965-1978.

Hillebrand H., Bennett D.M. & Cadotte M.W. (2008). Consequences of dominance: A review of evenness effects on local and regional ecosystem processes. *Ecology*, 89, 1510-1520.

Hiremath A.J. & Sundaram B. (2005). The fire-lantana cycle hypothesis in Indian forests. *Conservation and Society*, 3, 26-42.

Hobbs N.T. (1996). Modification of ecosystems by ungulates. *Journal of Wildlife Management*, 60, 695-713.

Holdo R.M., Holt R.D. & Fryxell J.M. (2009). Grazers, browsers, and fire influence the extent and spatial pattern of tree cover in the Serengeti. *Ecological Applications*, 19, 95-109.

Horvitz C.C. & Schemske D.W. (1995). Spatiotemporal variation in demographic transitions of a tropical understory herb: Projection matrix analysis. *Ecological Monographs*, 65, 155-192.

Howe H.F. & Miriti M.N. (2004). When seed dispersal matters. *BioScience*, 54, 651-660.

Isbell F., Calcagno V., Hector A., Connolly J., Harpole W.S., Reich P.B., Scherer-Lorenzen M., Schmid B., Tilman D., Ruijven J.V., Weigelt A., Wilsey B.J., Zavaleta E.S., Loreau M. & van Ruijven J. (2011). High plant diversity is needed to maintain ecosystem services. *Nature*, 47, 199-202.

Jongejans E. & De Kroon H. (2005). Space versus time variation in the population dynamics of three co-occurring perennial herbs. *Journal of Ecology*, 93, 681-692.

Jongejans E., Jorritsma-Wienk L.D., Becker U., Dostal P., Milden M., De Kroon H., Milde M. & Kroon H.D. (2010). Region versus site variation in the population dynamics of three short-lived perennials. *Journal of Ecology*, 98, 279-289.

Joyal E. (1996). The palm has its time: An ethnoecology of *Sabal uresana* in Sonora, Mexico. *Economic Botany*, 50, 446-442.

Kareiva P., Watts S., McDonald R. & Boucher T. (2007). Domesticated nature: Shaping landscapes and ecosystems for human welfare. *Science*, 316, 1866-1869.

Kathriarachchi H.S., Tennakoon K.U., Gunatilleke C.V.S., Gunatilleke I.A.U.N. & Ashton P.M.S. (2004). Ecology of two selected liana species of utility value in a lowland rain forest of Sri Lanka: Implications for management. *Conservation and Society*, 2, 273-288.

Keddy P.A. (1992). Assembly and response rules: Two goals for predictive community ecology. *Journal of Vegetation Science*, 3, 157-164.

Keystone Foundation (2009). *Report on Status of Village Forest Councils in the Nilgiri Biosphere Reserve – International Development Research Centre Case Study*. Keystone Foundation, Kotagiri, Tamil Nadu, India.

Kinnaird M.F. (1992). Competition for a forest palm: Use of *Phoenix reclinata* by human and nonhuman primates. *Conservation Biology*, 6, 101-107.

Kirkpatrick J., Marsden-Smedley J. & Leonard S. (2011). Influence of grazing and vegetation type on post-fire flammability. *Journal of Applied Ecology*, 48, 642-649.

Knight T.M. (2004). The effects of herbivory and pollen limiation on a declining population of *Trillium grandiflorum*. *Ecological Applications*, 14, 915-928.

Kodandapani N., Cochrane M.A. & Sukumar R. (2004). Conservation threat of increasing fire frequencies in the Western Ghats, India. *Conservation Biology*, 18, 1553-1561.

Kodandapani N., Cochrane M.A. & Sukumar R. (2009). Forest fire regimes and their ecological effects in seasonally dry tropical ecosystems in the Western Ghats, India. *Tropical Fire Ecology*, 335-354.

Kumar R. & Shahabuddin G. (2005). Effects of biomass extraction on vegetation structure, diversity and composition of forests in Sariska Tiger Reserve, India. *Environmental Conservation*, 32, 248.

Lagendijk G., Page B.R. & Slotow R. (2012). Short-term effects of single species browsing release by different-sized herbivores on sand forest vegetation community, South Africa. *Biotropica*, 44, 63-72.

Laliberté E., Declerck F., Metcalfe J., Catterall C.P., Sa D., Wells J.A., Metcalfe D.J., Queiroz C., Aubin I., Bonser S.P., Ding Y., Fraterrigo J.M., McNamara S., Morgan J.W., Merlos D.S., Vesk P.a. & Mayfield M.M. (2010). Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecology Letters*, 13, 76-86.

Laliberté E. & Legendre P. (2011). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91, 299-305.

Laliberté E. & Shipley B. (2011). FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-11.

Laughlin D.C. (2011). Nitrification is linked to dominant leaf traits rather than functional diversity. *Journal of Ecology*, 99, 1091-1099.

Lavorel S., Díaz S., Cornelissen J.H.C., Garnier E., Harrison S.P., Mcintyre S., Pausas J.G., Catherine N.P.-H. & Carlos R. (2007). Plant functional types: Are we getting any closer to the Holy Grail? In: *Terrestrial Ecosystems in a Changing World* (eds. Canadell JG, Pataki D & Pitelka L). Springer-Verlag, Berlin, pp. 149-160.

Lavorel S. & Garnier E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*, 16, 545-556.

Leisher C., Sanjayan M., Blockhus J., Kontoleon A. & Larsen S.N. (2010). *Does Conserving Biodiversity Work to Reduce Poverty? A State of Knowledge Review.* The Nature Conservancy, Washington, D.C., p. 32.

Lin B.B., Flynn D.F.B., Bunker D.E., Uriarte M. & Naeem S. (2011). The effect of agricultural diversity and crop choice on functional capacity change in grassland conversions. *Journal of Applied Ecology*, 48, 609-618.

Littell R.C., Milliken G.A., Stroup W.W., Wolfinger R.D. & Schabenberger O. (2006). *SAS for Mixed Models*. 2nd edn. SAS Institute, Inc., Cary, NC.

Lopez-Toledo L., Horn C. & Endress B.A. (2011). Distribution and population patterns of the threatened palm *Brahea aculeata* in a tropical dry forest in Sonora, Mexico. *Forest Ecology and Management*, 261, 1901-1910.

Loreau M., Naeem S., Inchausti P., Bengtsson J., Grime J., Hector A., Hooper D., Huston M., Raffaelli D., Schmid B., Tilman D. & Wardle A. (2001). Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science*, 294, 804-808.

Luck G.W., Harrington R., Harrison P.A., Kremen C., Berry P.M., Bugter R., Dawson T.R., Bello F., Díaz S., Feld C.K. & others (2009). Quantifying the contribution of organisms to the provision of ecosystem services. *Bioscience*, 59, 223-235.

Mace G.M., Norris K. & Fitter A.H. (2011). Biodiversity and ecosystem services: A multilayered relationship. *Trends in Ecology and Evolution*, 27, 19-26.

Madhusudan M.D. (2004). Recovery of wild large herbivores following livestock decline in a tropical Indian wildlife reserve. *Journal of Applied Ecology*, 41, 858-869.

Madhusudan M.D. (2005). The global village: Linkages between international coffee markets and grazing by livestock in a South Indian wildlife reserve. *Conservation Biology*, 19, 411-420.

Maron J.L. & Crone E.E. (2006). Herbivory: Effects on plant abundance, distribution and population growth. *Proceedings of the Royal Society B: Biological Sciences*, 273, 2575-2584.

Martínez-Ramos M., Anten N.P.R.R., Ackerly D.D., Martı M. & Nin E.E. (2009). Defoliation and ENSO effects on vital rates of an understorey tropical rain forest palm. *Journal of Ecology*, 97, 1050-1061.

Matthew K.M. (1983). *The Flora of the Tamilnadu Carnatic*. St. Joseph's College, Tiruchirapalli, India.

Matthew K.M. (1995). *An Excursion Flora of Central Tamilnadu, India*. Balkema, Rotterdam.

Mayer A.L. & Khalyani A.H. (2011). Grass trumps trees with fire. *Science*, 334, 188-189.

Mayfield M.M., Ackerly D.D. & Daily G.C. (2006). The diversity and conservation of plant reproductive and dispersal functional traits in human-dominated tropical landscapes. *Journal of Ecology*, 94, 522-536.

Mayfield M.M., Boni M.F., Daily G.C. & Ackerly D. (2005). Species and functional diversity of native and human-dominated plant communities. *Ecology*, 86, 2365-2372.

Mayfield M.M., Bonser S.P., Morgan J.W., Aubin I., McNamara S. & Vesk P.A. (2010). What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. *Global Ecology and Biogeography*, 19, 423-431.

Mayfield M.M. & Daily G.C. (2005). Countryside biogeography of neotropical herbaceous and shrubby plants. *Ecological Applications*, 15, 423-439.

Mazorelle M.J. (2011). AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 1.21.

McGraw J.B. & Furedi M.A. (2005). Deer browsing and population viability of a forest understory plant. *Science*, 307, 920-922.

McIntyre S., Lavorel S., Landsberg J. & Forbes T.D.A. (1999). Disturbance response in vegetation: Towards a global perspective on functional traits. *Journal of Vegetation Science*, 10, 621-630.

McKinney M. & Lockwood J. (1999). Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution*, 14, 450-453.

Menges E.S. (2000). Population viability analyses in plants: Challenges and opportunities. *Trends in Ecology and Evolution*, 15, 51-56.

Menges E.S. (2007). Integrating demography and fire management: An example from Florida scrub. *Australian Journal of Botany*, 55, 261-272.

Midgley J.J., Lawes M.J. & Chamaillé-Jammes S. (2010). Savanna woody plant dynamics: The role of fire and herbivory, separately and synergistically. *Australian Journal of Botany*, 58, 1-11.

Millennium Ecosystem Assessment (2005). *Ecosystems and Human Well-being: Synthesis*. Island Press, Washington, D.C.

Mittermeier R.A., Gil P.R., Hoffman M., Pilgrim J., Brooks T., Mittermeier C.G., Lamoreux J. & Da Fonseca G.A.B. (2005). *Hotspots revisited: Earth's biologically richest and most endangered terrestrial ecoregions*. Conservation International, Arlington, Virginia.

Mogenburg S.M. & Levey D.J. (2003). Do frugivores respond to fruit harvest? An experimental study of short-term responses. *Ecology*, 84, 2600-2612.

Moloney K.A. (1986). A generalized algorithm for determining category size. *Oecologia*, 69, 176-180.

Montúfar R., Anthelme F., Pintaud J.-C. & Balslev H. (2011). Disturbance and resilience in tropical American palm populations and communities. *The Botanical Review*, 77, 426-461.

Mora C. & Sale P.F. (2011). Ongoing global biodiversity loss and the need to move beyond protected areas: A review of the technical and practical shortcomings of protected areas on land and sea. *Marine Ecology Progress Series*, 434, 251-266.

Murali K.S., Shankar U., Uma Shaanker R., Ganeshaiah K.N. & Bawa K.S. (1996). Extraction of non-timber forest products in the forests of Biligiri Rangan Hills, India. 2. Impact of NTFP extraction on regeneration, population structure, and species composition. *Economic botany*, 50, 252-269.

Murphy P.G. & Lugo A.E. (1986). Ecology of tropical dry forest. *Annual Review of Ecology and Systematics*, 17, 67-88.

Myers N. (1988). Tropical forests: Much more than stocks of wood. *Journal of Tropical Ecology*, 4, 209-221.

Myers N., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A.B. & Kent J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853-858.

Naidoo R., Balmford A., Costanza R., Fisher B., Green R.E., Lehner B., Malcolm T.R. & Ricketts T.H. (2008). Global mapping of ecosystem services and conservation priorities. *Proceedings of the National Academy of Sciences*, 105, 9495.

Nath S. (2000). Non timber forest products in the Nilgiris – A case for local resource management. *Voices from the Forest*, 8, 5-10.

NREGA (The National Rural Employment Guarantee Act). (2005). No. 43, India Code (2004)

O'Hara J.L. (1999). A*n Ecosystem Approach to Monitoring Non-Timber Forest Products Harvest: The Case Study of Bayleaf Palm (*Sabal mauritiiformis*) In the Rio Bravo Conservation and management Area, Belize*. Ph.D. thesis. Yale University, New Haven, Connecticut.

Oba G., Mengistu Z. & Stenseth N.C. (2000). Compensatory growth of the African dwarf shrub *Indigofera spinosa* following simulated herbivory. *Ecological Applications*, 10, 1133-1146.

Odadi W.O., Karachi M.K., Abdulrazak S.A. & Young T.P. (2011). African wild ungulates compete with or facilitate cattle depending on season. *Science*, 333, 1753-1755.

Oesterheld M., Sala O.E. & McNaughton S.J. (1992). Effect of animal husbandry on herbivore-carrying capacity at a regional scale. *Nature*, 356, 234-236.

Oksanen J., Guillaume F., Blanchet R.K., Legendre P., Minchin P.R., O'Hara R.B., Simpson G.L., Solymos P., Wagner M., Stevens H.H. & Wagner H. (2011). vegan: Community ecology package. R package version 2.0-2.

Olden J.D. (2006). Biotic homogenization: A new research agenda for conservation biogeography. *Journal of Biogeography*, 33, 2027-2039.

Olden J.D., Leroy Poff N., Douglas M.R., Douglas M.E. & Fausch K.D. (2004). Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution*, 19, 18-24.

Olff H. & Ritchie M.E. (1998). Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution*, 13, 261-265.

Padmanabhan D. & Sudhersan C. (1988). Mass destruction of *Phoenix loureirii* in South India. *Principes*, 32, 118-123.

Petchey O.L. & Gaston K.J. (2006). Functional diversity: Back to basics and looking forward. *Ecology Letters*, 9, 741-758.

Peterson D.W. & Reich P.B. (2007). Fire frequency and tree canopy structure influence plant species diversity in a forest-grassland ecotone. *Plant Ecology*, 194, 5-16.

Pfister C.A. & Wang M. (2005). Beyond size: Matrix projection models for populations where size is an incomplete descriptor. *Ecology*, 86, 2673-2683.

Pickett S.T.A. & White P.S. (1985). *The ecology of natural disturbance and patch dynamics*. Academic Press, San Diego.

Pinheiro J., Bates D., DebRoy S., Sarkar D. & R Development Core Team (2011). nlme: Linear and nonlinear mixed effects models. R package version 3.1-102.

Polasky S., Calderone G., Duarte T.K., Goldstein J., Hannahs N., Ricketts T. & Tallis H. (2011). Putting ecosystem service models to work: Conservation, management and trade-offs. In: *Natural Capital: Theory and Practice of Mapping Ecosystem Services* (eds. Karieva P, Tallis H, Ricketts TH, Daily GC & Polasky S). Oxford University Press, Oxford, pp. 249-263.

Pulido M.T., Valverde T. & Caballero J. (2007). Variation in the population dynamics of the palm *Sabal yapa* in a landscape shaped by shifting cultivation in the Yucatan Peninsula, Mexico. *Journal of Tropical Ecology*, 23, 139.

Quintana-Ascencio P.F. & Morales-Hernández M. (1997). Fire-mediated effects of shrubs, lichens and herbs on the demography of *Hypericum cumulicola* in patchy Florida scrub. *Oecologia*, 112, 263-271.

R Development Core Team (2011). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing Vienna, Austria.

Ranganathan J., Daniels R.J.R., Chandran M.D.S., Ehrlich P.R. & Daily G.C. (2008). Sustaining biodiversity in ancient tropical countryside. *Proceedings of the National Academy of Sciences*, 105, 17852-17854.

Ratnam J., Bond W.J., Fensham R.J., Hoffmann W.A., Archibald S., Lehmann C.E.R., Anderson M.T., Higgins S.I. & Sankaran M. (2011). When is a 'forest' a savanna, and why does it matter? *Global Ecology and Biogeography*, 20, 653-660.

Ratsirarson J., Silander J.A. & Richard A.F. (1996). Conservation and management of a threatened Madagascar palm species, *Neodypsis decaryi*, Jumelle. *Conservation Biology*, 10, 40-52.

Rebarber R., Tenhumberg B. & Townley S. (2011). Global asymptotic stability of density dependent integral population projection models. *Theoretical Population Biology*, 81, 81-87.

Reddy C.S., Bagyanarayana G., Reddy K. & Raju V.S. (2008). *Invasive Alien Flora of India.* National Biological Information Infrastructure, United States Geological Survey, p. 35.

Reid L.A. (2005). *The Effects of Traditional Harvesting Practices on Restored Sweetgrass Populations*. M.S. thesis. State University of New York, Syracuse, NY, p. 73.

Rooney T.P. & Waller D.M. (2003). Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management*, 181, 165-176.

Rose K.E., Louda S.M. & Rees M. (2005). Demographic and evolutionary impacts of native and invasive insect herbivores on *Cirsium canescens*. *Ecology*, 86, 453-465.

Rose K.E., Russell F.L. & Louda S.M. (2011). Integral projection model of insect herbivore effects on *Cirsium altissimum* populations along productivity gradients. *Ecosphere*, 2, 1-19.

Roveta R.J. (2008). Traditional use of fire for the provision of ecosystem services: A case study in BRT Wildlife Sanctuary, India. In, p. 96.

Royal Botanic Gardens Kew (2008). Seed Information Database (SID) Version 7.1. Available online at http://data.kew.org/sid/.

Saha S. & Howe H.F. (2003). Species composition and fire in a dry deciduous forest. *Ecology*, 84, 3118-3123.

Sampaio M.B. & Scariot A. (2010). Effects of stochastic herbivory events on population maintenance of an understorey palm species (*Geonoma schottiana*) in riparian tropical forest. *Journal of Tropical Ecology*, 26, 151.

Sanderson E.W., Jaiteh M., Levy M.a., Redford K.H., Wannebo A.V. & Woolmer G. (2002). The human footprint and the last of the wild. *BioScience*, 52, 891.

Sankaran M. (2005). Fire, grazing and the dynamics of tall-grass savannas in the Kalakad-Mundanthurai Tiger Reserve, South India. *Conservation and Society*, 3, 4-25.

Sax D.F. & Gaines S.D. (2003). Species diversity: From global decreases to local increases. *Trends in Ecology and Evolution*, 18, 561-566.

Sax D.F., Stachowicz J.J., Brown J.H., Bruno J.F., Dawson M.N., Gaines S.D., Grosberg R.K., Hastings A., Holt R.D., Mayfield M.M., O'Connor M.I. & Rice W.R. (2007). Ecological and evolutionary insights from species invasions. *Trends in Ecology and Evolution*, 22, 465-471.

Saxena N.C. (1999). *Forest Policy of India*. WWF-India and International Institute for Environment and Development, New Delhi, p. 44.

Schleuning M., Huamán V. & Matthies D. (2008). Flooding and canopy dynamics shape the demography of a clonal Amazon understorey herb. *Journal of Ecology*, 96, 1045-1055.

Schmerbeck J. & Seeland K. (2007). Fire supported forest utilisation of a degraded dry forest as a means of sustainable local forest management in Tamil Nadu, South India. *Land Use Policy*, 24, 62-71.

Schmidt I.B. (2011). *Effects of Local Ecological Kowledge, Harvest and Fire on Golden-grass (*Syngonanthus nitens*, Eriocaulaceae), a Non-Timber Forest Product (NTFP) Species from the Brazilian Savanna*. Ph.D. thesis. University of Hawai‘i at Mānoa Honolulu, Hawai‘i, p. 212.

Schmidt I.B., Benedetti F.I. & Scariot A. (2007). Ethnobotany and effects of harvesting on the population ecology of *Sygonanthus nitens* (Bong.) Ruhland (Eriocaulaceae), a NTFP from Jalapão Region, Central Brazil. *Economic Botany*, 61, 73-85.

Schmidt I.B., Mandle L., Ticktin T. & Gaoue O.G. (2011). What do matrix population models reveal about the sustainability of non-timber forest product harvest? *Journal of Applied Ecology*, 48, 815-826.

Schmitt C., Senbeta F. & Denich M. (2010). Wild coffee management and plant diversity in the montane rainforest of southwestern Ethiopia. *African Journal of Ecology*, 48.

Sensenig R.L., Demment M.W. & Laca E.A. (2010). Allometric scaling predicts preferences for burned patches in a guild of East African grazers. *Ecology*, 91, 2898-2907.

Shaanker R.U., Ganeshaiah K.N., Krishnan S., Ramya R., Meera C., Aravind N.A., Kumar A., Rao D., Vanaraj G., Ramachandra J., Gauthier R., Ghazoul J., Poole N. & Reddy B.V.C. (2004a). Livelihood gains and ecological costs of non-timber forest product dependence: Assessing the roles of dependence, ecological knowledge and market structure in three contrasting human and ecological settings in South India. *Environmental Conservation*, 31, 242-253.

Shaanker R.U., Ganeshaiah K.N., Rao M.N. & Aravind N.A. (2004b). Ecological consequences of forest use: From genes to ecosystem – A case study in the Biligiri Rangaswamy Temple Wildlife Sanctuary, South India. *Conservation and Society*, 2, 347-363.

Shackleton C.M., Parkin F., Chauke M.I., Downsborough L., Oslen A., Brill G. & Weideman C. (2009). Conservation, commercialisation and confusion: Harvesting of *Ischyrolepis* in a coastal forest, South Africa. *Environmental Development and Sustainability*, 11, 229-240.

Shackleton S.E. (2005*). The significance of the local trade in natural resource products for livelihoods and poverty alleviation in South Africa*. Ph.D. thesis. Rhodes University Grahamstown, South Africa, p. 287.

Shankar U., Hegde R. & Bawa K.S. (1998a). Extraction of non-timber forest products in the forests of Biligiri Rangan Hills, India. 6. Fuelwood pressure and management options. *Economic Botany*, 52, 320-336.

Shankar U., Murali K., Shaanker R.U., Ganeshaiah K. & Bawa K.S. (1998b). Extraction of non-timber forest products in the forests of Biligiri Rangan Hills, India. 4. Impact on floristic diversity and population structure in a thorn scrub forest. *Economic Botany*, 52, 302-315.

Sinha A. & Brault S. (2005). Assessing sustainability of nontimber forest product extractions: How fire affects sustainability. *Biodiversity and Conservation*, 14, 3537-3563.

Sousa W.P. (1984). The role of disturbance in natural communities. *Annual Review of Ecology and Systematics*, 15, 353-391.

Souza A.F. & Martins F.R. (2004). Population structure and dynamics of a neotropical palm in fire-impacted fragments of the Brazilian Atlantic Forest. *Biodiversity and Conservation*, 1611-1632.

Staver A.C., Bond W.J., Stock W.D., Van Rensburg S.J. & Waldram M.S. (2009). Browsing and fire interact to suppress tree density in an African savanna. *Ecological Applications*, 19, 1909-19.

Stevens P.F. (2011). Angiosperm Phylogeny Website. Version 11. Available online at http://www.mobot.org/mobot/research/apweb.

Stott I., Townley S. & Hodgson D.J. (2011). A framework for studying transient dynamics of population projection matrix models. *Ecology Letters*, 959-970.

Stubben C. & Milligan B. (2007). Estimating and analyzing demographic models using the popbio Package in R. *Journal of Statistical Software*, 22, 1-23.

Sukumar R. (1990). Ecology of the Asian elephant in southern India. II. Feeding habits and crop raiding patterns. *Journal of Tropical Ecology*, 6, 33-53.

Sundararaj D.D. & Balasubramanyam G. (1986). *Guide to the Economic Plants of South India*. Periodical Expert Book Agency, Delhi, India.

ter Steege H. & Hammond D.S. (2001). Character convergence, diversity, and disturbance in tropical rain forest in Guyana. *Ecology*, 82, 3197-3212.

Terborgh J., Nunez-Iturri G., Pitman N.C.A., Valverde F.H.C., Alvarez P., Swamy V., Pringle E.G. & Paine C.E.T. (2008). Tree recruitment in an empty forest. *Ecology*, 89, 1757-1768.

Ticktin T. (2004). The ecological implications of harvesting non-timber forest products. *Journal of Applied Ecology*, 41, 11-21.

Ticktin T. & Nantel P. (2004). Dynamics of harvested populations of the tropical understory herb *Aechmea magdalenae* in old-growth versus secondary forests. *Biological Conservation*, 120, 461-470.

Tilman D., Lehman C.L. & Thomson K.T. (1997). Plant diversity and ecosystem productivity: Theoretical considerations. *Proceedings of the National Academies of Sciences*, 94.

Toniato M.T.Z. & de Oliveira-Filho A.T. (2004). Variations in tree community composition and structure in a fragment of tropical semideciduous forest in southeastern Brazil related to different human disturbance histories. *Forest Ecology and Management*, 198, 319-339.

Tscharntke T., Klein A.M., Kruess A., Steffan-Dewenter I. & Thies C. (2005). Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. *Ecology Letters*, 8, 857-874.

Vandenberghe C., Freléchoux F. & Buttler A. (2008). The influence of competition from herbaceous vegetation and shade on simulated browsing tolerance of coniferous and deciduous saplings. *Oikos*, 117, 415-423.

Vandermeer J. (1978). Choosing category size in a stage projection matrix. *Oecologia*, 32, 79-84.

Varghese A., Krishnamurthy V. & Ticktin T. (in press). Harvest, use and ecology of *Cycas cirincalis* L. – A case study in the Nilgiri Biosphere Reserve. *Botanical Review*.

Varghese A. & Ticktin T. (2008). Regional variation in non-timber forest product harvest strategies, trade, and ecological impacts: The case of black dammar (*Canarium strictum* Roxb.) use and conservation in the Nilgiri Biosphere Reserve, India. *Ecology and Society*, 13, 11.

Venables, W. N., & Ripley B.D. (2002). *Modern Applied Statistics with S*. 4th edn. Springer, New York.

Villéger S., Mason N.W.H. & Mouillot D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89, 2290-2301.

Weiher E., van der Werf A., Thompson K., Roderick M., Garnier E. & Eriksson O. (1999). Challenging Theophrastus: A common core list of plant traits for functional ecology. *Journal of Vegetation Science*, 10, 609-620.

Westoby M., Falster D.S., Moles A.T., Vesk P.a. & Wright I.J. (2002). Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, 33, 125-159.

Whelan R.J. (1995). *The Ecology of Fire*. Cambridge University Press, Cambridge.

Widayati A. & Carlisle B. (2012). Impacts of rattan cane harvesting on vegetation structure and tree diversity of Conservation Forest in Buton, Indonesia. *Forest Ecology and Management*, 266, 206-215.

Willis K.J. & Birks H.J.B. (2006). What Is natural? The need for a long-term perspective in biodiversity conservation. *Science*, 314, 1261-1265.

Wilsey B.J. (1996). Variation in use of green flushes following burns among African ungulate species: The importance of body size. *African Journal of Ecology*, 34, 32-38.

Winfree R., Cariveau D.P. & Bartomeus I. (2011). Native pollinators in anthropogenic systems. *Annual Review of Ecology, Evolution, and Systematics*, 42, 1-22.

Winter S.L., Fuhlendorf S.D., Goad C.L., Davis C.a., Hickman K.R. & Leslie Jr D.M. (2011). Restoration of the fire-grazing interaction in *Artemisia filifolia* shrubland. *Journal of Applied Ecology*, 49, 242-250.

Wisdom M.J., Vavra M., Boyd J.M., Hemstrom M.A., Ager A.A. & Johnson B.K. (2006). Understanding ungulate herbivory – Episodic disturbance effects on vegetation dynamics: Knowledge gaps and management needs. *Wildlife Society Bulletin*, 34, 283-292.

Wright S.J., Muller-Landau H.C., Calderón O. & Hernandéz A. (2005). Annual and spatial variation in seedfall and seedling recruitment in a neotropical forest. *Ecology*, 86, 848-860.

Yibarbuk D., Whitehead P.J., Russell-Smith J., Jackson D., Godjuwa C., Fisher A., Cooke P., Choquenot D. & Bowman D.M.J.S. (2001). Fire ecology and aboriginal land management in central Arnhem Land, Northern Australia: A tradition of ecosystem management. *Journal of Biogeography*, 28, 325-343.

Zanne A.E., Lopez-Gonzalez G., Coomes D.A., Ilic J., Jansen S., Lewis S.L., Miller R.B., Swenson N.G., Wiemann M.C. & Chave J. (2009). Data from: Towards a worldwide wood economics spectrum. Dryad Digital Repository. doi:105061/dryad/234.

Zhang C., Yang C. & Dong M. (2002). Clonal integration and its ecological significance in *Hedysarum laeve*, a rhizomatous shrub in Mu Us Sandland. *Journal of Plant Research*, 115, 0113-0118.

Zobel M. (1997). The relative role of species pools in determining plant species richness: An alternative explanation of species coexistence? *Trends in Ecology and Evolution*, 12, 266-269.

Zuidema Pieter A., Jongejans E., Chien P.D., During H.J. & Schieving F. (2010). Integral projection models for trees: A new parameterization method and a validation of model output. *Journal of Ecology*, 98, 345-355.

Zuidema P.A.A., de Kroon H. & Werger M.J.A. (2007). Testing sustainability by prospective and retrospective demographic analyses: Evaluation for palm leaf harvest. *Ecological Applications*, 17, 118-28.