Patterns and processes of Lantana camara *persistence in South Indian tropical dry forests*

Thesis submitted for the Degree of
Doctor of Philosophy

Thesis Submitted by
Bharath Sundaram

Reg No: 070900007

Thesis Submitted to
Manipal University
Manipal, 576104

Research carried out at
The Academy for Conservation Science and Sustainability Science
Ashoka Trust for Research in Ecology and the Environment (ATREE)
Bangalore

Acknowledgements

I am privileged to have enjoyed the fellowship offered by many people during the course of my doctoral research. My endeavor would not have seen fruition but for the help provided by these people.

Ankila Hiremath, my friend, philosopher, and guide. She has been a pillar of support throughout my studentship. Her constructive criticism and methodical thinking resulted in the improvement of all aspects of my work. Gladwin Joseph, member of my committee, for his unflagging encouragement. His keen eye for structure and detail has helped improve the way I write. Jagdish Krishnaswamy, member of my committee, for his valuable inputs at a stage when most of my ideas were half-baked. His inputs on experimental design and data analyses are of great value to me. Siddhartha Krishnan, for his help in the development of the chapter on Soliga local knowledge. He piloted me through uncharted waters, right from the design and implementation stages to the writing of the chapter. The same chapter also saw considerable improvement due to Nitin Rai's critical comments. Kavita Isvaran, for her patience and help with data analyses. My chapters on model selection to explain lantana invasions and on soil seed bank ecology would not be if not for her help. Devcharan Jathanna, black belt statistician and experiment designer, for his help and advice all the way through. M. C. Kiran, GIS analyst, for his help in assembling the GIS data that was the backbone of my work. R. Siddappa Setty, for sharing both his knowledge on BRT and his data on species distributions. His data set was invaluable in my research. Madhura Niphadkar, for making maps used in this thesis. N. A. Aravind's substantial help during the thesis submission stage helped me jump successfully through many an administrative hoop.

I greatly enjoyed the courses I took at ATREE, NCBS, and elsewhere, as part of my Ph.D. These courses provided much food for thought. Jagdish Krishnaswamy, Seema Purushothaman, Nitin Rai, Gladwin Joseph, Kartik Shanker, and Siddhartha Krishnan held courses at ATREE. Anindya Sinha and Mahesh Rangarajan taught courses at NCBS. I thank Ajith Kumar for letting me take these courses at NCBS. I also benefitted from the Statistics and Experimental design course conducted by Jason Tylianakis as part of the Association for Tropical Biology and Conservation meetings held in Malaysia and Thailand in 2007-08. I thank Rhett Harrison and Tomasso Savini for helping me get to these meetings from Bangalore.

My friends and colleagues at ATREE and elsewhere, Arundhati Das, Devcharan Jathanna, N. Samba Kumar, Robin Vijayan, Nandini Rajamani, Vivek Ramachandran, Kartik Shanker, Meera Anna Oommen, Nitin Rai, Mahesh Sankaran, Suhel Quader, Anirban Datta Roy, Ramesh Kannan, Ayesha Prasad, M. D. Madhusudan, Paramesha Mallegowda, Ravi Ramalingam, Dan Brockington, Ramesh Kannan, Samira Agnihotri, Muthatha Ramanathan, Pernille Sandemose, and C. Made Gowda were helpful in many ways during the course of my research. I enjoyed

their company, and enjoyed the many discussions I had with them about their research and mine. I offer my sincere apologies to Aarthi Sridhar, who has had to listen to first-cut versions of almost all my conference presentations related to my lantana work. Whether she likes it or not, she now knows much more about lantana than she would like.

The Writers' Bloc was created during August 2010 by Nandini Rajamani as an emergency measure to provide space for jaded thesis writers to enjoy coffee and snacks, and maybe get some writing done on the side. The Bloc invigorated my thesis writing, and ignited thoughts of a post-thesis-submission life, which in turn pushed me to write more.

When I was in New Delhi trying to get some writing done during May 2009, I came down with chicken pox, and was quarantined. Without Bansuri Taneja and Ankila's help during this time— which largely involved providing company, meals, and reading material — I would have either gone mad due to boredom or starved to death. This thesis was written because I survived, and thanks to them.

I would like to thank R. M Ray, Chief Wildlife Warden (retired) and R. Raju, Deputy Conservator of Forests (Chamrajnagar Wildlife Division), both of the Karnataka Forest Department, for facilitating my research in BRT.

T. R. Gopi, Sindhu Damodaran, Saji Damodaran, Umesha, Sunil, Ramesh N., and Lakshmikanthaiah N. provided crucial administrative and logistical support at various times during my research. These individuals kept ATREE's administrative machinery on a roll.

The International Foundation for Science, Sweden, and the Department of Science and Technology, India funded my field research. Grants to ATREE from the Jamsetji Tata Trust and Noragric partly funded my fellowship.

The BRT field station was my home for more than three years. Thanks to Renuka-amma, D. Rajanna, and Made Gowda for making the BRT field station a pleasure to work from. Field work at BRT was always going to be a challenge because of the terrain, and because of the thick lantana growth in most places. I would not have made it through—literally and figuratively— without the help of D. Kethe Gowda, M. Jadeya, Jade Swamy, R. Madeva, Nanje Gowda, M. Kethe Gowda, Jadeya 'Upendra' Gowda, M. R. Made Gowda, and Kumbhe Gowda. I owe much to these individuals for their help and for their cheerfulness in the face of adversity.

Much love to Amma, Appa, Sumi, Rakhi, and Chinna for all their love and support.

Executive summary

Invasive species have been recognized to be an important threat to biodiversity and ecosystem functioning. I examined the patterns of *Lantana camara* (hereafter, lantana) invasion and the effects of lantana invasion on native plant communities in a tropical dry forest in the Biligiri Rangaswamy Temple Wildlife Sanctuary (hereafter, BRT), Western Ghats, India. I then examined how patterns of lantana spread are related to factors such as disturbance (e.g., forest fires and historical habitat modification) and habitat structure. In order to link pattern with process, I investigated the role played by soil seed banks as a potential mechanism underlying lantana success in BRT. Lastly, I examined how local people perceive lantana invasions. I tabled results from both traditional ecological knowledge sources and scientific sources about the patterns and processes of lantana invasion and drew out implications for the future management of lantana-invaded landscapes.

Data on the distribution of lantana and native species in 1997 came from an existing study. In 1997, the entire 540 km^2 study area was overlaid with a 2-km grid to yield 134 cells, and an 80 m x 5 m plot was established in the centre of each grid cell. I re-visited the same set of plots in 2008 to arrive at the change in the density and distribution of lantana and native species. Additionally, I explored the effects of lantana density on the native woody species community, particularly diversity, abundance, evenness, size class distribution, and relative dominance. Over 11 years there was a tremendous increase in lantana abundance and density. Lantana was present in only 41% of plots inventoried in 1997, but by 2008 lantana had spread to 81 % of all plots. Lantana invasion was accompanied by a reduction in native species density and diversity. Lantana invasion was also accompanied by a reduction in evenness in the native community. In addition there was evidence for drastic reductions in the regenerating size classes of trees, suggesting that tree population declines may occur in the future. Lantana was found to be the most dominant species in BRT.

The BRT landscape has experienced and is experiencing a variety of disturbances. Historical disturbance factors, such as selective- and clear-felling of trees, extraction of bamboo and grass

resources, and slash-and-burn agriculture, could have created conditions favorable for lantana invasion. Contemporary disturbance factors, such as roads, and human-caused disturbance (e.g., collection of non-timber forest products or fuel-wood) may also play a role in driving lantana invasions. Lantana invasion could also be driven by an increase in fire frequency, since lantana resprouts in response to fire. Propagule pressure from sites already invaded by lantana could further enhance lantana invasion. Finally, lantana invasion would be influenced by the availability of suitable habitat. I modeled the rapid spread of lantana using explanatory variables such as historical habitat modification, current human disturbance, fire frequency, propagule pressure, and habitat suitability. Using an information-theoretic, model-selection approach, I focused the modeling exercise on the three distinct stages of biological invasion — arrival, establishment, and spread. Lantana arrival was best explained by propagule pressure, rather than disturbance factors or habitat suitability. Lantana establishment on the other hand, was limited by fire frequency. Lastly, I found that lantana spread was influenced largely by proximity to historical disturbance, such as old plantations.

Management efforts aimed at controlling the invasion of lantana and of other potentially problematic invasives are limited by the lack of information on the mechanisms that may enhance their success. The ecology of soil seed banks is one such mechanism. I explore the role played by soil seed banks in enhancing the success of two common invasives in BRT — lantana and *Chromolaena odorata* (hereafter, Chromolaena). Results from this study indicate that the soil seed bank is saturated with seeds of lantana and Chromolaena vis-à-vis native species. Lantana forms persistent seed banks, implying that for any kind of control, lantana seed output first has to be reduced. Reducing seed output could be achieved by reducing the density of adult lantana plants. Furthermore, repeated removals would have to be continued till lantana seed banks in soil are depleted. However, results from this study also indicate that lantana seed banks are negatively affected by fire. Repeated removals, combined with fire could be explored as a method to control lantana regeneration. Chromolaena, on the other hand, does not seem to be as pervasive as lantana.

Lastly, I explored how resident communities view lantana invasions. An indigenous community, the Soliga, have been residing in BRT for centuries. I used an open-ended interview schedule to

solicit Soliga thoughts on lantana invasion in BRT. The Soliga cited three main reasons for lantana spread: its copious fruit output and wide dispersal, the decrease in fire frequency, and the historical extraction of grass and bamboo resources. According to Soliga views, the nature of the lantana-fire relationship depended on lantana abundance. At a low lantana density, the occurrence of early dry-season fires was seen as a way to control lantana from spreading. At a high lantana density, the occurrence of forest fires was seen as beneficial for lantana, since fires were more intense and negatively affected native species due to the additional fuel provided by lantana biomass. The hampering of natural regeneration of native species due to the thick growth of lantana, which, in turn, curtailed native species seedlings from accessing light was also cited as a further contribution to lantana success. The Soliga believed that lantana invasion has had a negative effect on forest composition and structure, and on their livelihoods.

Tabling scientific knowledge with traditional ecological knowledge has led to an improvement in our understanding of lantana invasions in BRT. Some aspects of lantana invasion, such as the role of propagule pressure and response of native tree communities were corroborated by both traditional and scientific sources. However, some aspects, such as the role of fire in lantana invasion were surprisingly contradictory. According to the Soliga, at low lantana densities fire may play a role in limiting lantana, a view contrary to scientific studies that hypothesize a positive relationship between lantana and fire. However, both traditional and scientific knowledge sources agree that fires in high lantana density areas, if they occur, could be destructive for native species. The patterns of lantana spread indicate the serious threat posed by lantana to native plant biodiversity and the structure of this tropical dry forest landscape. Although fire frequency was observed to limit lantana establishment, and also appeared to reduce the density of viable lantana seeds stored in soil, a precautionary approach should be adopted before utilizing fire as a management tool to control or eradicate lantana. Since fires are likely to burn more intensely due to the build-up of lantana biomass, reducing biomass via lantana removal may be required before fires could be used to control lantana.

Table of contents

	Title	Page no.
1	Acknowledgements	i
2	Executive Summary	iii
3	Chapter 1: Introduction	1
4	Chapter 2: *Lantana camara* invasion in a heterogeneous landscape: patterns of spread and effects on native biodiversity	6
5	Chapter 3: Factors influencing the arrival, establishment, and spread of *Lantana camara*	33
6	Chapter 4: Soil seed bank ecology and invasive species success in a tropical dry forest	59
7	Chapter 5: Traditional Soliga knowledge on the ecology and impacts of the invasive *Lantana camara*	90
8	Chapter 6: Synthesis	117

List of Tables

Table no.	Description	Page no.
2.1	Classification of forest types in the Biligiri Rangaswamy Temple Wildlife Sanctuary. Plots were assigned to categories based on data from Ramesh (1989), Murali & Setty (2001) and Ganesan & Setty (2004).	09
2.2	Change in the density of lantana (stems/plot) and native species in the different forest types of BRT from 1997 to 2008. Sample sizes in each forest type are mentioned within parentheses. Note: t-tests were not conducted to compare change in mean density of lantana stems in the evergreen forest as lantana was present in only one plot in both 1997 and 2008.	15
2.3	Mean (± 1 standard error) basal area of lantana and of native species in 1997 and 2008 at the landscape scale and at the level of individual forest types in BRT. Sample sizes in each forest type, and for the entire landscape, are mentioned within parentheses.	17
2.4	Species richness, Shannon's diversity, *H'*, and evenness, *J,* in the different forest types of BRT in 1997 and 2008. Sample sizes in each forest type are mentioned within parentheses.	20
3.1	Models to explain lantana arrival with their corresponding number of parameters (K), corrected AIC (AIC_C), value of AIC_C in the i^{th} model – minimum value of AIC_C (Δ_i), Akaike weights, and percent deviance from the intercept-only model. The deviance of the intercept-only model was 75.256 .	45
3.2	Models to explain lantana establishment with their corresponding parameters (K), corrected AIC (AIC_c), value of AIC_c in the i^{th} model – minimum value of AIC_c (Δ_i), Akaike weights, and percent deviance from the intercept-only model. The deviance of the intercept-only model was 87.44.	46
3.3	Models to explain lantana spread with their corresponding parameters (K), corrected AIC (AIC_c), value of AIC_c in the i^{th} model – minimum value of AIC_c (Δ_i), Akaike weights, and percent deviance from the intercept-only model. The deviance of the intercept-only model was 7.057.	47

Table no.	Description	Page no.
3.4	Weight of evidence in favor of each variable for explaining lantana arrival, establishment, and spread. The weights for each variable were calculated by summing the Akaike weights of all models where the predictor variable of interest appears (Burnham and Anderson 2002). Greater weights indicate the importance of each predictor, relative to all other predictors.	48
4.1	Shrub and liana species (a) and tree species (b) emerging from seed rain and seed bank samples in the different seasons of sampling in BRT.	70
4.2	Relative abundance of shrub and liana species (a) and tree species (b) in the seed rain and seed bank samples across the different seasons in BRT.	71
4.3	Results from linear mixed-effects models to explain the variation of emergence of seeds from the soil seed bank as a response to random (block and sites over time) and fixed effects (treatment, layer, and time).	76
4.4	Results from linear mixed-effects models to explain the variation of seed arrival as a response to random (block and sites over time) and fixed effects (treatment and time).	77
5.1	The density (± 1 s.e.) of important NTFP species and canopy trees in 1997 and 2008.	105

List of Figures

Figure no.	Description	Page no.
2.1	Numbers of lantana stems per 400 m^2 plot encountered 1997 and in 2008. In 1997 134 plots were sampled; by 12 of these plots had been converted to other land uses, so only 122 plots were sampled.	13
2.2	Rank abundance profiles of all woody species by forest type in 1997 and 2008. Labels indicate the three most abundance species. Species codes (in alphabetical order) are ANOLAT = *Anogeissus latifolia*, ATAMON = *Atalantia monophylla*, CHLSWI = *Chloroxylon swietenia*, CIPBAC = *Cipadessa baccifera*, DIOOPP = *Dioscorea oppositifolia*, ERYMON = *Erythroxylon monogynum*, HELISO = *Helicteres isora*, JUSSPP = *Justicia spp.*, LANCAM = *Lantana camara*, LITDEC = *Litsea deccanensis*, MAEIND = *Maesa indica*, PSYSPP = *Psychotria spp*., RANDUM = *Randia dumetorum*.	16
2.3	The mean numbers of native trees/plot in each size class at the level of the landscape (a) and at the level of individual forest types, scrub-savanna (b), dry deciduous forest (c), and moist deciduous forest (d) in 1997 and 2008. Significant differences in tree density within a size class between 1997 and 2008 are indicated by * ($p<0.05$), ** ($p<0.01$), or *** ($p<0.001$). Note difference in y-axis scale in the case of the scrub-savanna.	18
2.4	The mean numbers of shrubs and lianas per plot in each size class at the level of the landscape (a) and at the level of individual forest types, scrub-savanna (b), dry deciduous forest (c), and moist deciduous forest (d) in 1997 and 2008. Significant differences in shrub and liana density within a size class between 1997 and 2008 are indicated by * ($p<0.05$), ** ($p<0.01$), or *** ($p<0.001$). Note differences in y-axis scale among panels.	21

Figure no.	Description	Page no.
2.5	Relationship between lantana density (stems/plot) and species richness, Shannon's diversity, and evenness at the landscape level in 1997 (n=134) and 2008 (n=122) in BRT. Lines denote significant ($p < 0.05$) linear relationships. Note the differences in x-axes range among panels.	23
2.6	Relationship between lantana density (stems/plot) and species richness, Shannon's diversity, and evenness in scrub-savanna (n=26 in 1997, n=22 in 2008), dry deciduous forest (n= 73 in 1997, n=73 in 2008) and moist deciduous forest (n=22 in 1997, n=20 in 2008) in 1997 and 2008. Lines denote significant linear relationships ($p< 0.05$) in the case of scrub-savanna (solid line), dry deciduous forest (dashed line), and moist deciduous forest (dotted line). Note the differences in x-axes range among panels.	24
3.1	Map of BRT showing sampling grids and roads (a), old podus, current podus, and areas of historical plantation activity (b), and streams (c). Inset map of India shows location of BRT.	36
3.2	Variables that best explain lantana arrival (a), establishment (b), and spread (c,d).	48
4.1	Mean density of viable seeds of lantana, other woody species, trees, and Chromolaena per season from the soil seed bank in the three different treatments (fire, invaded and uninvaded) in BRT.	72
4.2	Layer differences in the average density of viable seeds present in the soil seed bank of (a) lantana, (b) shrubs and lianas, (c) trees, and (d) Chromolaena in the three different treatments. Output from LME models indicating significant interactions ($p< 0.05$) between treatment and layer within plant categories are shown (*).	74
4.3	Variation in the mean seed arrival of lantana, shrubs and lianas, trees, and Chromolaena across the different treatments, averaged over seasons.	78

Figure no.	Description	Page no.
4.4	Seasonal variation in the soil seed bank density of (a) lantana, (b) other woody species, (c) trees, and (d) Chromolaena across all treatments. Model output from LMEs that showed significant interactions ($p < 0.05$) between seed arrival and season within plant categories are indicated (*).	78
4.5	Comparison between the density of viable seeds present in the soil seed bank and seed rain for the most dominant other woody species (a & b), the most dominant tree species (c & d), Chromolaena (e), and lantana (f), across the different seasons of sampling in BRT. Note differences in y-axis scale across panels.	79
4.6	Seasonal variation in total seed arrival of (a) lantana, (b) other woody species, (c) trees, and (d) Chromolaena across all treatments. Model output from LMEs that showed significant interactions ($p < 0.05$) between seed arrival and season within plant categories are indicated (*).	80
5.1	Numbers of lantana stems per 400 m^2 plot encountered in 1997 and in 2008. In 1997 134 plots were sampled by Murali and Setty (2001); by 2008, 12 of these plots had been converted to other land uses, and so only 122 plots were sampled by Sundaram and Hiremath (manuscript submitted).	97
5.2	Distribution of the responses (n= 47) related to the time of lantana spread in BRT.	101
5.3	The differences between mean basal area per plot of native species and of lantana in 1997 and 2008. Significant differences in the average values as identified by a *t* test are labeled with *. Error bars signify 1 standard deviation from the average basal area.	106

Chapter 1: Introduction

Invasive species are defined as non-native species that cause negative impacts in recipient systems (Colautti and MacIsaac 2004). Human beings have transported and introduced species outside their native habitat by accident or on purpose. Early agriculturists and pastoralists probably deliberately introduced species outside their native range. However, the rate of introductions (both accidental and deliberate) is likely to have increased with the development of commercial shipping routes by colonialists as early as eight centuries ago (Crosby 2004). With transport networks better developed than ever before, the rate and scale of contemporary species introductions are unprecedented. All introduced species do not become invasive. Those that do are often better competitors than native species. Factors such as young age to reproduction, prolific production of propagules, lack of dispersal limitation, efficient use of nutrients, escape from predators present in their native range ('enemy release'), and the ability to make use of ecosystem disturbances often weigh in favor of invasive species when compared to native species. Due to their negative effects in recipient systems, invasive species have been identified as one of the primary threats to biodiversity (Mack *et al*. 2000).

Just as species differ in their invasiveness (e.g., by being better competitors, or via enemy-release), ecosystems differ in their invasibility. Elton (1958) proposed the diversity-invasibility relationship, suggesting that species poor systems are more prone to invasion by non-native species than species-rich systems due to the availability of under-utilized niche space. However, as the field of biological invasions has evolved, contemporary studies suggest that conditions such as soil fertility are strongly correlated with both high native diversity and high invasive species diversity, implying that species-rich systems are not necessarily less invasible than species-poor systems (Stohlgren *et al*. 1999). Additionally, theoretical studies propose that large-scale disturbances, such as forest fires, could drastically increase invader abundance (Buckley *et al*. 2007).

Results from Stohlgren *et al*. (1999) imply that species rich biodiversity hotspots, such as the Western Ghats in India, could be negatively impacted by invasive species. Forests in the Western

Ghats biodiversity hotspot are affected by development and land-use changes, which are likely to further increase ecosystem invasibility. Several invasive species that occur pantropically, such as *Lantana camara*, *Chromolaena odorata*, *Eichhornia crassipes*, *Parthenium hysterophorus*, *Mikania micrantha*, *Cytisus scoparius*, and *Acacia mearnsii* are already present in the Western Ghats. Of these *L. camara* (hereafter, lantana) is widespread and present in a wide variety of land-use types (e.g., dry-to-moist deciduous forests, agricultural fallows, grazing lands), while the other species tend to occupy specific habitats like montane grasslands (*C. scoparius*), or freshwater wetlands (*E. crassipes*), or wet forests (*M. micrantha*).

Lantana was introduced into India from South America on multiple occasions beginning in 1809 (Cronk and Fuller 1995). Reports of the rapid spread of lantana began appearing from the early part of the 20th century from several parts of the country (e.g., Coorg in the Western Ghats; Tireman 1916, Kathgodam in Uttarakhand; Hakimuddin 1929, and Salem in Tamil Nadu; Iyengar 1933). Written from a forestry perspective, these anecdotal reports drew attention to the negative effects of lantana on the regeneration and survivorship of timber trees. However, reports about the effects of lantana on native biodiversity and forest structure are limited (see Sharma *et al*. 2005 for a review of lantana research in India). Gaps in our knowledge about lantana invasions, such as its effects on native biodiversity and the mechanisms influencing its spread are largely due to the absence of long-term research on lantana. For example, although the relationship between fire and lantana has been examined theoretically by a few studies in India (e.g., Sharma *et al*. 2005, Hiremath and Sundaram 2005), long-term data from the field were unavailable to either support of refute the hypothesized relationship. Research on the relationship between lantana and fire in Australia show that the effect of fire on lantana varies based on the habitat type. For example, in dry rainforests, Duggin and Gentle (1998) found that when compared to invaded areas that were left untreated, low intensity fires combined with native understory removal resulted in greater biomass accrual and survivorship of lantana. Additionally, greatest levels of lantana biomass and survivorship occurred in areas exposed to high intensity fires and overstory removals, implying that lantana invasion increased with disturbance intensity in dry rainforests (Duggin and Gentle 1998). Lantana invasions in Australian dry rainforests are now managed by restoring overstory canopies (Day *et al*. 2003). However, fires were found to be the cheapest way to control lantana in grazing lands, because repeated fires prevented lantana

establishment, along with minimal adverse effects on native flora (Day *et al*. 2003). Similarly, although the soil seed bank has been implicated as being an important factor underlying lantana invasion in Australia (Vivian-Smith and Panetta 2009), the role played by the soil seed bank in Indian forests invaded by lantana was unknown.

I examine different aspects of lantana invasion from a tropical dry forest landscape in the Western Ghats, the Biligiri Rangaswamy Temple Wildlife Sanctuary (hereafter, BRT). Invasive species success is dependent on a species' performance through the arrival, establishment, and spread phases (Sakai *et al*. 2001). Time lags are inherent to species invasions, implying that exotic species could remain at low densities for years after arriving on foreign shores. Although the earliest record of lantana in BRT is from 1934, there was evidence to suggest that its spread had occurred only over the past two decades. I examine the long-term change in lantana distribution and abundance in BRT from 1997-2008 (Chapter 2). Due to its prolific growth, lantana may negatively affect native species assemblages and forest structure. I therefore examine how variables that describe the native community, such as species richness, diversity, evenness, and population structure respond to lantana density. Since the habitat within BRT is heterogeneous, I examine how these variables respond at two scales: at the level of individual forest types and at the landscape-level.

Several factors could influence lantana invasion of the BRT landscape. Some, such as propagule pressure exerted by lantana and habitat suitability for lantana are a function of lantana ecology. Others, like forest fires, edges, and contemporary human-caused disturbance could also influence lantana invasion. I examine the drivers of lantana arrival, establishment and spread. After identifying primary drivers of lantana spread from the literature (Duggin and Gentle 1998, Day *et al*. 2003, Sharma *et al*. 2005), such as disturbance (forest fires, historical habitat modification, contemporary human-caused disturbance, and edges), habitat suitability for lantana, and propagule pressure, I use a model-selection approach to pinpoint drivers with the most influence (Chapter 3).

Propagule pressure has been recognized as one of the primary mechanisms underlying invasive species success. Invasive species often produce seeds in large quantities, fruit year-round, and

are not dispersal limited. All these factors give them an edge over annually fruiting native species. I examine how seed arrival and the soil seed bank influence lantana success in BRT (Chapter 4). Using an experimental approach, I examine patterns of seed arrival and storage in the soil seed bank — of both lantana and native species — across areas that are invaded, uninvaded and exposed to a disturbance such as fire. Using data from the seasonal patterns of seed arrival and soil-stored seeds to infer seed persistence, I attempt to identify whether seed arrival or seed persistence — or both — enhance lantana success in BRT.

Examining traditional ecological knowledge about the perceptions of invaders like lantana could improve our understanding of biological invasions. The Soliga, an indigenous community, have resided in BRT for centuries, and are likely to have evolved an understanding of lantana invasions. I interviewed members of the local Soliga community in BRT about patterns of lantana invasions, the effect of lantana invasions on forest composition and structure, and mechanisms driving lantana success (Chapter 5). By examining results from Soliga sources and scientific sources side-by-side, I attempt to seek a convergence between traditional and scientific knowledge to enrich our understanding of the ecology of lantana invasions and the management of areas invaded by lantana.

References

Buckley, Y. M., B. M. Bolker, and M. Rees. 2007. Disturbance, invasion and re invasion: managing the weed shaped hole in disturbed ecosystems. Ecology Letters **10**:809-817.

Colautti, R. I., and H. J. MacIsaac. 2004. A neutral terminology to define'invasive'species. Diversity and Distributions **10**:135-141.

Cronk, Q. C. B., and J. L. Fuller. 1995. Plant invaders. Chapman and Hall, London.

Crosby, A. W. 2004. Ecological imperialism: the biological expansion of Europe, 900-1900. Cambridge Univ Pr.

Day, M. D., C. J. Wiley, J. Playford, and M. P. Zalucki. 2003. Lantana: current management status and future prospects. Australian Centre for International Agriculture Research, Canberra, Australia.

Duggin, J. A., and C. B. Gentle. 1998. Experimental evidence on the importance of disturbance intensity for invasion of *Lantana camara* L. in dry rainforest-open forest ecotones in north-eastern NSW, Australia. Forest Ecology and Management **109**:279-292.

Elton, C. S. 1958. The ecology of invasions by animals and plants. . The University of Chicago Press, Chicago.

Hakimuddin, M. 1929. Lantana in northern India as a pest and its probable utility in solving the cowdung problem. Indian Forester **56**:405-410.

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

Iyengar, A. V. V. 1933. The problem of lantana. Current Science **1**:266-269.

Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications **10**:689-710.

Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. McCauley, P. O'Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. Annual Review of Ecology and Systematics **32**:305-332.

Sharma, G. P., A. S. Raghubanshi, and J. S. Singh. 2005. *Lantana* invasion: an overview. Weed Biology and Management **5**:157-165.

Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs **69**:25-46.

Tireman, H. 1916. Lantana in the forests of Coorg. Indian Forester **42**:384-392.

Vivian-Smith, G., and F. D. Panetta. 2009. Lantana (*Lantana camara*) seed bank dynamics: seedling emergence and seed survival. Invasive Plant Science and Management **2**:141-150.

Chapter 2: *Lantana camara* invasion in a heterogeneous landscape: patterns of spread and effects on native biodiversity

Introduction

Invasive species are significant drivers of ecosystem change. Invasive species alter or disrupt ecosystem processes such as nitrogen cycling (Ashton *et al*., 2005), hydrology (Strayer *et al*., 2006; Gordon, 1998), native plant-pollinator mutualisms (Traveset and Richardson, 2006), or below-ground mutualisms between native species and mycorrhizae (Stinson *et al*., 2006). Invasive species are often better competitors than native species in recipient habitat, resulting in community-level changes over the long-term (Strayer *et al*., 2006). In extreme cases, biological invasions lead to community disassembly due to competitive exclusion of native species by invasive species (Sanders *et al*., 2003), or rapid degradation of the entire ecosystem due to the predation of native species by invasive species (Fritts and Rodda, 1998).

While the effects of invasive species on ecosystem processes are relatively well known, the impacts of invasive species on native communities have received less attention, largely due to the paucity of long-term data (Strayer *et al*., 2006). In order to examine the effects of invasive species on native communities, examining the response of a suite of community variables, e.g., species richness, diversity, abundance, evenness, population structure, and dominance could potentially provide detailed insights into the effects of invasive species (e.g. Hejda *et al*., 2009).

Invasive species can have negative impacts on the diversity and abundance of native species (Clavero *et al*., 2009; Gooden *et al*., 2009a; Hejda *et al*., 2009; Sanders *et al*., 2003). Studies show that biological invasions can lead to the homogenization of native communities (Hejda *et al*., 2009; Hillebrand *et al*., 2008; Olden, 2006). Invasive species can also alter the population structure of native communities, leading to a change in the size class distributions of saplings or juveniles (Sharma and Raghubanshi, 2006; Litton *et al*., 2006) and changes in relative

dominance within invaded communities (Fisher *et al*., 2009). Sakai *et al*., (2001) propose that invasive species often have an edge over native species in the competition for space due to recruitment advantages. Such advantages can result from prodigious seed production and the lack of dispersal limitations for invasive species when compared to native species. Additionally, invasive species may gain competitive advantages in capturing space by the efficient use of resources in both high-nutrient (Huenneke *et al*., 1990) and low-nutrient (Funk and Vitousek, 2007) conditions vis-à-vis native species.

Change in community variables as a result of invasive species may not be uniform across heterogeneous landscapes as compared to homogeneous landscapes (Melbourne *et al*., 2007; Strayer *et al*., 2006; Pauchard and Shea, 2006). For example, forest type heterogeneity within landscapes is often determined by variations in topography and rainfall. Some forest types may be more invasible than others, while communities across different forest types may respond differentially to invasive species (Hejda *et al*., 2009). Therefore in heterogeneous landscapes, it is necessary to examine the response of community variables to invasive species at both the landscape scale and at the scale of individual forest types.

A large majority of studies that examine the effects of biological invasions on community structure or ecosystem processes use either historical records or space-for-time substitution (chronosequence) approaches to elucidate effects of invasive species on the structure of native communities. Studies that track the long-term response of native community diversity, abundance, evenness, population demography, and relative dominance to invasive species are rare, yet valuable (Strayer *et al*., 2006). The principal advantage of long-term studies is that they do not require making assumptions about the past condition of a site, unlike studies that substitute space for time (Johnson and Miyanishi, 2008; Landres *et al*., 1999).

In this study, I take advantage of unique long-term data to examine the patterns of spread of the invasive shrub, *Lantana camara* (Verbenaceae; hereafter, lantana), over 11 years. I examine its effects on native vegetation communities in different forest types of a landscape in the Western Ghats biodiversity hotspot, India. My specific objective is to examine the long-term change in lantana distribution and abundance at both the landscape level and at the level of individual

forest types. I predict that over the long term, native community variables such as (a) species richness, (b) diversity, (c) evenness, and (d) population structure will be negatively affected by an increasing lantana density, both at the landscape scale and at the scale of individual forest types.

Methods

Study area

I conducted this study in the 540 km^2 Biligiri Rangaswamy Temple Wildlife Sanctuary (77º – 77º 16´ E, and 11º 47´ – 12º 09´ N; hereafter, BRT). The BRT terrain is hilly, with elevation ranging from 600-1800 m above sea level. The sanctuary receives rainfall from both the southwest monsoon (June-September) and the northeast monsoon (October-December), with a pronounced dry period between January and March. There is considerable variation in rainfall with topography, with annual rainfall ranging from 898 - 1750 mm, depending on location. The mean annual temperature in the study area is 25.3 ºC, and varies between 11 ºC in winter to 42 ºC in summer (Murali *et al*., 1998). Soils in BRT are well-drained gravelly clays that have been classified as typic ustropepts (Anon., 1996).

The BRT sanctuary is part of the Western Ghats biodiversity hotspot (Myers, 2003; Mittermeier *et al*., 2004) and is located in the state of Karnataka, India. It was notified as a wildlife sanctuary in 1973 (Barve *et al*., 2005). The area is rich in biodiversity, with at least 1400 species of higher plants (Ramesh, 1989; Kammathy *et al*., 1967), and 254 species of birds (Srinivasan and Prashanth, 2005). The BRT landscape has 27 species of mammals, including large mammalian herbivores such as the Asian elephant (*Elephas maximus*), gaur (*Bos gaurus*), sambar (*Cervus unicolor*), and four-horned antelope (*Tetracerus quadricornis*), and carnivores such as the tiger (*Panthera tigris*), leopard (*Panthera pardus*), and dhole (*Cuon alpinus*).

The main vegetation types in BRT are scrub-savanna, dry deciduous forests, moist deciduous forests, riparian semi-evergreen forests, evergreen forests, and the shola-grassland mosaic (Table 2.1). Seasonally dry forests comprising the scrub-savanna, and dry deciduous and moist

deciduous forests, constitute approximately 90% of the study area (Ganesan and Setty, 2004) and are now extensively invaded by lantana.

Table 2.1: Classification of forest types in the Biligiri Rangaswamy Temple Wildlife Sanctuary. Plots were assigned to categories based on data from Ramesh (1989), Murali & Setty (2001) and Ganesan & Setty (2004).

Forest type	Average annual rainfall (mm)[§]	Elevation range (m asl)	Canopy height range (m)[1]	Characteristic species[2]
Scrub-savanna	898	600-800	4-6	*Acacia chundra, Diospyros melanoxylon, Chloroxylon swietenia*
Dry deciduous forest	1168	800-1100	8-12	*Anogeissus latifolia, Terminalia crenulata, Grewia tilaefolia*
Moist deciduous forest	1438	1100-1400	15-20	*Pterocarpus marsupium, Syzygium cuminii, Terminalia bellerica*
Evergreen forest	1750	>1400	20-25	*Persea macrantha, Litsea deccanensis, Elaeocarpus tuberculatus*
Shola-grassland	1750	>1400	12-18	*Memecylon umbellatum, Cinnamomum zeylanicum, Elaeocarpus serratus*

[§] Values are based on rainfall data from 1989-1999 from four recording stations situated in different areas of BRT; these stations correspond to the different forest types.

[1] Range of canopy heights gathered from Ramesh (1989).

[2] Data from this study and Ramesh (1989)

Lantana camara

Lantana camara is a woody straggling shrub native to Central and South America. Lantana was introduced to India on multiple occasions (Cronk and Fuller, 1995; Sharma *et al*., 2005), although its earliest documented introduction dates back to 1809 (Cronk and Fuller, 1995). Within just over a century of its introduction, there were reports of lantana's invasiveness (Tireman 1916, Iyengar, 1933, Anon., 1942). Lantana is today a common invader of dry forest landscapes, slash-and-burn fallows, and pasture lands all over India (Sharma *et al*., 2005).

Information regarding the exact year of introduction of lantana into BRT is unavailable. Forest working plans mention the presence of lantana in BRT as early as 1934 (Ranganathan, 1934), although interviews with the Soliga people, who have lived in BRT for centuries, suggest that the spread of lantana began during the 1970s (B. Sundaram, unpublished data).

Change in lantana distribution in BRT (1997-2008)

In order to arrive at change in the density and abundance of lantana and native species, I took advantage of an earlier study in BRT, in which a grid-based, systematic sampling method was used to sample all vegetation, including lantana, between January and April 1997 (Murali and Setty, 2001). I replicated this study in 2007-2008. The BRT area was overlaid by a 2 x 2 km grid, and a 5 x 80 m plot was laid at the centre of each grid cell. The GPS location of each plot in my study corresponded to the location of plots in the Murali and Setty (2001) study. Plots were located using a Garmin GPS 12XL fitted with an external antenna for added accuracy. Although I used the same geographical coordinates for my plots as Murali and Setty (2001), these plots may not have been in exactly the same locations due to errors associated with GPS triangulation. However, based on a comparison between the species encountered by Murali and Setty (2001) and the species I recorded, I believe I have closely approximated Murali and Setty's (2001) plots. Murali and Setty (2001) inventoried a total of 134 plots. However, by 2008, 12 plots had transitioned to non-forest (coffee plantation, human habitation, agriculture), leaving a total sample of 122 plots.

Within each 5 x 80 m plot, I recorded diameter at breast height (DBH) of all living woody vegetation ≥1 cm DBH. In case of multi-stemmed plants, all stems ≥1 cm DBH were counted, and their DBH was measured. Individuals of all woody species were identified in the field whenever possible; samples of unidentified species were brought back to the field station and identified using floras and herbarium records. Vegetation in these 122 plots was sampled between August 2007 and January 2008.

For each plot, lantana presence and absence values for 1997 and 2008 were extracted. The density of native species and lantana present during each sampling instance were calculated. For each plot, pair-wise differences in the density of lantana and native species between 2008 and 1997 were then computed. The contribution to total basal area by lantana and by all other native species was also estimated.

For examining the change in lantana distribution (presence/absence, density, basal area) by forest type, the following forest types were distinguished: scrub-savanna, dry deciduous, moist deciduous and evergreen forests. Plots were assigned to forest type categories using information on species associations, canopy height, and elevation (Table 2.1).

Effects of lantana on community structure

To examine the effects of lantana invasion on native communities over time, I computed (a) species richness (the total number of woody species in each plot), (b) Shannon's diversity index *H'*, and (c) Evenness, *J*. Values of community variables were calculated separately for the landscape level (which included all plots) and at the level of individual forest types (which included plots corresponding to each forest type), for 1997 and 2008. I also examined changes in relative dominance of all species between 1997 and 2008 in the different forest types by plotting rank-abundance curves. Rank abundance curves were plotted only at the level of individual forest type.

Shannon's diversity index, *H'*, was calculated as $H' = -\sum_{i=1}^{S} \frac{n_i}{N} \ln \frac{n_i}{N}$ where n_i is the abundance of the i^{th} species of *S* total species in the sample, and *N* is the total abundance of all species in the

sample (Stohlgren, 2007). Evenness, *J,* was calculated using the formula *H'*/ln(*S*), where *H'* is Shannon's diversity index, and *S* is species richness (Magurran, 1983). Since abundance is incorporated in the calculation of evenness, the index *J* is sensitive to dominance by any one or a few species. Values of *J* range from 0 to 1. Values closer to 0 indicate that the plot is dominated by a single species, while values of *J* closer to 1 indicate that all species are equally abundant.

In addition, I also examined changes in the population structure of trees on the one hand, and shrubs and lianas, on the other hand, between 1997 and 2008. Data were analyzed separately in two categories-- trees, and non-trees (shrubs and lianas). Tree data were partitioned into three diameter classes: $1 \geq x \geq 5$ cm (small stems), $5 > x \geq 10$ cm (medium stems), and $x > 10$ cm (large stems). Small stems represent young regenerating trees, while medium and large stems represent adult trees. For the shrub and liana data, four diameter classes were chosen to reflect their stature- $1 \geq x \geq 2$ cm DBH, $2 > x \geq 4$ cm DBH, $4 > x \geq 8$ cm DBH, and $x > 8$ cm DBH. Size class data were examined for the entire landscape, and then separately at the level of each forest type.

Statistical analyses

The change in means of various measures of community structure – species richness, *S*, Shannon's diversity, *H'*, and evenness, *J* – as a result of lantana spread between 1997 and 2008 were analyzed at both the landscape-level and at the level of individual forest types, using paired *t*-tests. For the *t*-tests, a Welch approximation to the degrees of freedom was used because sample variances were unequal (Crawley, 2007).

Species richness, Shannon's diversity, and evenness, were examined as a function of lantana density at the landscape scale and the forest-type scale using linear least-squares regression. This analysis was done for data from 1997 and 2008.

To determine changes in the population structure of woody native species (trees, and shrubs and lianas), the mean number of stems per size class per plot in 2008 was compared to corresponding values in 1997 using paired *t*-tests. A Welch approximation to the degrees of freedom was used

for the *t*-test because sample variances were unequal (Crawley, 2007). All statistical analyses were performed using R version 2.9.0. (R Development Core Team, 2009).

Results

Long-term changes in lantana distribution across different spatial scales

Over 11 years, there was a tremendous increase in lantana abundance and density, both at the landscape scale, and at the level of individual forest types. At the landscape scale, lantana was present in only 41% of the plots in 1997 (n=134). By 2008 lantana had spread to 81 % of all plots (n=122; Fig. 2.1). The mean density of lantana in 1997 was 14.5 ± 3.5 stems/plot. By 2008, the mean density of lantana had increased more than four-fold to 66.1 ± 10.2 stems/plot. Moreover, by 2008 more than a third of the invaded plots had a lantana density > 50 stems/plot compared with 1997, when only three of the invaded plots had a lantana density > 50 stems/plot.

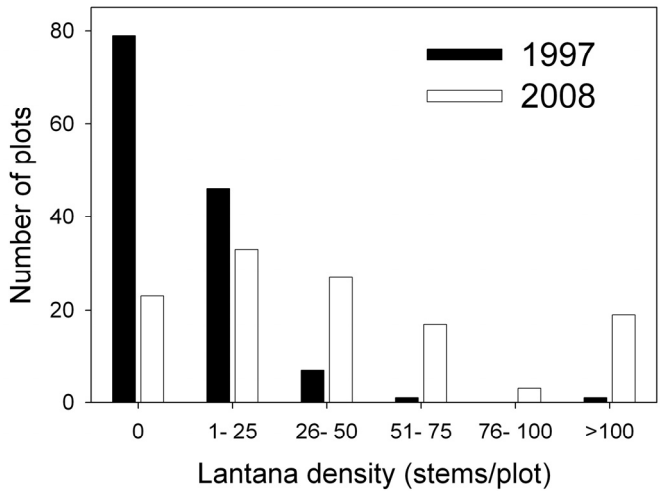

Figure 2.1: Numbers of lantana stems per 400 m^2 plot encountered in 1997 and in 2008. In 1997 134 plots were sampled; by 2008 12 of these plots had been converted to other land uses, and so only 122 plots were sampled.

The pattern of change in lantana density at the landscape level was closely mirrored at the level of individual forest types, particularly the scrub-savanna, the dry deciduous and the moist deciduous forests. The mean density of lantana increased more than ten-fold in the scrub-savanna and dry deciduous forests, and more than four-fold in the moist deciduous forests (Table 2.2). Lantana density did not show an increase in the evergreen forest plots. However, a large proportion of evergreen forest plots (6 of 13; almost 50%) had transitioned into non-forest types by 2008, and only one plot in the evergreen forest had lantana present on both sampling occasions. The mean density of stems of native species showed significant declines from 1997 to 2008 in the scrub-savanna as well as the dry deciduous forest (Table 2.2). However, native stem density did not differ significantly between 1997 and 2008 in the moist deciduous and evergreen forest plots (Table 2.2).

Although there was a tremendous increase in lantana density between 1997 and 2008, the proportion of total basal area accounted for by lantana in 2008 remained negligible when compared to the proportion of basal area contributed by all other native species at the landscape level (2%, Table 2.3). Lantana basal area did not contribute significantly to stand basal area at the level of individual forest types either (between 0% and 4% across different forest types; Table 2.3).

Changes in dominance, species richness, diversity, and evenness across different spatial scales

The dominance structure of three of the four forest types changed quite noticeably from 1997 to 2008. Lantana became the most dominant species (in terms of stem abundance) in the scrub-savanna and dry deciduous forests in 2008, displacing the canopy tree, *Anogeissus latifolia*, which was dominant in 1997 (Fig. 2.2). Interestingly, lantana was already the dominant species in the moist deciduous forest plots even in 1997, although it had augmented its dominance by 2008, with an almost two-fold increase in abundance (Fig. 2.2).

Table 2.2: Change in the density of lantana (stems/plot) and native species in the different forest types of BRT from 1997 to 2008. Sample sizes in each forest type are mentioned within parentheses. Note: t-tests were not conducted to compare change in mean density of lantana stems in the evergreen forest as lantana was present in only one plot in both 1997 and 2008.

Forest Type	Lantana density (stems/plot)						Native species stem density (stems/plot)					
	1997		2008		*t* value	p	1997		2008		*t* value	p
	mean	se	Mean	se			mean	se	mean	se		
Scrub-savanna (n=22)	3.22	1.29	44.71	8.53	4.53	0.0001	178.27	16.10	89.00	17.91	3.95	0.001
Dry deciduous forest (n=73)	4.79	1.42	48.99	6.98	6.26	0.00001	96.70	6.71	72.41	7.03	2.75	0.007
Moist deciduous forest (n=20)	12.65	8.22	60.25	16.55	2.42	0.0156	95.70	12.82	107.85	21.50	0.58	0.566
Evergreen forest (n=7)	7	7	0.29	0.29	-	-	149.43	36.23	112.57	30.57	0.89	0.407

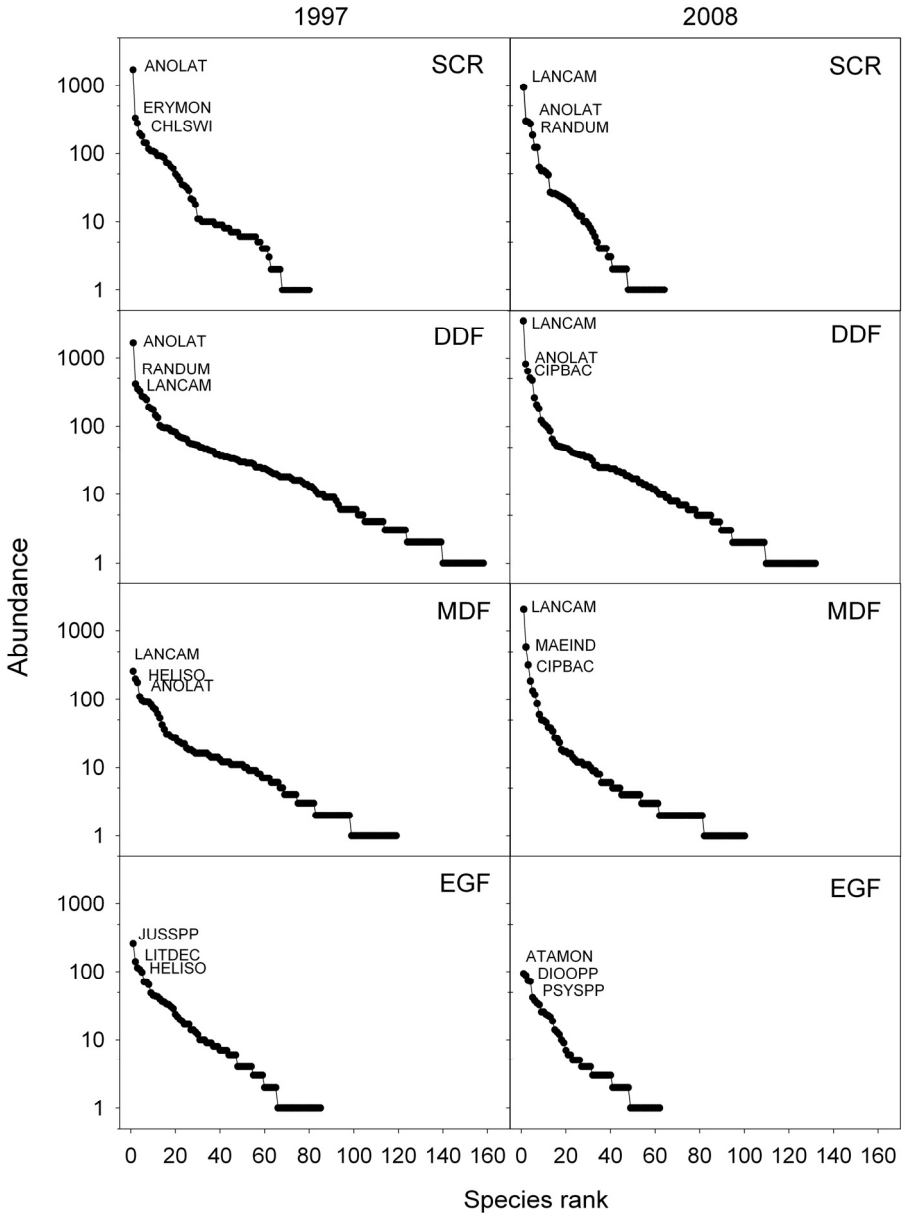

Figure 2.2: Rank abundance profiles of all woody species by forest type in 1997 and 2008. Labels indicate the three most abundance species. Species codes (in alphabetical order) are ANOLAT = *Anogeissus latifolia*, ATAMON = *Atalantia monophylla*, CHLSWI = *Chloroxylon swietenia*, CIPBAC = *Cipadessa baccifera*, DIOOPP = *Dioscorea oppositifolia*, ERYMON = *Erythroxylon monogynum*, HELISO = *Helicteres isora*, JUSSPP = *Justicia spp.*, LANCAM = *Lantana camara*, LITDEC = *Litsea deccanensis*, MAEIND = *Maesa indica*, PSYSPP = *Psychotria spp.*, RANDUM = *Randia dumetorum*.

There was a significant decline in species richness at the landscape scale from 1997 to 2008 (Table 2.4). From 1997 to 2008, there was a decrease in mean species richness in all forest types except for the evergreen forests. In the scrub-savanna and dry deciduous forests, the change in mean species richness between 1997 and 2008 was significant (Table 2.4).

At the landscape scale, the diversity of the woody species community was significantly lower in 2008 when compared to 1997 (Table 2.4). This was mirrored by the pattern of change in *H'* in the scrub-savanna, and in the dry- and moist-deciduous forests between 1997 and 2008. This decrease in diversity corresponded with a reduction in species richness in these forest types between 1997 and 2008, even though the reduction is species richness in the moist deciduous forest was non-significant during this time. Plots in the evergreen forest did not differ significantly in diversity from 1997 to 2008, mirroring patterns of similar species richness over the period 1997-2008 in this forest type (Table 2.4).

Table 2.3: Mean (± 1 standard error) basal area of lantana and of native species in 1997 and 2008 at the landscape scale and at the level of individual forest types in BRT. Sample sizes in each forest type, and for the entire landscape, are mentioned within parentheses.

	Basal area (m^2/ha) (lantana)		Basal area (m^2/ha) (all native species)	
	1997	2008	1997	2008
Entire landscape (n=122)	0.08 (0.02)	0.52 (0.07)	28.59 (2.15)	26.20 (2.08)
Scrub-savanna (n=22)	0.04 (0.01)	0.26 (0.02)	8.19 (0.39)	6.24 (0.43)
Dry deciduous forest (n=73)	0.05 (0.01)	0.55 (0.07)	27.36 (0.91)	24.48 (1.55)
Moist deciduous forest (n=20)	0.20 (0.05)	0.89 (0.11)	42.98 (2.80)	38.28 (2.33)
Evergreen forest (n=7)	0.11 (0.03)	0.001 (0.0001)	60.54 (2.16)	69.90 (2.94)

At the landscape level, values of evenness *J* were significantly lower in 2008 when compared to 1997 as a result of lantana dominance (Table 1.4). However, landscape-level patterns were not reflected in the patterns observed at the level of individual forest types. Reduced evenness was observed only in the dry deciduous and the moist deciduous forests (Table 1.4). There was no evidence for support of either increasing or decreasing evenness in the scrub-savanna and the evergreen forest plots (Table 2.4).

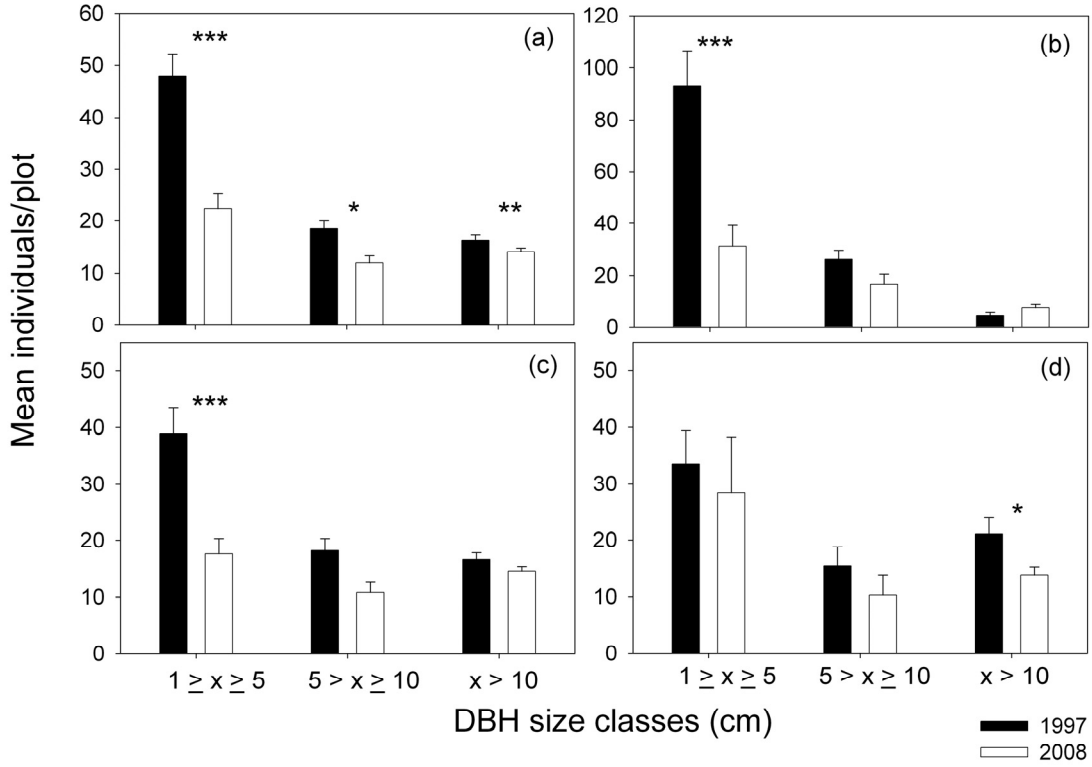

Figure 2.3: The mean numbers of native trees/plot in each size class at the level of the landscape (a) and at the level of individual forest types, scrub-savanna (b), dry deciduous forest (c), and moist deciduous forest (d) in 1997 and 2008. Significant differences in tree density within a size class between 1997 and 2008 are indicated by * ($p<0.05$), ** ($p<0.01$), or * ($p<0.001$). Note difference in y-axis scale in the case of the scrub-savanna.**

Changes in population structure of native species at different spatial scales

The size class distribution of trees changed markedly over time at the landscape scale. There were significant reductions over time in the average density of stems in all size classes (Fig. 2.3a). However, when data were analyzed separately by forest type, a significant reduction was evident only for small stems, and this was so in the scrub-savanna and dry deciduous forests (Figs. 2.3b and 2.3c). In the moist deciduous forests, on the other hand, the density of small stems remained unchanged over time but there was a significant reduction in the density of large stems (Fig. 2.3d). Tree data from the evergreen forest plots was not analyzed due to the small sample size.

The size class distribution of shrubs and lianas showed significant increases in the 1.0- 2.0 cm DBH class at the landscape scale (Fig. 2.4a). The changes in the density of stems in all other size class were not significant at this scale. Patterns of the change in the size class distribution of shrubs and lianas seen at the landscape scale were mirrored by the dry- and moist deciduous forest plots, with significant increases in the density of stems in the smallest size class (Figs. 2.4c and 2.4d). The changes in the density of shrubs in the rest of the size classes in these forests were not significant. In the scrub-savanna, there was no change in the population structure over time (Fig. 2.4). Shrub and liana data from the evergreen forest were not analyzed due to inadequate sample sizes.

Table 2.4: Species richness, Shannon's diversity, *H'*, and evenness, *J,* in the different forest types of BRT in 1997 and 2008. Sample sizes in each forest type are mentioned within parentheses.

Forest type	Community variable	1997		2008		*t* value	p
		mean	se	mean	se		
Entire landscape (n=122)	Species richness	15.84	0.51	12.34	0.50	4.80	0.0001
	Shannon's *H'*	2.05	0.04	1.57	0.05	7.85	0.0001
	Evenness *J*	0.76	0.01	0.65	0.01	6.10	0.0001
Scrub-savanna (n=22)	Species richness	17.00	0.92	10.95	1.32	3.687	0.0007
	Shannon's *H'*	1.93	0.07	1.61	0.10	2.589	0.013
	Evenness *J*	0.69	0.02	0.71	0.03	0.469	0.641
Dry deciduous forest (n=73)	Species richness	14.58	0.66	11.70	0.60	3.232	0.001
	Shannon's *H'*	2.02	0.05	1.52	0.06	6.598	0.0001
	Evenness *J*	0.77	0.01	0.64	0.02	5.849	0.0001
Moist deciduous forest (n=20)	Species richness	17.55	1.87	14.10	1.34	1.527	0.135
	Shannon's *H'*	2.14	0.12	1.46	0.13	3.997	0.0002
	Evenness *J*	0.77	0.03	0.56	0.01	4.336	0.0001
Evergreen forest (n=7)	Species richness	17.71	1.15	18.29	2.58	0.036	0.972
	Shannon's *H'*	2.16	0.12	2.32	0.16	0.177	0.863
	Evenness *J*	0.76	0.05	0.82	0.02	0.819	0.423

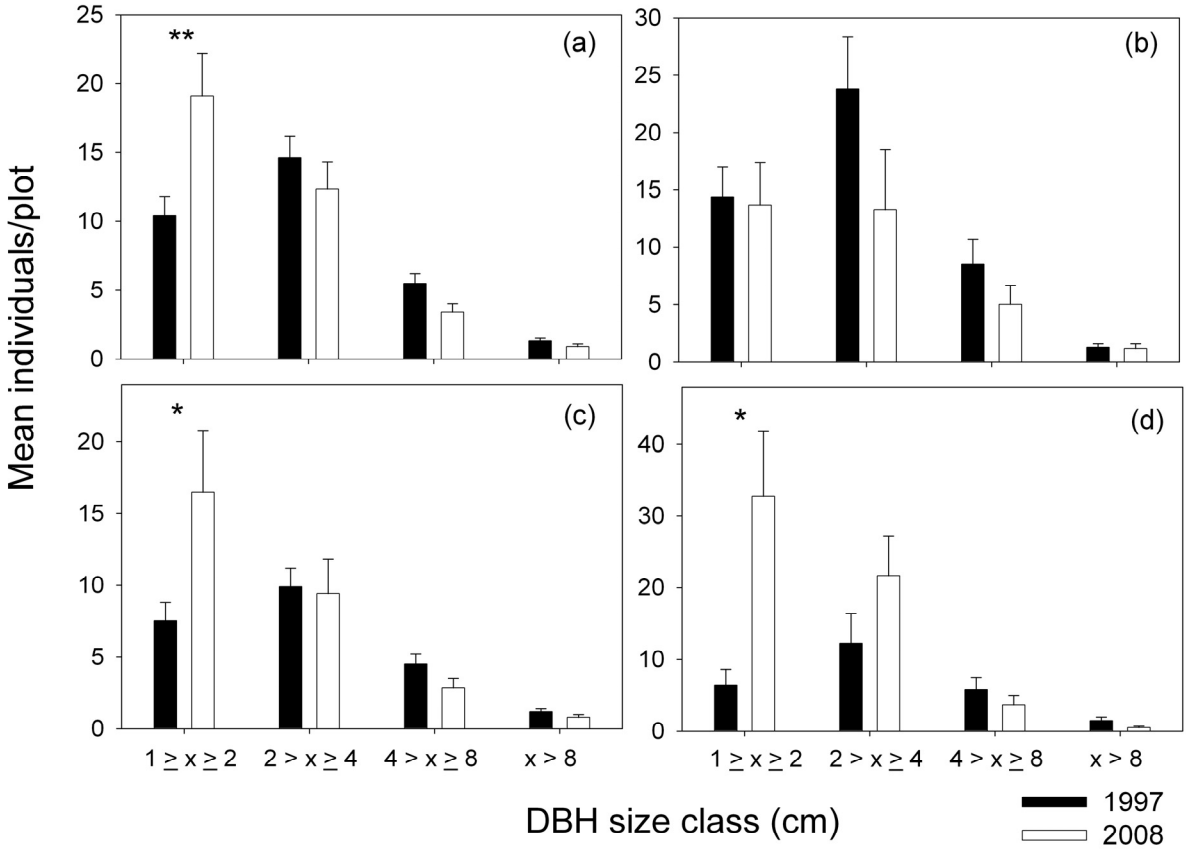

Figure 2.4: The mean numbers of shrubs and lianas per plot in each size class at the level of the landscape (a) and at the level of individual forest types, scrub-savanna (b), dry deciduous forest (c), and moist deciduous forest (d) in 1997 and 2008. Significant differences in shrub and liana density within a size class between 1997 and 2008 are indicated by * ($p<0.05$), ** ($p<0.01$), or * ($p<0.001$). Note differences in y-axis scale among panels.**

Relationship between lantana density and community structure at different spatial scales

At the landscape scale there was no discernible relationship between lantana density and community variables such as species richness, Shannon's diversity and evenness in 1997 (Fig. 2.5). The lack of pattern is not surprising, given that the majority of plots in 1997 either had no lantana, or had lantana at very low density. But by 2008, two community variables, Shannon's diversity and evenness, showed a significantly negative relationship with increasing lantana density at the landscape scale (Fig. 2.5). However, the relationship between lantana density and native species richness was not significant.

At the level of individual forest types the relationship between lantana density and community variables (species richness, Shannon's diversity and evenness) mirrored results obtained from the landscape level analysis in 1997: species richness, Shannon's diversity, and evenness did not vary as a function of lantana density in the scrub-savanna, dry deciduous or the moist deciduous forest plots in 1997 (Fig. 2.6). Analysis of the relationship between lantana density and species richness, diversity, and evenness was not conducted for the evergreen forest plots because lantana was present in only one of the plots in the evergreen forests in 1997.

By 2008, the relationship between lantana density and species richness, Shannon's diversity and evenness at the forest type level differed slightly from patterns observed at the landscape scale. Species richness remained unrelated to lantana density in all three forests (Fig. 2.6). On the other hand, lantana density emerged as a significant predictor of Shannon's diversity in the dry deciduous and moist deciduous forest though not in the scrub-savanna, and a significant predictor of evenness in all three forest types (Fig. 2.6).

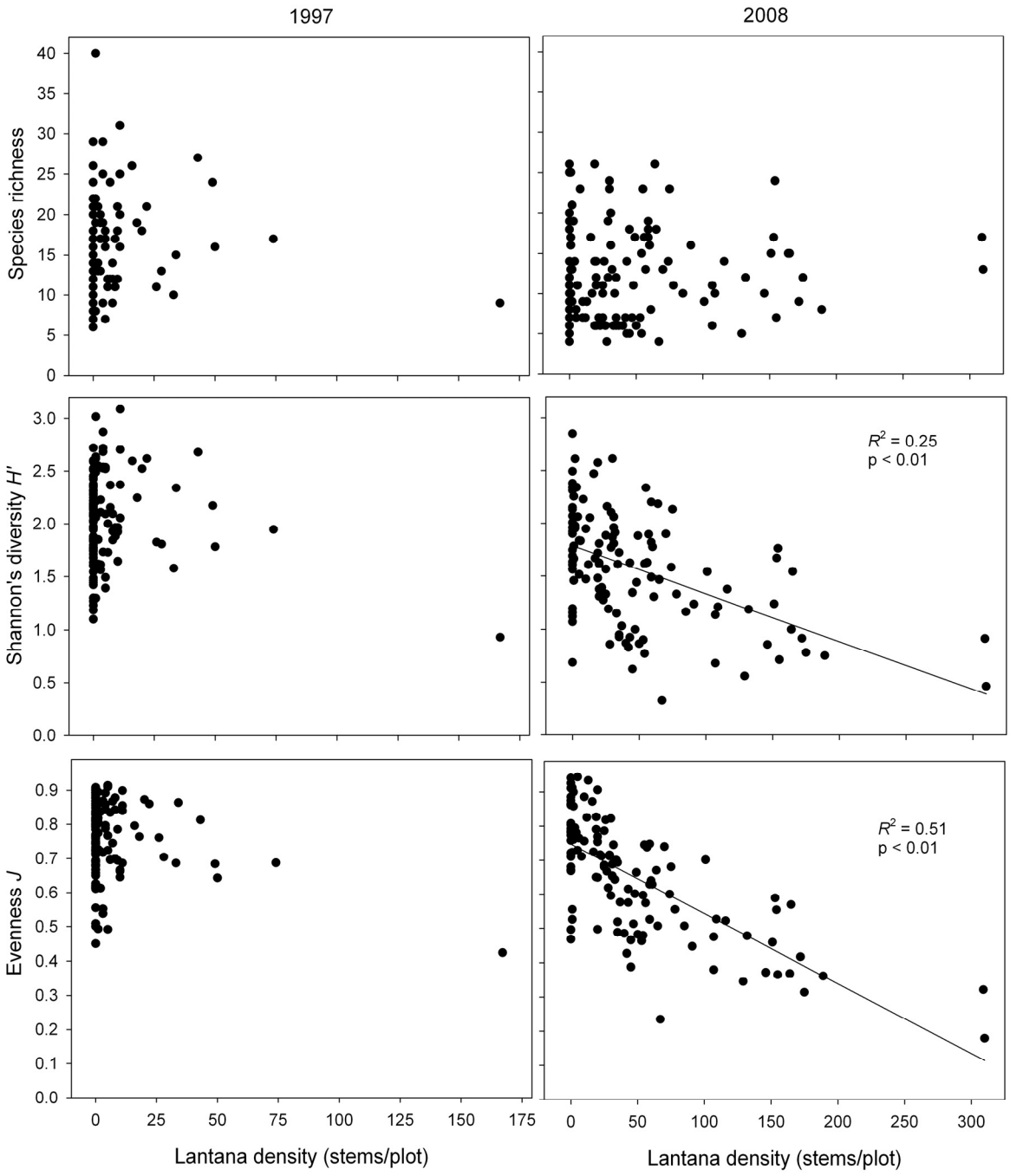

Figure 2.5: Relationship between lantana density (stems/plot) and species richness, Shannon's diversity, and evenness at the landscape level in 1997 (n=134) and 2008 (n=122) in BRT. Lines denote significant ($p < 0.05$) linear relationships. Note the differences in x-axes range among panels.

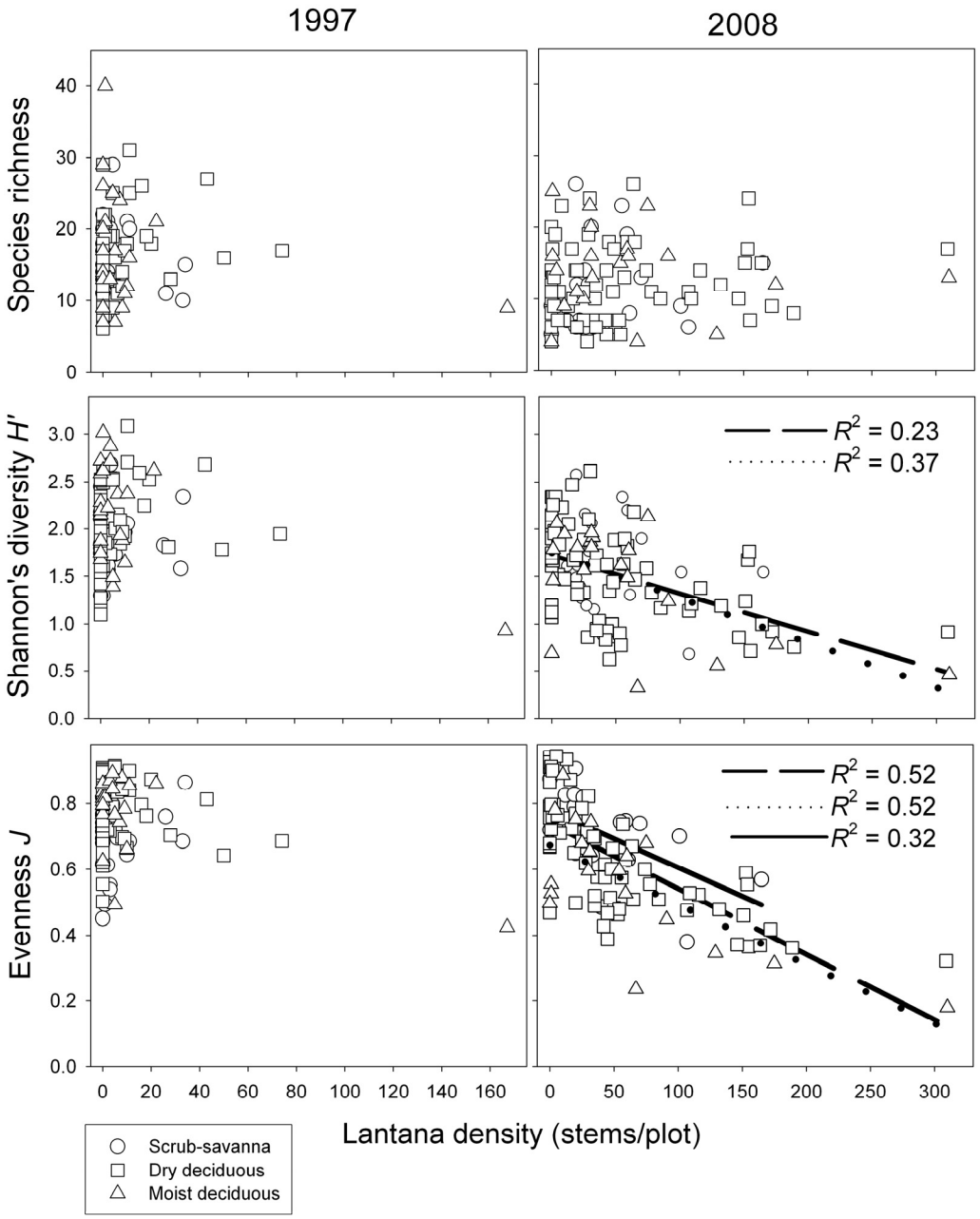

Figure 2.6: Relationship between lantana density (stems/plot) and species richness, Shannon's diversity, and evenness in scrub-savanna (n=26 in 1997, n=22 in 2008), dry deciduous forest (n= 73 in 1997, n=73 in 2008) and moist deciduous forest (n=22 in 1997, n=20 in 2008) in 1997 and 2008. Lines denote significant linear relationships ($p< 0.05$) in the case of scrub-savanna (solid line), dry deciduous forest (dashed line), and moist deciduous forest (dotted line). Note the differences in x-axes range among panels.

Discussion

Lantana as an 'ideal weed' in tropical dry forests

Baker (1965) describes the characteristics of an 'ideal weed' as a phenotypically-plastic perennial capable of germinating under a wide variety of conditions, exhibiting fast growth, flowering early, being self-compatible, producing copious amounts of seeds that are dispersed widely, reproducing vegetatively, and being an efficient competitor. Although this may seem a tall order, lantana typifies many of these characteristics. Lantana can form thickets up to 5 m tall, as well as climb into tree canopies 20 m above the ground (Tireman, 1916). It flowers early, and year-round, and is self-compatible (Day *et al*., 2003; Mathur and Ram, 1986). Lantana produces large amounts of fruit (Tireman, 1916) that are eaten by a wide variety of avian (Bhatt and Kumar, 2001; Corlett, 1998) and a few mammalian dispersers (e.g. wild pig [*Sus scrofa*] and sloth bear [*Melursus ursinus*]; personal observation). In addition to reproduction via seed, lantana can also resprout vegetatively from root stock (Day *et al*., 2003).

This study clearly shows that by 2008, the distribution and density of lantana had increased dramatically in BRT from its 1997 levels. Overall, the increase in lantana density has been the most in the deciduous forest types (scrub-savanna, dry-, and moist deciduous forests). Gooden *et al*. (2009a) found that native species richness, diversity, abundance, and population structure are negatively affected by lantana invasion. However, removing lantana from sites resulted in increased species richness and native species recruitment, indicating that active management, including follow-up removals, could potentially mitigate the negative effects of lantana invasion (Gooden *et al*., 2009a).

Invasive species spread and the invasibility of heterogeneous landscapes

Forest type heterogeneity has been found to influence levels of invasion in many areas, with some forest types like grasslands and lowlands being more prone to invasion than heathlands and uplands (Chytry *et al*., 2009; Stohlgren *et al*., 2002). In this study, even though forest types differ in their physical structure, high levels of lantana invasion are seen in the deciduous forest types

which have an open canopy for up to 3 months of the year. Canopy openness has been reported to be a key factor that influences lantana invasibility in many forest types across the world. In the wet sclerophyllous forests of Australia, lantana's invasive capacity increases with understory and overstory canopy removal (Duggin and Gentle, 1998). Similarly, studies in the dry forests of Uganda report that gap size and canopy openness are key factors that govern lantana population size and reproductive effort (Totland *et al*., 2005). There is also evidence for lantana cover being much higher in areas with a low native canopy cover (Raizada *et al*., 2008). Canopies in the deciduous forests of BRT are largely leafless during February- March every year (R. Siddappa Setty, unpublished data). Canopy openness in the deciduous forest types could thus explain presence of lantana in the deciduous forests of BRT.

In addition to canopy openness, there could be other factors that enhance lantana success in BRT. There is evidence that seed germination and seedling establishment rates of lantana increase with light availability and disturbance such as fire and understory clearing (Duggin and Gentle, 1998). There is also evidence that lantana exerts tremendous propagule pressure — particularly from invaded areas— that enables it to colonize uninvaded sites over time (Sundaram *et al*. unpublished manuscript). Therefore, habitat heterogeneity, combined with the proximity of lantana seed sources (i.e. sources of propagule pressure), may be playing a role in influencing ecosystem invasibility.

Invasive species spread and effects on native communities

Lantana invasion in BRT has been accompanied by significant reductions in species richness, diversity and evenness, at both the landscape scale and in the deciduous forest types. Although lantana was reported from BRT almost eight decades ago, lantana density was relatively negligible in 1997 when compared to 2008. The recent and rapid spread of lantana in BRT, despite its relatively long presence in the area, supports the idea of lag phases in invasive species spread within heterogeneous habitats (Sakai *et al*., 2001). After arrival, invasive species are sometimes able to lie in wait for long periods of time before expanding their range or increasing in abundance (Wangen and Webster, 2006; Crooks, 2005; Shigesada *et al*., 1995).

The reduction in species richness, diversity, and evenness with increasing lantana density could possibly occur directly or indirectly. Sakai *et al*. (2001) broadly classify interactions between native and invasive species as either being direct (via predation or competition) or indirect (via habitat alteration). Community-level declines in species richness, diversity, and evenness observed in BRT indicate that both direct and indirect interactions may be occurring simultaneously. Decreasing species richness and diversity along a lantana invasion gradient in BRT indicate direct effects of competition. Some native species are probably being out-competed by lantana, possibly because lantana—like other invasive species—utilizes limiting resources efficiently (e.g. Funk and Vitousek, 2007). Additionally, due to the dominance of lantana in BRT, indirect effects on native species due to alteration of habitat are also possible. Indirect effects on native species may occur due to the poor survival of light-demanding seedlings of native tropical dry forest species (Vieira and Scariot, 2006) under conditions of high lantana abundance and shade.

Changes in the demography of native woody species

Invasive species affect native biodiversity by suppressing new recruitment (Litton *et al*., 2006) and by changing the physical structure of invaded forests (Gooden *et al*., 2009b). The size class structure of trees and shrubs in BRT have changed over time with an increase in lantana abundance. Lantana invasion is most likely resulting in recruitment limitation for small trees. However, in a heterogeneous landscape like BRT, examining the effects of lantana on size-class distributions at both the landscape scale and at the scale of individual forest types has proved to be illuminating. The landscape-level patterns of size class distributions in 1997 and 2008 indicate that recruitment limitation is occurring in all size class of trees. However, analysis of tree size class distributions within each forest type revealed that the recruitment of small stems in the scrub-savanna and dry deciduous forests has been severely affected. Lantana could impede the recruitment of young tree individuals by successfully competing for space and light, and is a pattern that has been observed in Australia (Gooden *et al*., 2009a). Additionally, studies from a neighboring tropical dry forest indicate that tree populations are bereft of saplings in lantana-invaded areas (Prasad 2010). Lastly, the reduction in the density of adult trees in the moist deciduous forests could probably be due to the effects of other disturbances (such as fire) that

occur in the study area. The frequency and intensity of forest fires in the tropical dry forests of the Western Ghats is on the increase (Kodandapani *et al*., 2004). It is also possible that fires occurring in areas heavily invaded by lantana are more intense (Hiremath and Sundaram, 2005) with lantana possibly creating ladder fuels that lead to canopy fires (Tireman, 1916). Prasad (2009) suggests that tree mortality is higher in areas with a dense lantana understory, especially along roads, when compared to areas free of lantana and away from roads. Therefore, the reduction in the population of large trees in the moist deciduous forests of BRT may be due to the combined effects of forest fires occurring in lantana-invaded sites. However, more experimental work will be required to investigate the mechanistic links between reduced tree recruitment and lantana invasion.

Unlike the size class distribution of trees, where recruitment limitations have been observed, lantana invasion has been accompanied by an increase in the density of juvenile shrubs at the landscape level. Patterns of increased juvenile shrub recruitment seen at the landscape level have been mirrored by patterns observed in the dry- and moist deciduous forests. The increase in the density of small shrubs was largely driven by the recruitment of two species: *Maesa indica*, and *Cipadessa baccifera*. These two species are probably responding positively to the same factors that promote lantana. Both *M. indica* and *C. baccifera* share characteristics shown by lantana: both species are understory shrubs, have fruits that are bird dispersed, and are unpalatable to wild herbivores (M.D. Madhusudan, personal communication). The possible lack of dispersal limitation and escape from herbivory may be resulting in population increases for both *M. indica* and *C. baccifera*.

Changes in the population structure of trees and shrubs in BRT are likely to result in a change in the physical structure of the forest over the long term. Recruitment limitations seen for tree populations in BRT is likely to be amplified over the long term, since there will be fewer recruits available to replace dying adult trees. Simultaneously, an increase in the population of shrubs such as *M. indica* and *C. baccifera* is likely to make the deciduous forests of BRT shrubbier than what it is presently. Community level changes that occur due to the effects of invasive species often result in a shift in the physical structure of the forest. For example, lantana invaded forests in Australia have shown a gradual shift in physical structure from tall woodland to short-statured

shrubland (Gooden *et al*., 2009b). Results from this study indicate that active and large-scale lantana removal coupled with restoration efforts will be required to arrest and reverse the negative effects of lantana in the BRT landscape.

References

Anonymous (1942) Control of lantana in Madras. *Nature*, **150**, 399-400.

Anonymous (1996) *Map of Karnataka soils.* National Bureau of Soil Survey and Land-Use Planning, Indian Council for Agriculture Research, Nagpur.

Ashton, I.W., Hyatt, L.A., Howe, K.M., Gurevitch, J. & Lerdau, M.T. (2005) Invasive species accelerate decomposition and litter nitrogen loss in a mixed deciduous forest. *Ecological Applications*, **15**, 1263-1272.

Baker, H.G. (1965) Characteristics and modes of origin of weeds. *The genetics of colonizing species* (ed. by H.G. Baker & C.L. Stebbins), pp. 147-169. Academic Press, New York.

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

Bhatt, D. & Kumar, A. (2001) Foraging ecology of red-vented bulbul *Pycnonotus cafer*, in Haridwar, India. *Forktail*, **17**, 109-110.

Chytry, M., Pysek, P., Wild, J., Pino, J., Maskell, L.C. & Vila, M. (2009) European map of alien plant invasions based on the quantitative assessment across habitats. *Diversity and Distributions*, **15**, 98-107.

Clavero, M., Brotons, L., Pons, P. & Sol, D. (2009) Prominent role of invasive species in avian biodiversity loss. *Biological Conservation*, **142**, 2043-2049.

Corlett, R.T. (1998) Frugivory and seed dispersal by birds in Hong Kong shrubland. *Forktail*, **13**, 23-27.

Crawley, M.J. (2007) *The R Book*. Wiley, New Jersey.

Cronk, Q.C.B. & Fuller, J.L. (1995) *Plant invaders.* Chapman and Hall, London.

Crooks, J.A. (2005) Lag times and exotic species: the ecology and management of biological invasions in slow-motion. *Ecoscience*, **12**, 316-329.

Day, M.D., Wiley, C.J., Playford, J. & Zalucki, M.P. (2003) *Lantana: current management status and future prospects.* Australian Centre for International Agriculture Research, Canberra, Australia.

Duggin, J.A. & Gentle, C.B. (1998) Experimental evidence on the importance of disturbance intensity for invasion of *Lantana camara* L. in dry rainforest-open forest ecotones in north-eastern NSW, Australia. *Forest Ecology and Management*, **109**, 279-292.

Fisher, J.L., Loneragan, W.A., Dixon, K., Delaney, J. & Veneklaas, E.J. (2009) Altered vegetation structure and composition linked to fire frequency and plant invasion in a biodiverse woodland. *Biological Conservation*, **142**, 2270-2281.

Fritts, T.H. & Rodda, G.H. (1998) The role of introduced species in the degradation of island ecosystems: a case history of Guam. *Annual Review of Ecology and Systematics*, **29**, 113-140.

Funk, J.L. & Vitousek, P.M. (2007) Resource-use efficiency and plant invasion in low-resource systems. *Nature*, **446**, 1079-1081.

Ganesan, R. & Setty, R.S. (2004) Regeneration of *amla*, an important non-timber forest product from southern India. *Conservation and Society*, **2**, 365-375.
Gooden, B., French, K. & Turner, P.J. (2009a) Invasion and management of a woody plant, *Lantana camara* L., alters vegetation diversity within wet sclerophyll forest in southeastern Australia. *Forest Ecology and Management*, **257**, 960-967.
Gooden, B., French, K., Turner, P.J. & Downey, P.O. (2009b) Impact threshold for an alien plant invader, Lantana camara L., on native plant communities. *Biological Conservation*, **142**, 2631-2641.
Gordon, D.R. (1998) Effects of invasive, non-indigeneous plant species on ecosystem processes: lessons from Florida. *Ecological Applications*, **8**, 975-989.
Hejda, M., Pysek, P. & Jarosik, V. (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology*, **97**, 393-403.
Hillebrand, H., Bennett, D.M. & Cadotte, M.W. (2008) Consequences of dominance: a review of evennes effects on local 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.
Huenneke, L.F., Hamburg, S.P., Koide, R., Mooney, H.A. & Vitousek, P.M. (1990) Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology*, **71**, 478-491.
Iyengar, A.V.V. (1933) The problem of the lantana. *Current Science*, **1**, 266-269.
Johnson, E.A. & Miyanishi, K. (2008) Testing the assumptions of chronosequences in succession. *Ecology Letters*, **11**, 419-431.
Kammathy, R.V., Rao, A.S. & Rao, R.S. (1967) A contribution towards a flora of Biligirirangan Hills. *Mysore State Bulletin: Botanical Survey of India*, **9**
Kodandapani, N., Cochrane, M.A. & Sukumar, R. (2004) Conservation threat of increasing fire frequencies in the Western Ghats, India. *Conservation Biology*, **18**, 1553-1561.
Landres, P.B., Morgan, P. & Swanson, F.J. (1999) Overview of the use of natural variability concepts in managing ecological systems. *Ecological Applications*, **9**, 1179-1188.
Litton, C.M., Sandquist, D.R. & Cordell, S. (2006) Effects of non-native grass invasion on aboveground carbon pools and tree population structure in a tropical dry forest of Hawaii. *Forest Ecology and Management*, **231**, 105-113.
Magurran, A.E. (1983) *Ecological diversity and its measurement.* Croom Helm, London.
Mathur, G. & Ram, H.Y.M. (1986) Floral biology and pollination of Lantana camara. *Phytomorphology*, **36**, 79-100.
Melbourne, B.A., Cornell, H.V., Davies, K.F., Dugaw, C.J., Elmendorf, S., Freestone, A.L., Hall, R.J., Harrison, S., Hastings, A., Holland, M., Holyoak, M., Lambrinos, J., Moore, K. & Yokomizo, H. (2007) Invasion in heterogeneous world: resistance, coexistence or hostile takeover? *Ecology Letters*, **10**, 77-94.
Mittermeier, R.A., Robles-Gil, P., Hoffman, M., Pilgrim, J.D., Brooks, T.M., Mittermeier, C.G., Lamoreux, J.L. & Fonseca, G. (2004) *Hotspots revisited: Earth's biologically richest and most endangered terrestrial ecoregions.* . CEMEX, Mexico City.
Murali, K.S., Setty, R.S., Ganeshaiah, K.N. & R, U.S. (1998) Does forest type classification reflect spatial dynamics of vegetation? An analysis using GIS techniques. *Current Science*, **75**, 220-227.

Murali, K.S. & Setty, R.S. (2001) Effect of weeds Lantana camara and Chromelina odorata growth on the species diversity, regeneration and stem density of tree and shrub layer in BRT sanctuary. *Current Science*, **80**, 675-678.
Myers, N. (2003) Biodiversity hotspots revisited. *Bioscience*, **53**, 916-917.
Olden, J.D. (2006) Biotic homogenization: a new research agenda for conservation biogeography. *Journal of Biogeography*, **33**, 2027-2039.
Pauchard, A. & Shea, K. (2006) Integrating the study of non-native plant invasions across spatial scales. *Biological Invasions*, **8**, 399-413.
Prasad, A.E. (2010) Effects of an Exotic Plant Invasion on Native Understory Plants in a Tropical Dry Forest. *Conservation Biology*, **24**, 747-757.
Prasad, A.E. (2009) Tree community change in a tropical dry forest: the role of roads and exotic plant invasion. *Environmental Conservation*, **36**, 201-207.
R Development Core Team. (2009) *R: A language and environment for statistical computing.* R Foundation for Statistical Computing.
Raizada, P., Sharma, G.P. & Raghubanshi, A.S. (2008) Ingress of lantana in dry tropical forest fragments: edge and shade effects. *Current Science*, **94**, 180-182.
Ramesh, B.R. (1989) *Flora of Biligirirangan Hills.* Madras University, Chennai.
Ranganathan, C.R. (1934) *Working plan, Kollegal Forest Division.* Government of India, Madras.
Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N. & Weller, S.G. (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics*, **32**, 305-332.
Sanders, N.J., Gotelli, N.J., Heller, N.E. & Gordon, D.M. (2003) Community disassembly by an invasive species. *Proceedings of the National Academy of Sciences*, **100**, 2474-2477.
Sharma, G.P., Raghubanshi, A.S. & Singh, J.S. (2005) *Lantana* invasion: an overview. *Weed Biology and Management*, **5**, 157-165.
Sharma, G.P. & Raghubanshi, A.S. (2006) Tree population structure, regeneration and expected future composition at different levels of *Lantana camara* L. invasion in the Vindhyan tropical dry deciduous forest of India. *Lyonia*, **11**, 27-39.
Shigesada, N., Kawasaki, K. & Takeda, Y. (1995) Modeling stratified diffusion in biological invasions. *Am Nat*, **146**, 229-251.
Srinivasan, U. & Prashanth, N.S. (2005) Additions to the avifauna of the Biligirirangan Hills, Karnataka. *Indian Birds*, **1**, 103.
Stinson, K.A., Campbell, S.A., Powell, J.R., Wolfe, B.E., Callaway, R.M., Thelen, G.C., Hallett, S.G., Prati, D. & Klironomos, J.N. (2006) Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. *PLoS Biology*, **4**, 727.
Stohlgren, T.J., Chong, G.W., Schell, L.D., Rimar, K.A., Otsuki, Y., Lee, M., Kalkhan, M.A. & Villa, C.A. (2002) Assessing vulnerability to invasion by nonnative plant species at multiple spatial scales. *Environmental Management*, **29**, 566-577.
Stohlgren, T.J. (2007) *Measuring plant diversity: lessons from the field.* Oxford University Press, New York.
Strayer, D.L., Eviner, V.T., Jeschke, J.M. & Pace, M.L. (2006) Understanding the long-term effects of species invasions. *Trends in Ecology and Evolution*, **21**, 645-651.
Tireman, H. (1916) Lantana in the forests of Coorg. *Indian Forester*, **42**, 384-392.

Totland, O., Nyeko, P., Bjerknes, A.-L., Hegland, S.J. & Nielsen, A. (2005) Does forest gap size affect population size, plant size, reproductive success and pollinator visitation in *Lantana camara*, a tropical invasive shrub? *Forest Ecology and Management*, **215**, 329-338.

Traveset, A. & Richardson, D.M. (2006) Biological invasions as disruptors of plant reproductive mutualisms. *Trends in Ecology & Evolution*, **21**, 208-216.

Vieira, D.L.M. & Scariot, A. (2006) Principles of natural regeneration of tropical dry forests for restoration. *Restoration Ecology*, **14**, 11-20.

Wangen, S.R. & Webster, C.R. (2006) Potential for multiple lag phases during biotic invasions: reconstructing an invasion of the exotic tree Acer platanoides. *Journal of Applied Ecology*, **43**, 258-268.

Chapter 3: Factors influencing the arrival, establishment, and spread of *Lantana camara*

Introduction

The success of any invasive species is contingent upon its performance in the arrival, establishment and spread stages (Sakai *et al*. 2001, Vermeij 1996). Introduced species that are unsuccessful in any of these three stages rarely become invasive (Marchetti *et al*. 2004, Kolar and Lodge 2002). Therefore information on the factors influencing invasive species arrival, establishment, and spread is of interest to biologists and managers alike (Von Holle and Simberloff 2005). Unfortunately, there are very few empirical studies that identify factors driving invasive species success within an area (but see Tobin *et al*. 2009, Kolar and Lodge 2002), often due to the absence of long-term information on the temporal change in distribution and abundance of invasive species, as well as lack of data on the factors that may influence the performance of the invasive in the arrival, establishment and spread phases.

Species invasions are driven by a synergy between mechanistic factors related to the biology of the invasive species (Sakai *et al*. 2001, Rejmanek and Richardson 1996) and the disturbance regime prevalent in the area (Shea and Chesson 2002, Hobbs and Huenneke 1992). Biological advantages possessed by invasive species, such as high propagule output and the lack of dispersal limitation (Traveset and Richardson 2006), enhance their success by conferring on them a competitive edge over native species in recipient habitats (Sakai *et al*. 2001, Blossey and Notzold 1995). Furthermore, reduced regulation by herbivores or predators ("enemy-release") in their introduced range also enhances invasive species' success in recipient habitats (Keane and Crawley 2002). The disturbance regime prevalent in an area also plays a pivotal role in influencing the success of invasive species (Levine *et al*. 2003). For example, some invasive species are successful because they alter the fire regime to their advantage in areas they invade (D' Antonio and Vitousek 1992). Similarly invasive species are better able to take advantage of historical disturbance such as clear-cutting to successfully establish (Brown and Gurevitch 2004, Seabloom *et al*. 2003). Other disturbance factors, such as the presence of roads, may also provide

pathways for the successful spread and establishment of invasives (Bradley and Mustard 2006, Forman and Alexander 1998). An analysis of an invasive species' success, which examines the performance of the invasive species separately during the arrival, establishment and spread phases, could enrich our knowledge of biological invasions and help manage habitat affected by invasive species (Levine *et al*. 2003).

I examine the factors influencing the arrival, establishment, and spread of *Lantana camara* L. (hereafter, lantana) in a tropical dry forest in the Western Ghats, India, where rapid invasion has occurred over the past decade (Sundaram and Hiremath, manuscript submitted). The study area is an ideal system to examine the drivers of lantana success for several reasons. First, the occurrence of forest fires enables examination of the role played by disturbance on lantana invasion. Second, lantana invasion as a result of legacy effects created by historical forestry activities and slash-and-burn agriculture can also be examined in the area. Third, the presence of different habitat types in the area enables examination if some types are more vulnerable than others to lantana invasion. Fourth, the presence of human settlements enables examination of the role played by contemporary human habitation on lantana invasion. Lastly, since data on the presence and abundance of lantana is available for 1998 (Murali and Setty 2001), it is possible to examine the effect of local arrival on lantana invasion. Lantana is considered amongst the world's hundred most invasive species (Lowe *et al*. 2000), and is widely distributed in India. Although the invasive nature of lantana in India has been acknowledged for almost a century (Tireman 1916, Iyengar 1933), its spread in Indian forests has continued unabated. However, lantana invasion has not progressed at the same speed across different forests in India (Sharma *et al*. 2005), possibly due to variation of factors such as fire frequency, habitat suitability for lantana, landscape history, contemporary disturbance, edge effects, and propagule pressure (Raizada *et al*. 2008, Colautti *et al*. 2007, Hiremath and Sundaram 2005). Given the apparent multivariate nature of the factors that influence lantana invasion, I use an information-theoretic, model-selection approach (Burnham and Anderson 2002) to determine the relative importance of fire frequency, landscape history, habitat suitability, contemporary disturbance, edge effects, and propagule pressure on the arrival, establishment, and spread of lantana in a tropical dry forest landscape in the Western Ghats, India.

Methods

Study area

This study was conducted in the Biligiri Rangaswamy Temple Wildlife Sanctuary (hereafter, BRT) in Karnataka, India. The sanctuary is part of the Western Ghats biodiversity hotspot. The sanctuary is 540 km^2 in area, and is located between 77º – 77º 16′ E, and 11º 47′ – 12º 09′ N. The terrain in BRT is undulating, and elevation ranges from about 600 m in the foothills to about 1800 m in the upper reaches. Annual rainfall in the study area is also highly variable, ranging from ca 900 mm at low elevations to ca 1750 mm at higher elevations. The mean annual temperature in the study area is 25.3 ºC, but varies with elevation. Winter temperatures come down to a mean minimum of 11 °C in the higher elevations, while summer temperatures soar to mean maximum of 42 °C in the foothills (Murali *et al*. 1998). Soils in BRT are well-drained gravelly clays that have been classified as typic ustropepts (Anon. 1996). The study area was declared a Wildlife Sanctuary in 1973 (Barve *et al*. 2005), after which logging and plantation activities (both clear- and selection-felling) were suspended, and most human settlements within the area were relocated to settlements located in the park's periphery (Fig. 3.1).

The study area has a long history of human habitat modification and use. Forestry activities in the area began in earnest during the 1930s (Ranganathan 1934), with the establishment of forest blocks to harvest sandalwood (*Santalum album*), bamboo (both *Bambusa arundanacea* and *Dendrocalamus strictus*), and timber (via selection- and clear-felling). In addition to disturbance generated by forestry activities, shifting agriculture was practiced by the Soliga in several sites across the BRT landscape over centuries, and this entailed the slashing and burning of understory vegetation prior to planting (Madegowda 2009). The Soliga also collect non-timber forest products such as Indian gooseberry (*Phyllanthus emblica* and *Phyllanthus indofischierii*) and honey. Although collection rights of forest products were suspended or curtailed after the creation of the wildlife sanctuary in 1973, Soliga collection rights were protected by recent legislation such as the Wildlife (Protection) Amendment Act 2007.

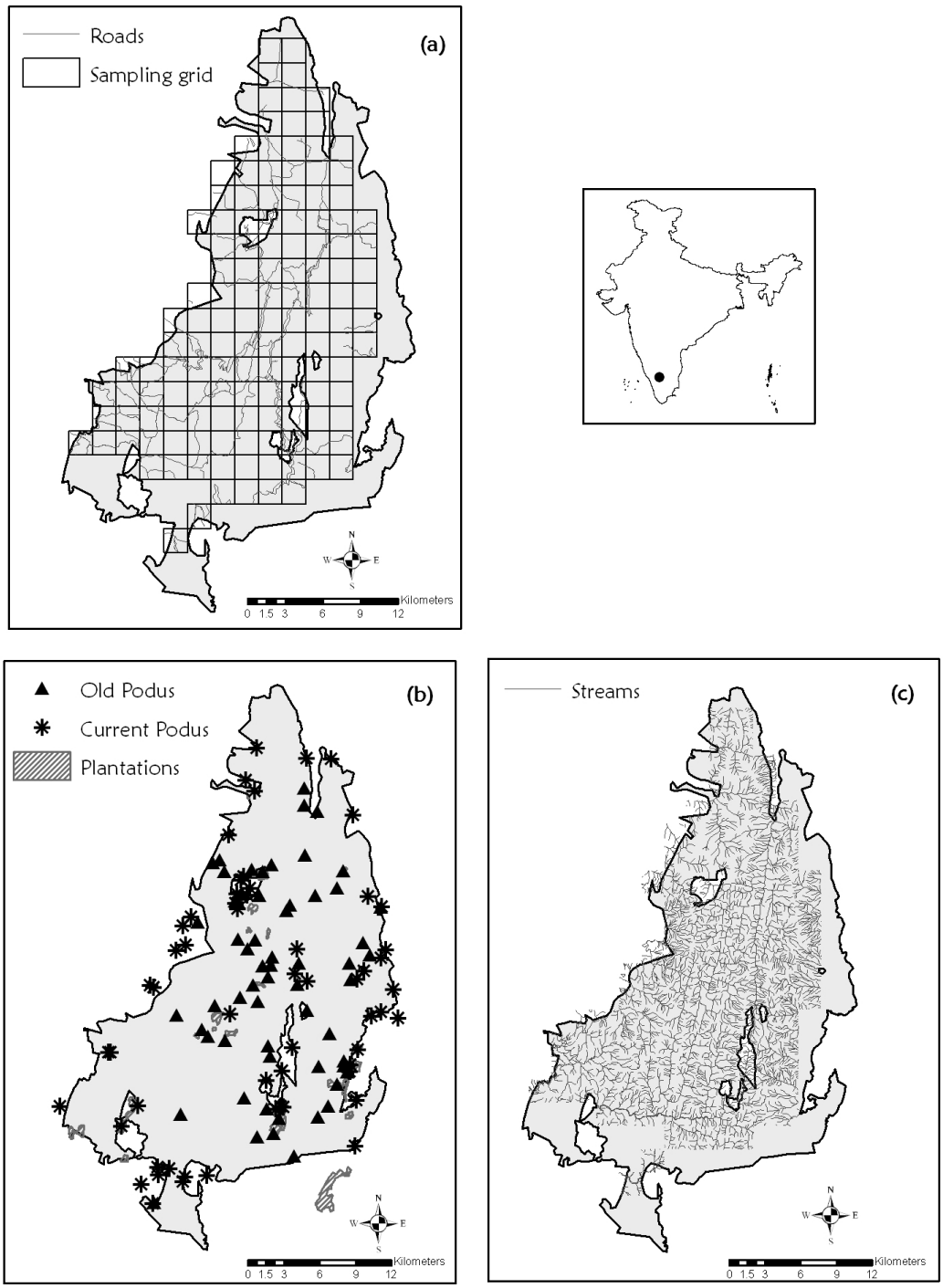

Fig. 3.1: Map of BRT showing sampling grids and roads (a), old podus, current podus, and areas of historical plantation activity (b), and streams (c). Inset map of India shows location of BRT.

There are several forest types in BRT. Of these, the seasonally dry forests constitute approximately 90% of the study area (Ganesan and Setty 2004) and include the scrub-savanna, dry deciduous and moist deciduous forests. These forests are extensively invaded by *Lantana camara* (Sundaram and Hiremath, manuscript submitted).

Lantana was introduced to India on multiple occasions almost two centuries ago, and is one of the most widespread plant invasive species in India (Hiremath and Sundaram 2005). The success of lantana in Indian forests could be associated with lantana's ability to resprout in response to fire, and to the lack of propagule and dispersal limitations (Hiremath and Sundaram, manuscript submitted). The spatial extent of lantana in BRT has increased dramatically from 1997 to 2008. Lantana was present only in ~ 40 % of plots across BRT in 1997 (Murali and Setty 2001), but had spread to ~ 80 % of the same plots by 2008 (Sundaram and Hiremath, manuscript submitted). Simultaneously, there has been a significant decrease in native species diversity in the scrub-savanna and dry deciduous forests of BRT over this period (Hiremath and Sundaram, manuscript submitted).

Lantana arrival, establishment, and spread

Information on lantana distribution in BRT from 1997 was gathered from a published source (Murali and Setty 2001). Between January and April 1997, Murali and Setty (2001) first overlaid a 2 x 2 km grid over the entire study area. They then counted and identified all vegetation $\geq$ 1 cm diameter at breast height (DBH) from a total of 134 plots – one plot at the center of every grid cell. Plots were 80 x 5 m in size, with the long axis of the plot oriented north-south.

To enable assessment of lantana arrival, establishment, and spread since 1997, I employed the same plot locations and field protocol used by Murali and Setty (2001). Field work to ascertain contemporary distribution of species was conducted from August 2007 to January 2008. Twelve of the original 134 plots were found to occur in habitation or plantation during my survey, presumably as a result of a change in land-use at these locations between 1997 and 2008. Data from these plots were therefore excluded from analyses.

Drivers of lantana arrival, establishment, and spread

A set of important predictor variables were identified from a survey of published sources related to the characteristics of lantana invasion, both in BRT (e.g., Murali and Setty 2001) and elsewhere (Babu *et al*. 2009), and invasion by other species in general. The key predictor variables identified were fire frequency (Hiremath and Sundaram 2005, Day *et al*. 2003, Duggin and Gentle 1998), habitat suitability for lantana (Babu *et al*. 2009, Totland *et al*. 2005, Sharma *et al*. 2005), proximity to historical disturbances such as plantations and sites of human habitation (Brown and Gurevitch 2004, Levine *et al*. 2003), proximity to current habitation (Barve *et al*. 2005), proximity to habitat edges such as roads and streams (Raizada *et al*. 2008, Bradley and Mustard 2006), and propagule pressure (Colautti *et al*. 2006, Lockwood *et al*. 2005).

Previous studies have hypothesized that an increase in fire frequency may lead to an increase in lantana invasion (Sharma *et al*. 2005, Hiremath and Sundaram 2005). The mapping of areas burnt by forest fires was conducted each year from 1997-2002 (R. Siddappa Setty *et al*. unpublished data), and 2004-2007 (this study), yielding fire maps for 10 of the 11 years over which change in lantana distribution has been assessed. Each year during April-May, the entire road network within BRT was traversed by vehicle. Burnt areas visible from the roads were marked on a topographical sheet (scale 1:50000, or 1 cm = 500 m). Additional burnt areas that were not visible from the roads were mapped from vantage points within BRT. There were at least 17 locations that were consistently used as vantage points every year. The topographical sheet on which fires were mapped was scanned and burnt areas were digitized using MapInfo software. Based on fire maps from 1997-2002 and 2004-2007 fire frequency was calculated for each grid cell as the total number of times the cell burned across the sampling period (i.e., between 1997 and 2007). In case the grid was incompletely burnt, the grid cell was scored as burnt only if the grid centre (where plots were located) was burnt.

Choosing an appropriate variable to quantify habitat suitability for lantana was a challenging task. From previous studies, it was apparent that lantana does not occur in areas that have an evergreen forest canopy (Sharma *et al*. 2005). In the Western Ghats, phenological attributes, e.g., vegetation evergreen-ness, is highly correlated with environmental conditions such as rainfall

(Champion and Seth 1968). Published information (Gentle and Duggin 2006, Day *et al*. 2003) and experience from my study area also suggests that lantana is successful in dry- and moist deciduous environments vis-à-vis wet, evergreen environments. The target variable or index that describes lantana habitat suitability should therefore incorporate a measure of evergreen-ness (or its opposite- deciduousness). The degree of evergreen-ness or deciduousness is often derived through the inter-seasonal variation in canopy biomass, with the assumption that high canopy biomass values, combined with low variance in how canopy biomass fluctuates inter-seasonally are indicative of evergreen canopies (Roderick *et al*. 1999, Running *et al*. 1994). On the other hand, relatively lower canopy biomass, combined with high variance in canopy biomass across seasons, are indicative of deciduous canopies (Roderick *et al*. 1999, Running *et al*. 1994). A recent index, the '*eco-climatic distance'* developed by Krishnaswamy *et al*. (2009) and Krishnaswamy *et al*. (2004) for the Western Ghats and BRT was used because it takes evergreen-ness and canopy biomass into account. Eco-climatic distance (ECD) is a Mahalanobis distance that uses remotely-sensed, multi-date Normalized Difference Vegetation Index (NDVI) to arrive at a degree of deciduousness for each pixel (Krishnaswamy *et al*. 2009). Each pixel in the Krishnaswamy *et al*. (2009) study was 23.5 m^2, while the plot size used in this study is 400 m^2. To account for the difference in size between remotely-sensed ECD and plots from which ground data was gathered, values of ECD were averaged for all pixels encompassed within each plot.

The satellite images that were used for the derivation of ECD by Krishnaswamy *et al*. (2009) was from 1998-1999, which was fortuitous for this study. One can assume that the density of lantana in BRT was negligible during this period, as we know from the survey carried out just one year prior to this (Murali and Setty 2001). By 2007-08 lantana density had increased dramatically (Sundaram and Hiremath, manuscript submitted). Had more recent satellite imagery been used to calculate ECD the increased presence of lantana would have contributed substantially to remotely sensed NDVI values, thereby confounding any model-building exercise using ECD as a predictor for lantana occurrence and spread.

Field observations from BRT indicated that a large proportion of historical plantation and agricultural sites are heavily invaded by lantana. It is possible that these were the original

locations of lantana, which could have provided a potential source of lantana propagules. Information about the locations of historical clear- and selection-felling sites was obtained from the field (using a hand-held GPS unit) and from historical records of the Karnataka Forest Department (Ranganathan 1934) for the entire study area. In addition, locations of sites of historical habitation were obtained from an ongoing study that documents the historical use of BRT by its long-term residents, the Soliga (Madegowda 2009).

Several studies (Raizada *et al*. 2008, Totland *et al*. 2005, Day *et al*. 2003) indicate that edge effects and contemporary disturbance may play an important role in lantana invasion. In the context of BRT, sites of present-day habitation, roads, and streams were all included in this category of 'contemporary disturbance.' The location of current habitation, roads, and streams was recorded in the field using a GPS. All geographical information was then digitized and minimum proximity (m) of each plot from each predictor (present-day habitation, roads, streams) was calculated using MapInfo software.

The lantana neighborhood index is an indirect estimate of the propagule pressure (*sensu* Colautti *et al*. 2006, Lockwood *et al*. 2005) that confronts each grid cell. To calculate the neighborhood extent of lantana in 1997, I used data on lantana presence/absence from Murali and Setty (2001). Each grid cell in the study area was scored as 0 (lantana absent) or 1 (lantana present). For each grid cell, its four immediate neighbors (grids that were directly connected) were listed. Lantana presence/absence scores were then averaged for immediate neighbors of a given focal cell. This process was repeated for all grid cells in the study area, and a lantana neighborhood index (LNI) for each grid cell was generated.

Response variables, model selection, and data analyses

An information-theoretic, model-selection approach (Burnham and Anderson 2002) was adopted to evaluate suitability of various predictors to describe three response variables— lantana arrival, establishment, and spread. For examining arrival, I used the subset of plots that were uninvaded by lantana in 1997, but were invaded by 2008 (n= 78), with lantana presence in 2008 as the response variable. For examining establishment, I first picked the subset of plots that were

invaded by lantana in 1997 (n= 55). I then calculated the change in lantana density that had occurred by 2008 (2008 lantana density values/ 1997 lantana density values). Change in lantana density was log-transformed to yield the response variable to examine establishment. Lastly, for examining lantana spread (sensu Lockwood *et al*. 2005), I defined spread as the present-day extent of lantana in each plot, relative to total stems. I picked all plots that showed lantana presence by 2008 (n= 96), regardless of whether or not they has lantana in them in 1997. I then calculated the proportion of lantana stems vis-à-vis total stems in the plot, including those of native species. Lantana proportion data were logit transformed.

After response variables were derived, candidate sets of models were developed *a priori* to examine factors underlying lantana arrival, establishment, and spread. For each candidate set, the explanatory variables used were identical, and each predictor variable was used an equal number of times in each candidate set. Having a balanced model set was necessary for the purposes of calculating the importance of each predictor variable individually (Burnham and Anderson 2002, Johnson and Omland 2004). The explanatory variables used in all candidate sets of models were (a) fire frequency (FF), (b) eco-climatic distance (ECD), (c) minimum proximity to historical disturbance (both plantations and habitation; HD), (d) minimum distance to contemporary disturbance (existing habitation; CD), (e) minimum proximity to edge (both roads and streams; EDGE), and lastly, (f) lantana neighborhood index (LNI).

Each candidate set contained a global model that included all predictors. The global models of lantana arrival and lantana establishment included only two-way interactions (e.g., fire frequency * proximity to edge) between predictors. Three-, four- and five-way interactions could not be included on account of small sample size. The global model to describe lantana spread included two-, three-, four-, and five-way interactions between predictors. After defining the global model in each candidate set, a sub-set of separate single-predictor models were then added (a total of six models, one for each predictor). Finally, a sub-set of separate two-way additive models containing all unique combinations of predictor variables were added (a total of 15 models). Thus each candidate set had a total of 22 models (1 global + 6 single predictor + 15 two-way additive = 22 models).

Models that incorporate only LNI can be compared to a null model (e.g. Colautti *et al*. 2006), one that assumes changes in lantana presence/absence and lantana distribution to be only a result of propagule pressure, with no other biophysical variable playing a part in influencing pattern. However, since additive effects of a lantana neighborhood and other predictor variables cannot be biologically discounted (Colautti *et al*. 2006, Sakai *et al*. 2001), two-way additive models that included lantana neighborhood index were also incorporated in each candidate set of models.

A generalized linear model (GLM) with binomial errors and a logit link was used to model lantana arrival. For modeling lantana establishment, a GLM with Gaussian errors and a log link was used. Lantana spread was examined using a GLM with Gaussian errors and a logit link function. For each candidate set of models, a set of background tests were conducted before progressing to the model-selection stage (Burnham and Anderson 2002). The fit of the global model (% variance explained) was first examined. The data were then checked for overdispersion. Overdispersion is a phenomenon by which the sampling variance exceeds the theoretical (model-based) variance in the global model (Burnham and Anderson 2002). The overdispersion parameter $\hat{c}$, is the goodness-of-fit chi-square (χ^2)/degrees of freedom of the global model. Values of $\hat{c} > 1$ are an indication of overdispersed data (Burnham and Anderson 2002), and necessitate the use of quasi-likelihood methods for analysis (Pemberton and Liu 2009). After checking for overdispersion in the data, Akaike's Information Criterion, corrected for small sample sizes (AIC_c; Burnham *et al*. 2002, Johnson and Omland 2004) was calculated for each model. By including a bias correction term for complexity and small sample sizes, AIC_c estimates provide a maximum-likelihood based parsimonious measure of model fit (Johnson and Omland 2004). For each model in a candidate set, Δ_i (value of AIC_c in the i^{th} model – minimum value of AIC_c occurring within the candidate model set) was calculated (Burnham and Anderson 2002). Based on Δ_i values, Akaike weights (relative likelihood of a focal model versus all hypothesized models) were calculated (Burnham and Anderson 2002). Lastly, by summing the Akaike weights for all models where a particular predictor appears, the "weight of evidence of support" (e.g., Marchetti *et al*. 2004) for each predictor was calculated across all models within a candidate set. Data analysis was conducted using R version 2.9.0. (R Development Core Team 2009).

Results

Lantana arrival

In 1997, 78 out of 134 plots were uninvaded by lantana. By 2008, a large majority of these uninvaded plots (54/78= 69 %) were invaded. The global model (all predictors individually, and all two-way additive interactions of predictors) explained 51.1 % of the deviance from the intercept-only model. Lantana arrival data was not overdispersed, with ĉ= 0.12.

Lantana arrival increased with an increase in the extent of lantana neighborhoods around each plot in 1997 (a proxy for propagule pressure; Fig. 3.2a). The model that used only lantana neighborhoods as a predictor of lantana presence had the lowest AIC_c value and the highest Akaike weight when compared to all other models (Table 3.1). The lantana neighborhood index explained 6.2 % of the deviance from the intercept-only model for lantana arrival data. Additionally, parameter averaging indicated that lantana neighborhoods had the highest evidence of support as a predictor of lantana arrival when compared to all other covariates (Table 3.4). Surprisingly, other disturbance factors that affect the study area, such as fire frequency and proximity to edge, did not emerge as being important for explaining lantana arrival when compared to propagule pressure alone.

Lantana establishment

Of the total 55 plots that were invaded in 1997, lantana density increased in 37 plots, remained the same in 2 plots, and decreased in 12 plots. Data from four plots were not analyzed because they had transitioned to plantations or habitation by 2008. The global model containing all predictors and their interactions explained 56.8 % of the deviance from the intercept-only model for lantana establishment data. Overdispersion in lantana establishment data was not evident (ĉ = 0.43).

The frequency of fire in each grid cell during 1997-2008 emerged as the best predictor of lantana establishment. Surprisingly, an increase in fire frequency led to a decrease in lantana density

(Fig. 3.1b). The model using fire frequency alone as a predictor of lantana establishment emerged as the most parsimonious model (lowest AIC_c, highest Akaike weight) and explained 23.6 % of the deviance from the intercept-only model for the data (Table 3.2). Surprisingly, the extent of lantana neighborhoods (which was found to be an important factor driving lantana arrival) did not play a large role in influencing lantana establishment (Table 3.2). Summing the Akaike weights across all models where fire frequency appeared as a predictor revealed that fire frequency had the highest evidence for support when compared to all other predictors (Table 3.4).

Lantana spread

The relative proportion of lantana stems vis-à-vis that of total stems within plots, including stems of native species, ranged from ≈ 0 – 0.93, with a median value of 0.43 (n=96). The global model containing all predictors and interactions explained 77.2 % of the deviance from the intercept-only model for the data. There was no evidence of data overdispersion ($\hat{c}$ = 0.14).

None of the single-predictor models within the candidate set of models were able to sufficiently explain patterns of lantana spread within a plot (Table 3.3). However, the model containing predictors HDIST + ECD emerged to be the most parsimonious model, and accounted for 7.47 % of deviance from the intercept-only model. The proportion of lantana in each plot increased with an increase in eco-climatic distance (Fig. 3.2c), and decreased as the distance from historical disturbance increased (Fig. 3.2d). The model containing HDIST alone had a slightly higher AIC_c value of 28.88 when compared to the HDIST + ECD model (AIC_c = 27.72), but could explain only 3.26 % of the deviance from the intercept-only model in the data (Table 3.3). However, summing the Akaike weights in favor of each predictor over all models where they appeared revealed that the proximity to historical disturbance has the greatest weight over other predictors, closely followed by ECD (Table 3.4).

Table 3.1: Models to explain lantana arrival with their corresponding number of parameters (K), corrected AIC (AIC_C), value of AIC_C in the i^{th} model – minimum value of AIC_C (Δ_i), Akaike weights, and percent deviance from the intercept-only model. The deviance of the intercept-only model was 75.256.

Model	K	AIC_c	Δi	Akaike weights	% deviance explained
Lantana arrival (n= 71)					
Global*	23	116.05	38.27	0.000	51.12
Fire frequency (FF)	3	81.70	3.92	0.047	< 1
Eco-climatic distance (ECD)	3	82.19	4.41	0.036	< 1
Proximity to historical disturbance (HD)	3	82.04	4.26	0.039	< 1
Proximity to contemporary disturbance (CD)	3	82.26	4.48	0.035	< 1
Proximity to edge (EDGE)	3	82.42	4.64	0.032	< 1
Neighborhood index (NI)	3	77.78	0.00	0.330	6.19
FF+ECD	4	84.39	6.61	0.012	1.60
FF+HD	4	84.56	6.78	0.011	1.34
FF+CD	4	84.61	6.83	0.011	1.27
FF+EDGE	4	84.82	7.04	0.010	< 1
ECD+HD	4	84.30	6.52	0.013	1.69
ECD+CD	4	85.13	7.36	0.008	< 1
ECD+EDGE	4	85.27	7.49	0.008	< 1
HD+CD	4	85.04	7.26	0.009	< 1
HD+EDGE	4	85.16	7.39	0.008	< 1
CD+EDGE	4	85.36	7.59	0.007	< 1
NI+FF	4	80.44	2.66	0.087	6.81
NI+ECD	4	80.68	2.90	0.077	6.50
NI+HD	4	79.96	2.18	0.111	7.45
NI+CD	4	80.02	2.24	0.108	7.38
NI+EDGE	4	123.41	45.63	0.000	6.24

Table 3.2: Models to explain lantana establishment with their corresponding parameters (K), corrected AIC (AIC_c), value of AIC_c in the i^{th} model – minimum value of AIC_c (Δ_i), Akaike weights, and percent deviance from the intercept-only model. The deviance of the intercept-only model was 87.44.

Model	K	AIC_c	Δi	Akaike weights	% deviance explained
Lantana establishment (n=55)					
Global*	23	219.71	50.76	0.000	56.75
Fire frequency (FF)	3	168.94	0.00	0.400	23.59
Eco-climatic distance (ECD)	3	182.67	13.72	0.000	< 1
Proximity to historical disturbance (HD)	3	182.51	13.57	0.000	< 1
Proximity to contemporary disturbance (CD)	3	182.64	13.70	0.000	< 1
Proximity to edge (EDGE)	3	181.98	13.03	0.001	1.35
Neighborhood index (NI)	3	182.36	13.42	0.000	< 1
FF+ECD	4	172.12	3.17	0.083	23.69
FF+HD	4	171.27	2.32	0.127	24.95
FF+CD	4	172.15	3.20	0.082	23.65
FF+EDGE	4	170.31	1.37	0.204	26.35
ECD+HD	4	185.69	16.74	0.000	< 1
ECD+CD	4	185.87	16.93	0.000	< 1
ECD+EDGE	4	185.18	16.24	0.000	1.41
HD+CD	4	185.71	16.77	0.000	< 1
HD+EDGE	4	185.11	16.16	0.000	1.56
CD+EDGE	4	185.21	16.27	0.000	1.36
NI+FF	4	171.74	2.79	0.100	24.26
NI+ECD	4	185.60	16.65	0.000	< 1
NI+HD	4	185.27	16.32	0.000	1.25
NI+CD	4	185.57	16.63	0.000	< 1
NI+EDGE	4	184.94	16.00	0.000	1.88

Table 3.3: Models to explain lantana spread with their corresponding parameters (K), corrected AIC (AIC_c), value of AIC_c in the i^{th} model – minimum value of AIC_c (Δ_i), Akaike weights, and percent deviance from the intercept-only model. The deviance of the intercept-only model was 7.057.

Model	K	AIC_c	Δi	Akaike weights	% deviance explained
Lantana spread2 (n=96)					
Global	65	228.57	200.85	0.000	77.16
Fire frequency (FF)	3	31.36	3.64	0.042	< 1
Eco-climatic distance (ECD)	3	30.98	3.26	0.051	1.12
Proximity to historical disturbance (HD)	3	28.88	1.16	0.146	3.26
Proximity to contemporary disturbance (CD)	3	31.15	3.43	0.047	< 1
Proximity to edge (EDGE)	3	30.50	2.78	0.065	1.62
Neighborhood index (NI)	3	31.97	4.25	0.031	< 1
FF+ECD	4	33.20	5.48	0.017	2.03
FF+HD	4	31.07	3.35	0.049	4.18
FF+CD	4	33.49	5.77	0.015	1.74
FF+EDGE	4	32.52	4.80	0.024	2.73
ECD+HD	4	27.72	0.00	0.261	7.47
ECD+CD	4	33.29	5.57	0.016	1.95
ECD+EDGE	4	32.85	5.13	0.020	2.39
HD+CD	4	30.98	3.26	0.051	4.27
HD+EDGE	4	30.81	3.09	0.056	4.45
CD+EDGE	4	32.26	4.54	0.027	2.99
NI+FF	4	34.36	6.64	0.009	< 1
NI+ECD	4	34.05	6.33	0.011	1.17
NI+HD	4	31.74	4.02	0.035	3.51
NI+CD	4	34.11	6.39	0.011	1.11
NI+EDGE	4	33.52	5.80	0.014	1.71

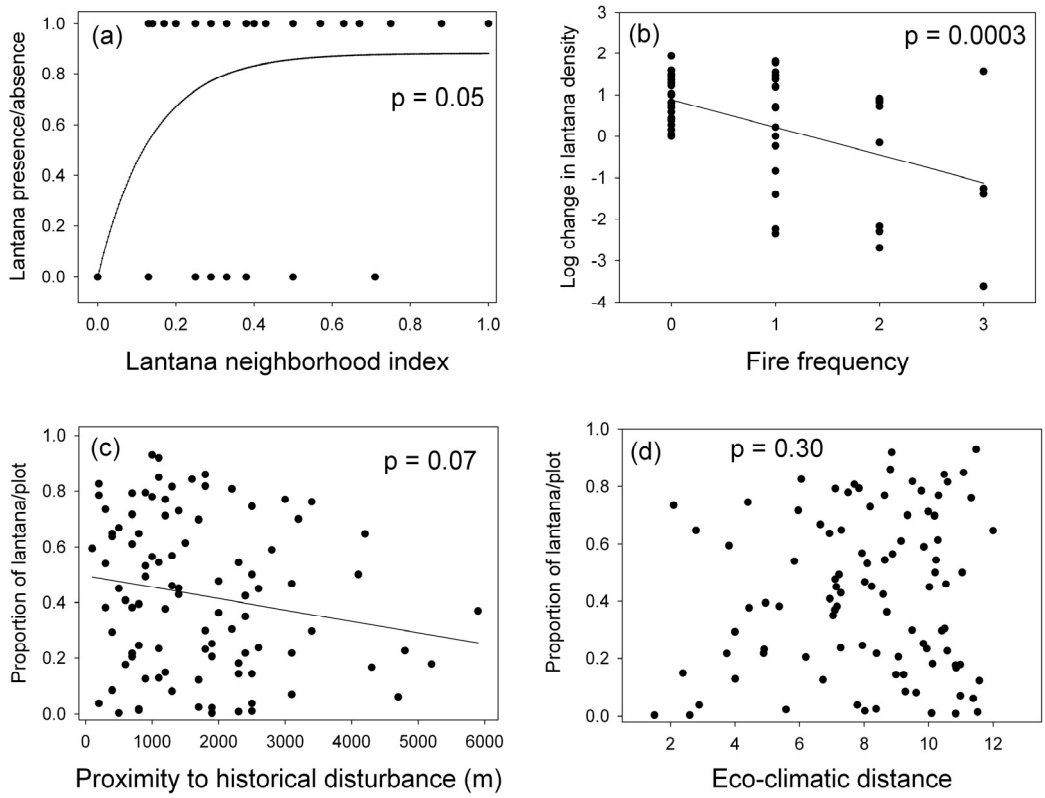

Fig. 3.2: Variables that best explain lantana arrival (a), establishment (b), and spread (c,d).

Table 3.4: Weight of evidence in favor of each variable for explaining lantana arrival, establishment, and spread. The weights for each variable were calculated by summing the Akaike weights of all models where the predictor variable of interest appears (Burnham and Anderson 2002). Greater weights indicate the importance of each predictor, relative to all other predictors.

Predictor variables	Arrival	Establishment	Spread
Fire frequency	0.12	0.62	0.10
Eco-climatic distance	0.10	0.05	0.23
Proximity to historical disturbance	0.13	0.08	0.37
Proximity to contemporary disturbance	0.12	0.05	0.10
Proximity to edge	0.04	0.13	0.13
Neighborhood index	0.48	0.06	0.07

Discussion

Success in the invasion process is defined by the performance of the invasive during the arrival, establishment and spread stages (Sakai *et al*. 2001, Vermeij 1996). There are very few empirical examples that look at all three stages in the same place (but see Tobin *et al*. 2009, Kolar and Lodge 2002). To the best of my knowledge, this is the first empirical study to report important factors driving the arrival, establishment and spread of lantana using long-term field data. Results from this study indicate that different factors are important during different stages of lantana invasion. At the initial stages of lantana invasion, propagule pressure plays an overwhelming role in increasing the probability of arrival. Following lantana arrival, the frequency of forest fires seems to be the most important factor limiting the establishment of lantana. Lastly, the spread of lantana within sites is largely driven by how close the site is to historical habitat disturbance, such as selective- and clear-felling locations, and old human habitation sites.

Although a few factors have emerged as being vital drivers of the lantana invasion process, it is important to note that the three other disturbance factors taken into account in this study (lantana habitat suitability, distance to current human habitation, and distance to edge) also play a role in our understanding of the lantana invasion process. The fit of the data to the global models containing all predictors was high (all global models accounted for > 50 % of the variance in the data) and indicates that the importance of these variables is by no means negligible, although their relative weights remain low in comparison to the primary drivers.

Lantana arrival and the importance of propagule pressure

Propagule pressure has been found to act as an important trigger in the invasion process (Reaser *et al*. 2007, Colautti *et al*. 2006, Von Holle and Simberloff 2005, Lockwood *et al*. 2005). For example, in an experimental study using forest understory plants, Von Holle and Simberloff (2005) found that the successful invasions were largely contingent upon the number of propagules arriving *in situ*, when compared to other factors such as resident diversity and the flooding regime. Additionally, Colautti *et al*. (2006), in their meta-analysis of characteristics of

invasive species world-wide also found that propagule pressure was a significant predictor of both the invasiveness of species and the invasibility of landscapes. However, propagule pressure is dependent upon life history characteristics such as time taken to reach reproductive maturity and dispersal mode, with rapidly maturing species with abiotically dispersed seeds being more successful vis-à-vis slow-maturing biotically dispersed species (Daehler 1998). Lantana plants sometimes take just 6 months to reach maturity (personal observation).

Lantana produces large fruit crops, sometimes up to 10^4 per plant over a single fruiting season in BRT (Monika Kaushik, unpublished data). It is likely that arrival of lantana propagules is enhanced by the year-round fruiting of the species combined with the lack of dispersal limitation. Indeed, studies in the Reunion Islands have shown that a greater population of dispersers (e.g., the invasive red-whiskered bulbul) are supported in areas invaded by four bird-dispersed invasive plants that produce seeds year-round (including lantana), indicating that the lack of dispersal limitation enhances propagule pressure (Mandon-Dalger *et al*. 2004). It is also possible that positive feedback occurs between presence of propagules and presence of dispersers (Mandon-Dalger *et al*. 2004). Bulbuls are responsible for the dispersal of lantana seeds in India as well, with lantana fruit forming up to 10 % of their diet (Bhatt and Kumar 2001). Studies from Hong Kong show that lantana's sugar-rich berries also attract other birds (e.g., Light-vented bulbul; Corlett 1998). Although there are no studies on lantana seed dispersal by mammals, lantana seeds have been observed in the fecal matter of wild pigs and sloth bears in BRT (Bharath Sundaram, personal observation). Thus, an increase in lantana propagule pressure may be driven by the additive effects of both high fruit production and lack of dispersal limitation in BRT.

Information about the exact year of lantana introduction into BRT is unavailable, but forest management plans cite the presence of lantana in the forests of BRT in 1934 (Ranganathan 1934). Although lantana has been present in the BRT landscape for at least 70 y, anecdotal evidence would suggest that it may only have become abundant about 30 years ago, i.e., in the 1970s. Moreover, long-term monitoring suggests that extensive lantana invasion within BRT has occurred only over the past decade (Sundaram and Hiremath, manuscript submitted). Multiple lag phases are inherent in species invasions (Crooks 2005) and introduced species present at low

density could be lying in wait to fund future spread via the build-up of propagule pressure (Colautti *et al*. 2006). In the case of lantana in BRT, the build-up of propagule pressure may have taken up a large part of the time since its introduction into BRT.

Although the weight of evidence in favor of propagule pressure as the primary driver of lantana arrival was high, other predictors were by no means unimportant. The weight of evidence in favor of all predictors associated with disturbance, such as distance to edge, fire frequency, and distance to both contemporary and historical disturbance, were not negligible. Both Colautti *et al*. (2006) and Daehler (1998) observe that synergy between factors that influence both the invasiveness of species and the invasibility of landscapes is the rule, rather than the exception. Similarly, the relatively lower weight of evidence in favor of habitat suitability for lantana (the eco-climatic distance) when compared to propagule pressure may be related to the relative representation of different forest types within the BRT landscape. A large chunk of the BRT landscape is deciduous (~ 90 %; Ganesan and Setty 2004). Thus the eco-climatic distance within the deciduous forests is likely more homogenous.

Lantana establishment and fire frequency as a limiting factor

Theoretical studies of lantana invasibility have hypothesized that an increase in fire frequency could potentially lead to an increase in lantana establishment (Sharma *et al*. 2005, Hiremath and Sundaram 2005). These reviews suggest that since lantana readily resprouts in response to fire, and has a potential advantage over native species that are not fire resistant, an increase in fire frequency could theoretically lead to an increase in lantana establishment (Sharma *et al*. 2005, Hiremath and Sundaram 2005). Results from this study indicate an opposite effect: an increase in fire frequency leads to lower establishment of lantana.

These results are consistent with observed fire effects on lantana in Australia (Day *et al*. 2003). Regular and repeated fires are used in dry forests and pastures to control lantana density, and fire is considered one of the cheapest methods to control lantana (Day *et al*. 2003). Adult lantana, although able to resprout after single or a few instances of fire, do not seem to be able to recover from repeated burning (Day *et al*. 2003). Additionally, there is some evidence from experimental

studies to suggest that surface fires may reduce the density of viable seeds stored in soil (Sundaram and Hiremath, manuscript submitted). However, collateral damage to native species has been recognized to be an important issue while using fire to control lantana in Australia, especially in wet-sclerophyll forests, where fires injure or kill thin-barked trees of native species (Day *et al*. 2003). Although fires are not an uncommon occurrence in Indian tropical dry forests, adult trees of native species that cannot resprout in response to fire are killed by fires, particularly if they occur frequently (Saha and Howe 2003). Additionally, saplings of non-resprouting species, unable to escape from ground fires, are also killed over time (Saha 2002). Further research is therefore required to improve our understanding of the effects of fire on native vegetation communities in tropical dry forests, both above ground in standing vegetation, and below ground in soil seed banks.

Although lantana establishment was best explained by fire frequency, other predictors also play a role, albeit to a lesser extent. Other predictors that were related to disturbance, e.g., distance to historical- and contemporary disturbance, and distance to edge do not play a large role vis-à-vis fire frequency, probably because after lantana arrival aspects of lantana's biology that enhance its invasiveness (e.g., fruit output) are affected more by fire than by other disturbance factors. However, the minimal role played by eco-climatic distance as a factor driving lantana establishment was contrary to my expectations. Studies from Australia and Africa show that lantana establishment is enhanced by the presence of open canopies or gaps (Day *et al*. 2003, Totland *et al*. 2005). However, the effects of eco-climatic distance are probably masked by the large spatial extent of deciduous forests in BRT vis-à-vis other forest types. Lastly, propagule pressure predictably does not play much of a role in influencing lantana establishment. After the arrival of lantana in a site, allochthonous seed dispersal may cease to be important, due to the young age to maturity of lantana and resulting autochthonous seed arrival.

Lantana spread and the importance of landscape history

Legacy effects of historical habitat disturbance on ecosystem invasibility by either a single or suite of invasive species have been noted in many studies (Mosher *et al*. 2009, DeGasperis and Motzkin 2007, Brown *et al*. 2006, Brown and Gurevitch 2004). A case in point is that of

Japanese barberry (*Berberis thunbergii*) invasion in central Massachusetts, USA, where invasion occurred more frequently and with greater abundance in sites that had been cultivated in the past, possibly as a result of changes in soil (DeGasperis and Motzkin 2007). Historical soil disturbance may have played a role in increasing lantana spread in BRT, since tree plantations in BRT were maintained by understory clearing using fire, or manual clearing via the uprooting of shrubby vegetation (Ranganathan 1934). Additionally, shifting agriculture may also have caused soil disturbance. However, information on the actual mechanisms by which soil disturbance could enhance lantana invasion in BRT is lacking.

In addition to historical habitat disturbance, lantana spread was also influenced by eco-climatic distance. Results from this study show that the proportion of lantana stems to total stems in a plot increases with an increase in the degree of deciduousness. This is consistent with existing studies on lantana in BRT, where the deciduous forest types are heavily invaded (Sundaram and Hiremath, manuscript submitted). Similar to patterns seen in Australia (Gooden *et al*. 2009), deciduous conditions probably offer the best conditions for lantana spread in BRT.

Management implications

Lantana camara invasion in BRT is the product of the complex interplay between lantana habitat suitability, frequency of forest fires, proximity to historical and contemporary disturbance, proximity to edge, and propagule pressure. Different factors have been found to be important at different stages of lantana invasion. Propagule pressure plays a driving role in enhancing the probability of lantana arriving in sites. Lantana establishment was limited by fire frequency. Clearly, therefore, land managers and biologists must take into account the inherent multivariate nature of lantana invasion when coordinating invasive species control activities or when planning future research.

The official position taken by forest managers in India is that forest fires cause forest degradation, and result in other adverse ecological impacts (Bahuguna and Upadhyay 2002). Managers of BRT expend significant resources for the control of forest fires, including the maintenance of fire-breaks, and the manning of fire-fighting camps during summer. But

conducting fire-fighting operations in BRT is an onerous task owing to the highly undulating terrain, and explains why fires are not an uncommon occurrence in BRT. This study shows that fire occurrence may not encourage lantana, contrary to previous studies, that hypothesized a positive relationship between fire frequency and lantana dominance (Hiremath and Sundaram 2005). However, a change in fire management regimes to control lantana via fire is not warranted by examining the results from this study alone. Future studies that conduct experimental *in-situ* research exploring the effects of repeated fire on lantana and native species in different forest types will be required to evaluate whether fire can indeed be used as a management tool to control lantana in BRT.

Several studies have examined ways to reduce propagule pressure exerted by invasive species, especially in aquatic systems (e.g. Wonham *et al*. 2005, Herborg *et al*. 2007), mainly as a way to limit their arrival. Once established, the reduction of propagule pressure is a challenging task (Lockwood *et al*. 2005). Limiting propagule pressure by physical removal of lantana has been found to be successful e.g., in Australia (Day *et al*. 2003) and South Africa (Van Wilgen *et al*. 2004), although costs of removal are prohibitive when the area of operation is large. Additionally, removal activities have to be conducted repeatedly in the same area over time because of lantana re-growth (Day *et al*. 2003). However, prioritizing lantana removal activities in heavily invaded areas could help reduce propagule pressure in the long run (Chornesky *et al*. 2005, Mack and Lonsdale 2002).

References

Anonymous. 1996. Map of Karnataka soils. National Bureau of Soil Survey and Land-Use Planning, Indian Council for Agriculture Research, Nagpur.

Babu, S., A. Love, and C. R. Babu. 2009. Ecological restoration of lantana-invaded landscapes in Corbett Tiger Reserve, India. Ecological Restoration **27**:468-478.

Bahuguna, V. K., and A. Upadhyay. 2002. Forest fires in India: policy initiatives for community participation. International Forestry Review **4**:122-127.

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

Bhatt, D., and A. Kumar. 2001. Foraging ecology of red-vented bulbul *Pycnonotus cafer*, in Haridwar, India. Forktail **17**:109-110.

Blossey, B., and R. Notzold. 1995. Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. Journal of Ecology **83**:887-889.
Bradley, B. A., and J. F. Mustard. 2006. Characterizing the landscape dynamics of an invasive plant and risk of invasion using remote sensing. Ecological Applications **16**:1132-1147.
Brown, K. A., and J. Gurevitch. 2004. Long-term impacts of logging on forest diversity in Madagascar. Proceedings of the National Academy of Sciences, USA **101**:6045-6049.
Brown, K. A., F. N. Scatena, and J. Gurevitch. 2006. Effects of an invasive tree on community structure and diversity in a tropical forest in Puerto Rico. Forest Ecology and Management **226**:145-152.
Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.
Champion, H. G., and S. K. Seth. 1968. A revised survey of the forest types of India. Government of India Press, Dehra Dun.
Chornesky, E. A., A. M. Bartuska, G. H. Aplet, K. O. Britton, J. Cummings-Carlson, F. W. Davis, J. Eskow, D. R. Gordon, K. W. Gottschalk, and R. A. Haack. 2005. Science priorities for reducing the threat of invasive species to sustainable forestry. Bioscience **55**:335-348.
Colautti, R. I., I. A. Grigorovich, and H. J. MacIsaac. 2006. Propagule pressure: a null model for biological invasions. Biological Invasions **8**:1023-1037.
Corlett, R. T. 1998. Frugivory and seed dispersal by birds in Hong Kong shrubland. Forktail **13**:23-27.
Crooks, J. A. 2005. Lag times and exotic species: the ecology and management of biological invasions in slow-motion. Ecoscience **12**:316-329.
Daehler, C. C. 1998. The taxonomic distribution of invasive angiosperm plants: ecological insights and comparison to agricultural weeds. Biological Conservation **84**:167-180.
D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics **23**:63-87.
Day, M. D., C. J. Wiley, J. Playford, and M. P. Zalucki. 2003. Lantana: current management status and future prospects. Australian Centre for International Agriculture Research, Canberra, Australia.
DeGasperis, B. G., and G. Motzkin. 2007. Windows of opportunity: historical and ecological control on *Berberis thunbergii* invasions. Ecology **88**:3115-3125.
Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics **29**.
Ganesan, R., and R. S. Setty. 2004. Regeneration of *amla*, an important non-timber forest product from southern India. Conservation and Society **2**:365-375.
Gentle, C. B., and J. A. Duggin. 2006. *Lantana camara* L. invasions in dry rainforest-open forest ecotones: the role of disturbances with fire and cattle grazing. Austral Ecology **22**:298-306.
Herborg, M.-M., C. L. Jerde, D. M. Lodge, G. M. Ruiz, and H. J. MacIsaac. 2007. Predicitng invasion risk using measures of introduction effort and environmental niche models. Ecological Applications **17**:663-674.
Hiremath, A. J., and B. Sundaram. 2005. The fire-lantana cycle hypothesis in Indian forests. Conservation and Society **3**:26-42.

Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology **6**:324-337.
Holle, B. V., and D. Simberloff. 2005. Ecological resistance to biological invasions overwhelmed by propagule pressure. Ecology **86**:3212-3218.
Iyengar, A. V. V. 1933. The problem of lantana. Current Science **1**:266-269.
Johnson, J. B., and K. S. Omland. 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution **19**:101-108.
Keane, R. M., and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology & Evolution **17**:164-170.
Kolar, C. S., and D. M. Lodge. 2002. Ecological predictions and risk assessment for alien fishes in Noth America. Science **298**:1233-1236.
Krishnaswamy, J., K. S. Bawa, K. N. Ganeshaiah, and M. C. Kiran. 2009. Quantifying and mapping biodiversity and ecosystem sevices: Utility of a multi-season NDVI based Mahalanobis distance surrogate. Remote Sensing of Environment **In press**.
Krishnaswamy, J., M. C. Kiran, and K. N. Ganeshaiah. 2004. Tree model based eco-climatic vegetation classification and fuzzy mapping in diverse tropical deciduous ecosystems using multi-season NDVI. International Journal of Remote Sensing **25**:1185-1205.
Levine, J. M., M. Vila, C. M. D. Antonio, J. S. Dukes, K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society of London (Biology) **270**:775-781.
Lockwood, J. L., P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology and Evolution **20**:223-228.
Lowe, S., M. Browne, S. Boudjelas, and M. De Poorter. 2000. 100 of the world's worst invasive alien species a selection from the global invasive species database. Published by The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN), 12pp. First published as special lift-out in Aliens **12**.
Mack, R. N., and W. M. Lonsdale. 2002. Eradicating invasive plants: hard-won lessons for islands. Turning the tide: the eradication of invasive species. Invasive Species Specialty Group of the World Conservation Union (IUCN), Auckland, New Zealand:164–172.
Madegowda, C. 2009. Traditional Knowledge and Conservation. Economic & Political Weekly **44**:21-65.
Mandon-Dalger, I., P. Clergeau, J. Tassin, J. N. Rivière, and S. Gatti. 2004. Relationships between alien plants and an alien bird species on Reunion Island. Journal of Tropical Ecology **20**:635-642.
Marchetti, M. P., P. B. Moyle, and R. Levine. 2004. Alien fishes in California watersheds: characteristics of successfull and failed invaders. Ecological Applications **14**:587-596.
Mosher, E. S., J. A. Silander, and A. M. Latimer. 2009. The role of land-use history in major invasions by woody plant species in the northeastern North American landscape. Biological Invasions **11**:2317-2328.
Murali, K. S., and R. S. Setty. 2001. Effect of weeds Lantana camara and Chromelina odorata growth on the species diversity, regeneration and stem density of tree and shrub layer in BRT sanctuary. Current Science **80**:675-678.
Murali, K. S., R. S. Setty, K. N. Ganeshaiah, and R. Uma Shaanker. 1998. Does forest type classification reflect spatial dynamics of vegetation? An analysis using GIS techniques. Current Science **75**:220-227.

Pemberton, R. W., and H. Liu. 2009. Marketing time predicts naturalization of horticultural plants. Ecology **90**:69-80.
R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Raizada, P., G. P. Sharma, and A. S. Raghubanshi. 2008. Ingress of lantana in dry tropical forest fragments: edge and shade effects. Current Science **94**:180-182.
Ranganathan, C. R. 1934. Working plan, Kollegal Forest Division. Government of India, Madras.
Reaser, J. K., L. A. Meyerson, and B. V. Holle. 2008. Saving camels from straws: how propagule pressure-based prevention policies can reduce the risk of biological invasion. Biological Invasions **10**:1085-1098.
Rejmanek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? Ecology **77**:1655-1661.
Roderick, M. L., I. R. Noble, and S. W. Cridland. 1999. Estimating woody and herbaceous vegetation cover from time series satellite observations. Global Ecology and Biogeography **8**:501-508.
Running, S. W., T. R. Loveland, and L. L. Pierce. 1994. A vegetation classification logic based on remote sensing for use in global biogeochemical models. Ambio **23**:77-81.
Saha, S., and H. F. Howe. 2003. Species composition and fire in a dry deciduous forest. Ecology **84**:3118-3123.
Saha, S. 2002. Anthropogenic fire regime in a deciduous forest of central India. Current Science **82**:1144-1147.
Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. McCauley, P. O'Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. Annual Review of Ecology and Systematics **32**:305-332.
Seabloom, E. W., W. S. Harpole, O. J. Reichman, and D. Tilman. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. Proceedings of the National Academy of Sciences of the United States of America **100**:13384.
Sharma, G. P., A. S. Raghubanshi, and J. S. Singh. 2005. *Lantana* invasion: an overview. Weed Biology and Management **5**:157-165.
Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology and Evolution **17**:170-176.
Tireman, H. 1916. Lantana in the forests of Coorg. Indian Forester **42**:384-392.
Tobin, P. C., C. Robinet, D. M. Johnson, S. L. Whitmire, O. N. Bjornstad, and A. M. Liebhold. 2009. The role of Allee effects in gypsy moth, *Lymantria dispar* (L.), invasions. Population Ecology **51**:373-384.
Totland, O., P. Nyeko, A.-L. Bjerknes, S. J. Hegland, and A. Nielsen. 2005. Does forest gap size affect population size, plant size, reproductive success and pollinator visitation in *Lantana camara*, a tropical invasive shrub? Forest Ecology and Management **215**:329-338.
Traveset, A., and D. M. Richardson. 2006. Biological invasions as disruptors of plant reproductive mutualisms. Trends in Ecology and Evolution **21**:208-216.
Vermeij, G. J. 1996. An agenda for invasion biology. Biological Conservation **78**:3-9.

Van Wilgen, B. W, M. P. de Wit, H. J. Anderson, D. C. L. Maitre, I. M. Kotze, S. Ndala, B. Brown, and M. B. Rapholo. 2004. Costs and benefits of biological control of invasive alien plants: case studies from South Africa. . South African Journal of Science **100**:113-122.

Wonham, M. J., M. A. Lewis, and H. J. MacIsaac. 2005. Minimizing invasion risk by reducing propagule pressure: a model for ballast-water exchange. Frontiers in Ecology and the Environment **3**:473-478.

Chapter 4: Soil seed bank ecology and invasive species success in a tropical dry forest

Introduction

The success of invasive species in recipient habitat is often enhanced by effective regeneration mechanisms (Sakai *et al*. 2001, Mack *et al*. 2000). Several life-history characteristics of invasives, such as large quantum of seed production, lack of dispersal limitation, and young age to reproductive maturity result in effective regeneration, and possibly, in their successful persistence vis-à-vis native species (Theoharides and Dukes 2007, Rejmanek and Richardson 1996). Although invasive plant regeneration can occur asexually by root suckering and sexually by seed production, range expansion of invasive species is strongly associated with their capacity to produce large quantities of seed that are dispersed widely by biotic or abiotic means (Sakai *et al*. 2001, Rejmanek 1996). Other than seeds that succumb to post-dispersal mortality, dispersed seeds could either germinate immediately, or some proportion of dispersed seeds could enter and persist in the soil seed bank. Seed arrival and seed storage below-ground have been identified as important mechanisms of invasive species success that enables them to take advantage of favorable regeneration opportunities when they occur (Colautti *et al*. 2006, Chambers and MacMahon 1994).

Invaded areas often show a disproportionately higher density of arriving and soil-stored seeds of invasive species compared to seeds of native species (Buckley *et al*. 2004, Lonsdale *et al*. 1988). Successful invasive species are often characterized by high rates of seed arrival (Buckley *et al*. 2006). However, invasive species that saturate the soil seed bank with their seeds are also successful (Lonsdale *et al*. 1988). A comparison of the seasonal variation in seed arrival and the soil-stored seeds of invasive species vis-à-vis native species between invaded and un-invaded sites could thus improve our understanding of the mechanisms underlying invasive species success. The formation of a soil seed bank is a function of seed arrival and seed persistence. Depending on the seasonal variation in seed arrival and whether or not seeds persist in soil, four different scenarios are possible: (a) species have low seed arrival and short persistence in soil,

i.e., seed storage is low, and no seed bank is built up, (b) species have low seed arrival, but long persistence in soil, i.e., seed storage occurs, leading to the formation of a seed bank, (c) species have high seed arrival but short persistence in soil, i.e., seed storage is low (cf 'a'), but seeds may be available through the year and, (d) species have high seed arrival, and long persistence in soil, i.e., seed storage is high, leading to the formation of a growing seed bank. Each of these scenarios could potentially have different implications for invasive species success. Persistent seeds, rather than propagule pressure, are likely to contribute to invasive species success in (b). On the other hand, propagule pressure, rather than persistent seeds could contribute to invasive species success in (c). Lastly, persistent seeds, combined with propagule pressure, would drive invasive species success if (d) occurs. In the case of (a), neither seed persistence nor propagule pressure is likely to result in invasive species success.

Based on the seasonal patterns of seed arrival and germination from the soil seed bank, seed persistence has been classified into 3 broad syndromes: transient, persistent, and pseudo-persistent (Thompson and Grime 1979, Garwood 1989). According to Garwood (1989), transient species produce seeds that are briefly present in the soil following dispersal. Persistent species, on the other hand, have seeds that are present in soil irrespective of time of dispersal. Lastly, pseudo-persistent species are those whose seeds are dispersed and present in soil year-round, but whose density in soil is directly proportional to the density of seed arrival. The classification developed by Garwood (1989) is particularly useful to study soil seed banks in tropical dry forest systems that are invaded by non-native species because seed persistence of native species rarely exceeds a year in these systems (Vieira and Scariot 2006). Invasive species on the other hand, may produce persistent seeds, thus giving them a competitive edge over native species.

Drake (1998) examined the persistence of native and invasive species in a Hawaiian forest using the classification developed by Garwood (1989) by comparing the seasonal patterns of seed arrival and seeds emerging from the soil seed bank. He found that native species, although dominating seed arrival through the year, did not persist in soil. Invasive species, on the other hand, had lower amounts of seeds arriving, but these seeds persisted in the soil. Thus, invasive species like *Myrica faya* and *Setaria gracilis*, despite low seed arrival, could dominate the soil seed bank over time due to their high seed persistence (Drake 1998).

Successful persistence following seed arrival and possible soil seed bank enrichment could enable invasive species to make use of favorable regeneration opportunities presented by disturbance events. At a global scale, disturbances such as fire, or nitrogen deposition, have been found to facilitate invasion (Theoharides and Dukes 2007, Hobbs and Huenneke 1992). In tropical dry forests, disturbances that occur at landscape scales, such as fire, have been found to promote invasion by alien species, especially grasses (Fine 2002, D'Antonio and Vitousek 1992). However, the regeneration of non-grass species (both native and invasive) could be hindered due to seeds present in soil being killed by fire. Studies have found that fires result in the reduction of viable seeds (of both native and invasive species) in the top 3 cm of soil (Kennard *et al*. 2002). However, in tropical dry forests, the effect of fire on the density of seeds present in depths beyond 3 cm is unknown. Since fire is a disturbance that regularly occurs in tropical dry forests worldwide, examining the effects of fire on seed storage of native and invasive species across different depths could provide further mechanistic insights into the role played by soil seed banks in the regeneration of native and invasive species. Although there are studies that examine the differences in soil seed bank ecology between native and invasive species (Vivian-Smith and Panetta 2009, Keeley *et al*. 2005, Witkowski and Wilson 2001, Drake 1998), there are very few studies that examine the effects of disturbance, seasonality, and depth, on soil seed banks in tropical dry forests affected by invasive species.

Two species of plant invaders, *Lantana camara* (Verbenaceae; hereafter lantana) and *Chromolaena odorata* (formerly *Eupatorium odoratum*, Asteraceae; hereafter Chromolaena) are successful invaders in seasonally dry tropical forests of the Western Ghats, India. There is evidence to suggest that propagule pressure from invaded neighborhoods strongly influences lantana colonization of uninvaded sites (Sundaram *et al*. manuscript submitted). Preliminary data also suggests that lantana fruits year-round, with some plants producing 10^4 fruits each season (Monika Kaushik, unpublished data). Lantana seeds are consumed by birds like bulbuls (Bhatt and Kumar 2001) that may result in their wide dispersal. Year-round fruit production coupled with wide dispersal could potentially result in the year-round arrival of lantana seeds. Chromolaena on the other hand, is a perennial herb with wind-dispersed seeds that are produced seasonally (Zachariades *et al*. 2009). Seeds of Chromolaena have been found to remain viable in

the soil for up to a year, after which germinability rapidly declines (Zachariades *et al*. 2009). Information from elsewhere suggests that both lantana and Chromolaena form short-term persistent seed banks (Vivian-Smith and Panetta 2009, Witkowski and Wilson 2001). However, there is no information on the soil seed bank dynamics of either lantana or Chromolaena from Indian tropical dry forests.

I examine the seed arrival and the soil seed bank in a tropical dry forest invaded by lantana and Chromolaena in the Western Ghats, India. On the basis of the fruiting phenology of the two species, I predict that (a) lantana success is a function of high seed arrival, rather than high persistence in the soil seed bank, (b) Chromolaena success on the other hand, is a function of persistence in the soil seed bank rather than seed arrival. Lastly, I predict that (c) for both invasive and native species, fire will have a negative effect on the density of seeds stored in the topmost layer of soil vis-à-vis other deeper layers. However, lantana, with its aseasonal fruiting phenology, would be best able to take advantage of the opportunity for regeneration following fire.

Methods

Study area

This study was carried out in the Biligiri Rangaswamy Temple Wildlife Sanctuary (hereafter, BRT) in Karnataka, India. The sanctuary is part of the Western Ghats biodiversity hotspot. The sanctuary is 540 km^2 in area, and is located between 11º 47´ – 12º 09´ N latitude and 77º – 77º 16´ E longitude. The terrain in BRT is highly undulating, and elevation ranges from 600 m above sea level (asl) in the foothills, to 1800 m asl in the upper reaches. Annual rainfall in the study area varies with elevation. While areas in the foothills (600 m asl) receive 900 mm of rain annually, the forests at higher elevations receive 1750 mm of precipitation annually. The study area receives rainfall from both the southwest monsoon during June to September as well as the northeast monsoon during October to December. A pronounced dry season prevails from January to March each year. The mean annual temperature in the study area is 25.3 ºC, and varies between 11 ºC in winter to 42 ºC in summer (Murali *et al*. 1998). Soils in BRT are well-drained

gravelly clays that have been classified as typic ustropepts (Anon. 1996). The area is rich in plant biodiversity, with at least 1400 species of angiosperms (Kammathy *et al*. 1967).

The topographic and climatic diversity within BRT has resulted in several forest types within this relatively small area, with dry scrub-savanna at low elevations, dry-deciduous and moist-deciduous forests at intermediate elevations, and evergreen and shola forests at higher elevations. Of these forest types, the seasonally dry forests constitute approximately 90% of the study area (Ganesan and Setty 2004) and include the scrub-savanna, dry deciduous and moist deciduous forests.

Seasonally dry forests in BRT are extensively invaded by the invasive species *Lantana camara*. Lantana is native to Central and South America, and was introduced into India more than two centuries ago as an ornamental hedge plant (Sharma *et al*. 2005, Cronk and Fuller 1995). Lantana is now widespread in dry forest landscapes, slash-and-burn fallows, and pasture lands all over India (Hiremath and Sundaram 2005). Although information regarding the exact year of introduction of lantana into BRT is unavailable, forest management plans cite the presence of lantana in the park as early as 1934 (Ranganathan 1934). The spread of lantana in BRT has not occurred gradually and is a recent phenomenon. A systematic survey of vegetation in BRT in 1997 indicated that lantana was present in ~ 40 % of sampled plots, with a mean density of 362.5 ± 35.0 stems ha^{-1} (Murali and Setty 2001). A resurvey of plots used by Murali and Setty (2001) in 2008, indicated that lantana had spread to ~ 80% of sampled plots, and was accompanied by a four-fold increase in density to 1652.5 ± 102.0 stems/ha in a period of 11 years (Sundaram and Hiremath, manuscript submitted).

Lantana is a woody scrambling shrub that was introduced into India during the early 19^{th} century (Sharma *et al*. 2005). Lantana seems to prefer seasonally dry forests as opposed to closed-canopy evergreen forests in BRT. Lantana success may be driven by multiple factors. Lantana produces fruit throughout the year (Day *et al*. 2003), and its fruits are largely — and widely — dispersed by birds (Bhatt and Kumar 2001, Swarbrick *et al*. 1998).

Chromolaena odorata (Syn. *Eupatorium odoratum*) has also been recognized as an important invasive species in BRT (Murali and Setty 2001). The species was introduced into India during the 1840s (Zachariades *et al*. 2009). Successful Chromolaena spread has been attributed to the species' remarkable reproductive output. An adult plant may produce as many as one million seeds during the course of a single year (Epp 1987).

In BRT Chromolaena was present in more than half the plots surveyed in 1997 (Murali and Setty 2001) and 2008 (Bharath Sundaram unpublished data) indicating that it is a widespread invasive. However, Chromolaena is not perceived as a threat to the forests of BRT in the same way as lantana is despite its wide distribution in the area because of its low density with respect to lantana. Chromolaena is similar to lantana in the kinds of forest types it occupies — it is largely present only in the seasonally dry forests, and is rarely seen in evergreen forests.

Study design

Soil seed banks and seed rain were sampled from five sites spread across the sanctuary. Sites were chosen in areas that were invaded by lantana and showed the presence of Chromolaena, but each site also had areas that were uninvaded by either invasive species within close proximity (< 100 m). Three plots of size 25 m x 25 m were demarcated within each site. One plot was lantana-invaded and had Chromolaena present and formed the invaded treatment. A second plot free from lantana and Chromolaena constituted the uninvaded control. In the remaining plot the understory (largely consisting of lantana) was slashed and burnt, and formed the fire treatment. Plots that were assigned to the lantana-fire treatment were burnt during January 2006.

Within each plot, a nested rectangular area measuring 10 m x 20 m was demarcated for sampling of the soil seed bank and seed rain. The total basal area of trees ≥ 1 cm DBH (diameter at breast height) in plots varied from 0.16 - 1.29 m^2/ha, with an average tree basal area of 0.57 m^2/ha. The canopy cover over plots varied from 41.2 % - 90.3 %, with a mean canopy cover of 44.7 %. Plots nested within treatments did not significantly differ in values of tree basal area ($F_{2, 12} = 1.113$, $p = 0.36$) or canopy cover ($F_{2, 12} = 0.0312$, $p = 0.96$). Similarly, across the study area, plots nested

within sites did not have significantly different values of basal area ($F_{4, 10} = 1.9233$, $p = 0.18$) or canopy cover ($F_{4, 10} = 0.9996$, $p = 0.45$).

Soil seed bank sampling

Within each plot, soil samples were taken from 10 randomly chosen locations using a soil corer. Cores were 5 cm in diameter and 10 cm deep. I initially sampled down to a depth of 15 cm, but as no seeds occurred below 10 cm, subsequent samples were restricted to a depth of 10 cm. The 10 soil cores per plot were composited by depth (0-2 cm, 2-5 cm, and 5-10 cm). Samples were transported to the nursery in the Biligiri Field Station, BRT. Soil seed bank samples were spread thinly (≈ 0.5 cm; as suggested by Dalling *et al*. (1994) to maximize seed germination) on trays lined with sterilized sand in a shade house (50% shade cloth). To avoid contamination of samples, sand that was used to line trays was sterilized by boiling in water for 24 h to kill any seeds that could be present. Rectangular trays (76 cm x 45 cm) were fabricated from galvanized iron. The bottoms of all trays were perforated to allow water to drain. The trays were kept well-watered.

Seedling emergence was noted weekly, and observations continued till emergence of seedlings ceased (12 weeks). Germinating seedlings were classified into 5 categories: herbs, trees, other woody species (shrubs and lianas), lantana, and Chromolaena. Each week, all emerging seedlings were removed after data were recorded. Removing emerging seedlings from trays after data collection each week served two purposes. Removed seedlings were transferred to pots to enable identification once the true leaves appeared. Additionally, removing seedlings on a weekly basis eliminated confusion in counting freshly emerging seedlings the following week. To account for seed contamination arising from the nursery area, five trays containing only sterilized coconut husk peat spread over sand were used as "blanks." Three species of herbs were found emerging from blanks and were removed from the data.

To examine the effect of seasonality on soil seed bank dynamics, samples were taken in February, June, September, and December 2006. The total area sampled at each instance, i.e., in February, June, September, and December 2006, in each treatment was 0.02 m^2.

Seed rain sampling

Seed rain traps were placed in three randomly chosen locations within each plot. Seed rain traps were fashioned from rectangular metal trays of size 76 cm x 45 cm (0.34 m^2). All trays were lined with sterilized coconut husk peat, and were sunk into the ground flush with the soil surface. At the first sampling in February 2006, I found several trays had been stolen. Thus, for subsequent seed rain samples metal trays were not used. Instead, depressions of the same size and depth as the trays were made on the soil surface and lined with sterilized peat. The peat was left *in situ* for 3 months. At each collection instance, the peat along with seeds that may have been deposited on it was collected and then transported to the nursery. Seed rain samples were treated in a manner identical to that of soil seed bank samples.

In order to examine seasonal patterns of seed arrival, seed rain was sampled during February, May, September, and December 2006. Seed rain samples were indicative of seeds accumulated over a 3-month period preceding the collection date. The locations of seed rain traps were chosen randomly for each collection period. The total area sampled in each instance (in February, May, September, and December 2006) in each treatment was 1.03 m^2.

Persistence of seeds

The persistence of seeds in soil was examined for the two most numerically dominant species of trees and other woody species in comparison with the persistence of lantana and Chromolaena. To examine seed persistence in soil, a method similar to that used by Drake (1998) was adopted. For each season, the density of seeds in the top 2 cm of the soil seed bank and the density of seed rain were calculated across the different treatments. Temporal patterns of seed arrival were then visually compared with temporal patterns of seed emergence from the soil seed bank.

Depending on the patterns of seed arrival and emergence of seeds from soil, species were classified as being transient, persistent, or pseudo-persistent (sensu Garwood 1989). Species were classified as being transient if their seeds were only briefly present in soil after seed arrival.

On the other hand, species were classified as being persistent if their seeds emerged from the soil seed bank across all seasons, irrespective of seed arrival. Lastly, species were classified as pseudo-persistent if their seeds emerged from soil year-round, but their emergence fluctuated in proportion to seed arrival.

Data analysis

A linear mixed effects model framework (LME; Pinheiro and Bates 2000) was used for analyzing both soil seed bank and seed rain data. Due to the experimental design used, the quantification of two sources of error was necessary. These were: (a) random error originating from the five sites ('blocks') from which data were collected and (b) random error originating from data being collected from the same plots over time. Random effects that come from the same block are likely to be correlated. For example, density of lantana seeds present in soil from block#1 could inherently be low due to high soil moisture that results in high seed mortality, vis-à-vis other blocks. Similarly, since density was a repeated-measure in plots over time, correlated estimates of density from a particular plot over time would contribute to error originating from this source as well. Correlated estimates contravene fundamental assumptions of independent errors required by most statistical models (Crawley 2007). However, using an LME framework allows for the analysis of data originating from hierarchical experiments by quantifying errors associated with both spatial (e.g., block) and temporal (e.g., plots over time) replication (Crawley 2007).

Soil seed bank data was analyzed at two levels. At the first level, the total density of all species (native and invasive) was examined as a response to the fixed effects of treatment and layer, and an interaction between treatment and layer. The effect of time was not included in this analysis because *a priori* information indicated that the seed germination of native species was likely to be seasonal (Vieira and Scariot 2006), while seed germination of invasive species was likely to be aseasonal (Day *et al*. 2003). Therefore, analyzing the effects of time in a combined data set containing species with very different patterns of germination would not be valid. At the next level, data pertaining to each plant category (lantana, trees, other woody species, and Chromolaena) were analyzed separately as a response to treatment, layer, time, and an

interaction between treatment and layer. For both levels of analyses (overall total density, and density of individual plant categories), errors associated with block and plots over time was quantified. Additionally, for both levels of analyses, since the tree and the other woody species categories were composed of multiple species, the average emergence per species (total emergence/number of species) was calculated. Details of significant interaction terms (e.g., treatment x layer interactions within individual plant categories) from the LME analyses were depicted via graphical exploration of soil seed bank density data.

Analyses of seed rain data was conducted in a way similar to the analyses of soil seed bank data. Two levels of LME were used: one to quantify the response of total seeds arriving to treatment, and the other to quantify the response of each plant category to treatment and time. Similar to the analysis of the soil seed bank data, average emergence of the tree and other woody species categories was first calculated. Error structure for the seed rain analyses were identical to error structure defined for the analyses of soil seed bank data. Lastly, results from LME analyses were juxtaposed with graphical patterns of seed arrival versus treatment and season within plant categories. The maximum likelihood method was used within all LMEs to produce F-statistics and significance values (Crawley 2007). All statistical analyses were performed using the NLME package (Pinheiro and Bates 2000) within the R 2.9.0. statistics and computing environment (R Development Core Team 2009).

Results

Seed bank and seed rain composition

Over the course of one year, a total of 2316 seedlings emerged from the seed bank samples taken from all three treatments. Herbaceous vegetation formed a large proportion (59 %) of emerging vegetation, followed by other woody species (19%), lantana (11%), trees (6%), and Chromolaena (5%). In all, 47 species were recorded, including lantana and Chromolaena, in seeds germinated from the soil seed bank samples. These included 26 species of herbs, 6 species of shrubs, 4 species of lianas, and 9 species of trees (Table 4.1). Herbaceous vegetation was excluded from further analyses. The two most abundant tree species emerging from the soil seed bank were

Oroxylum indicum and *Trema orientalis*. These two tree species accounted for 91% of all tree seedlings that emerged from the soil through the year from all plots (Table 4.2). The two most abundant species in the other woody species category were *Solanum torvum* and *Cipadessa baccifera*, both shrubs. These two species accounted for 97% of all other woody species seedlings that emerged from the soil through the year in all plots (Table 4.2).

Patterns in the total density of seeds (all plant categories combined) in soil were then examined after partitioning data into layers from which seedlings emerged (0-2 cm, 2-5 cm, 5-10 cm). There were no differences in total seed densities across different soil depths ($F_{2, 159}= 0.40$, $p = 0.67$). Additionally, the total density of seeds was unaffected by interactions between treatment and layer ($F_{4, 159}= 1.69$, $p = 0.16$). Variation across blocks accounted for very little of the residual variation ($SD_{block}= 0.22$, residuals= 657.26). However the part played by errors associated with repeated-measures in plots over time was more substantial ($SD_{time/plots}= 170.39$, residuals= 657.26).

When model results were examined separately by plant category, there were significant differences in density with soil depth. For example, the density of lantana seeds stored in soil varied significantly across layers (Table 4.3) with density in the topmost layer of soil significantly higher than other layers in the invaded and in the uninvaded treatments (Fig. 4.2a). The density of Chromolaena seeds in soil also varied significantly with layer (Table 4.3). Similar to lantana, significantly higher density of seeds of Chromolaena was present in the topmost layer of soil in invaded sites (Fig. 4.2d). The density of soil stored seeds of trees and other woody species did not vary across layers (Table 4.3). Random effects of block accounted for more than two-thirds of the residual variation present in the model that examined the density of lantana seeds in soil, while random effects related to making repeated measures in plots over time accounted for a fifth of all residual variation in lantana seed density data (Table 4.3). Similarly, almost half the residual variation in the model to describe density of tree seeds in soil was contributed by repeated-measures in plots over time (Table 4.3). Random effects (both block, and plots over time) on other plant categories (Chromolaena and other woody species) were negligible (Table 4.3).

Table 4.1: Shrub and liana species (a) and tree species (b) emerging from seed rain and seed bank samples in the different seasons of sampling in BRT.

	SEED RAIN				SEED BANK			
(a) Other woody species	**Jun.**	**Sep.**	**Dec.**	**Feb.**	**Jun.**	**Sep.**	**Dec.**	**Feb.**
Allophylus cobbe				x				
Cipadessa baccifera	x	x	x	x	x	x	x	
Clematis gouriana	x							
Derris heyneana							x	
Dioscorea bulbifera	x							
Diplocyclos palmatus							x	
Helicteres isora	x		x					
Jasminum species	x							
Solanum torvum	x	x	x	x	x	x	x	x
Toddalia asiatica	x		x		x	x	x	
(b) Trees								
Oroxylum indicum	x	x	x	x	x	x	x	
Anogeissus latifolia	x		x	x	x			
Bischofia javanica		x				x		
Elaeaocarpus serratus				x				
Grewia tileaefolia				x				
Litsea deccanensis	x						x	
Mallotus philippensis		x		x				
Meliosma pinnata		x	x	x			x	
Michelia champaka			x					
Persea macrantha	x							
Phyllanthus emblica			x	x				
Premna serratifolia	x							
Randia dumetorum	x				x			
Scolopia crenulata				x	x			
Syzygium cuminii	x	x			x			
Trema orientalis	x	x	x	x	x	x	x	

Table 4.2: Relative abundance of shrub and liana species (a) and tree species (b) in the seed rain and seed bank samples across the different seasons in BRT.

Season	Seed rain		Seed bank	
	Species	Relative abundance	Species	Relative abundance
(a) Other woody species				
February	*Cipadessa baccifera*	0.882	*Solanum torvum*	1.000
	Solanum torvum	0.104		
	Others	0.014		
June	*Cipadessa baccifera*	0.639	*Solanum torvum*	0.667
	Toddalia asiatica	0.139	*Toddalia asiatica*	0.278
	Solanum torvum	0.056	*Cipadessa baccifera*	0.056
	Jasminum spp.	0.056		
	Dioscorea bulbifera	0.056		
	Others	0.056		
September	*Solanum torvum*	0.940	*Cipadessa baccifera*	0.429
	Cipadessa baccifera	0.060	*Solanum torvum*	0.286
			Others	0.286
December	*Solanum torvum*	0.823	*Solanum torvum*	0.976
	Cipadessa baccifera	0.113	*Derris heyneana*	0.012
	Toddalia asiatica	0.032	*Cipadessa baccifera*	0.005
	Others	0.032	Others	0.007
(b) Trees				
February	*Oroxylum indicum*	0.337	No emergence	
	Trema orientalis	0.193		
	Meliosma pinnata	0.157		
	Mallotus philippensis	0.145		
	Anogeissus latifolia	0.120		
	Others	0.048		
June	*Syzygium cuminii*	0.325	*Trema orientalis*	0.633
	Trema orientalis	0.250	*Oroxylum indicum*	0.228
	Anogeissus latifolia	0.142	*Syzygium cuminii*	0.101
	Oroxylum indicum	0.117	Others	0.038
	Persea macrantha	0.108		
	Others	0.058		
September	*Trema orientalis*	0.680	*Trema orientalis*	0.712
	Oroxylum indicum	0.200	*Oroxylum indicum*	0.269
	Mallotus philippensis	0.060	*Bischofia javanica*	0.019
	Others	0.060		
December	*Oroxylum indicum*	0.529	*Trema orientalis*	0.474
	Trema orientalis	0.353	*Oroxylum indicum*	0.421
	Anogeissus latifolia	0.039	*Litsea deccanensis*	0.053
	Michelia champaka	0.039	*Meliosma pinnata*	0.053
	Others	0.039		

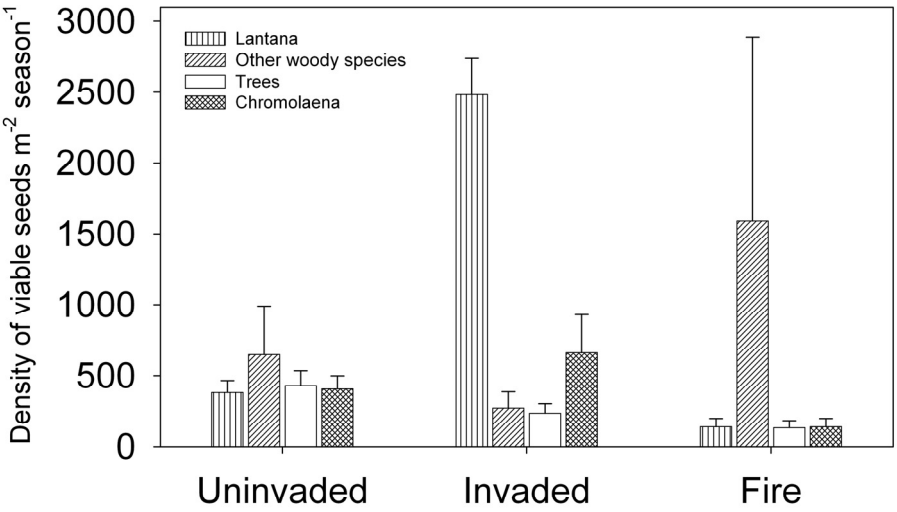

Figure 4.1: Mean density of viable seeds of lantana, other woody species, trees, and Chromolaena per season from the soil seed bank in the three different treatments (Fire, invaded and uninvaded) in BRT.

A total of 3725 seedlings emerged from the seed rain samples over the year of sampling. The composition of the seed rain was similar to that of the seed bank, with herbaceous vegetation accounting for 58% of all seedlings, followed by lantana (19%), other woody species (10%), trees (9%), and lastly, Chromolaena (5%). A total of 66 species were recorded from seed rain samples over the course of a year. These included, in addition to lantana and Chromolaena, 40 species of herbs, 8 species of shrubs and lianas, and 16 species of trees (Table 4.1). Herbaceous vegetation was excluded from further analyses. The two most abundant tree species that dominated seed arrival, as with the seed bank, were *Oroxylum indicum* and *Trema orientalis* (Table 4.2). These two species accounted for 58% of all viable tree seeds arriving into plots over the year, and were also the only two tree species to arrive into plots throughout the year, i.e., during all sampling occasions. Two other woody species, *Solanum torvum* and *Cipadessa baccifera* (both shrubs) accounted for 95% of all viable other woody species seed arriving into plots through the year (Table 4.2).

Treatment differences in soil seed bank and seed rain density

The density of viable seeds (all plant categories combined) emerging from the soil seed bank did not vary across treatment ($F_{2, 8}= 0.37$, $p = 0.70$). However, when data were analyzed separately by plant category, there were significant treatment differences in the case of lantana (Table 4.3). The density of lantana seeds in invaded sites was much higher than the density of lantana seeds in other treatments (Fig. 4.1). However, the density of seeds of all other plant categories (Chromolaena, trees, and other woody species) was not affected by treatment (Table 4.3).

Similar to patterns observed in soil seed bank data, the density of seed arrival did not vary across treatment when pooled data were analyzed ($F_{2, 8} = 0.85$, $p = 0.46$). However, when data from plant categories were examined separately, strong treatment effects emerged for lantana, but not for other plant categories (Table 4.4). Lantana seed arrival into sites already invaded was much higher than sites either presently uninvaded, or sites where lantana was cut and burned (Fig. 4.3).

Temporal patterns of soil seed bank and seed rain

Seasonality in the emergence of seeds from soil was detected for Chromolaena and other woody species, but not for lantana or tree species (Table 4.3). Chromolaena showed significantly seasonal seed emergence from soil, with higher emergence during the rainy season in June (Fig. 4.4). Other woody species, on the other hand, had peak seed emergence from soil in December (Fig. 4.4).

Similarly, seasonality in seed arrival was clearly apparent for trees and Chromolaena, but not so for lantana and other woody species (Table 4.4). While the arrival of trees and Chromolaena seeds was maximal in June, there was high variance associated with the arrival of seeds of lantana and other woody species year-round (Fig. 4.6).

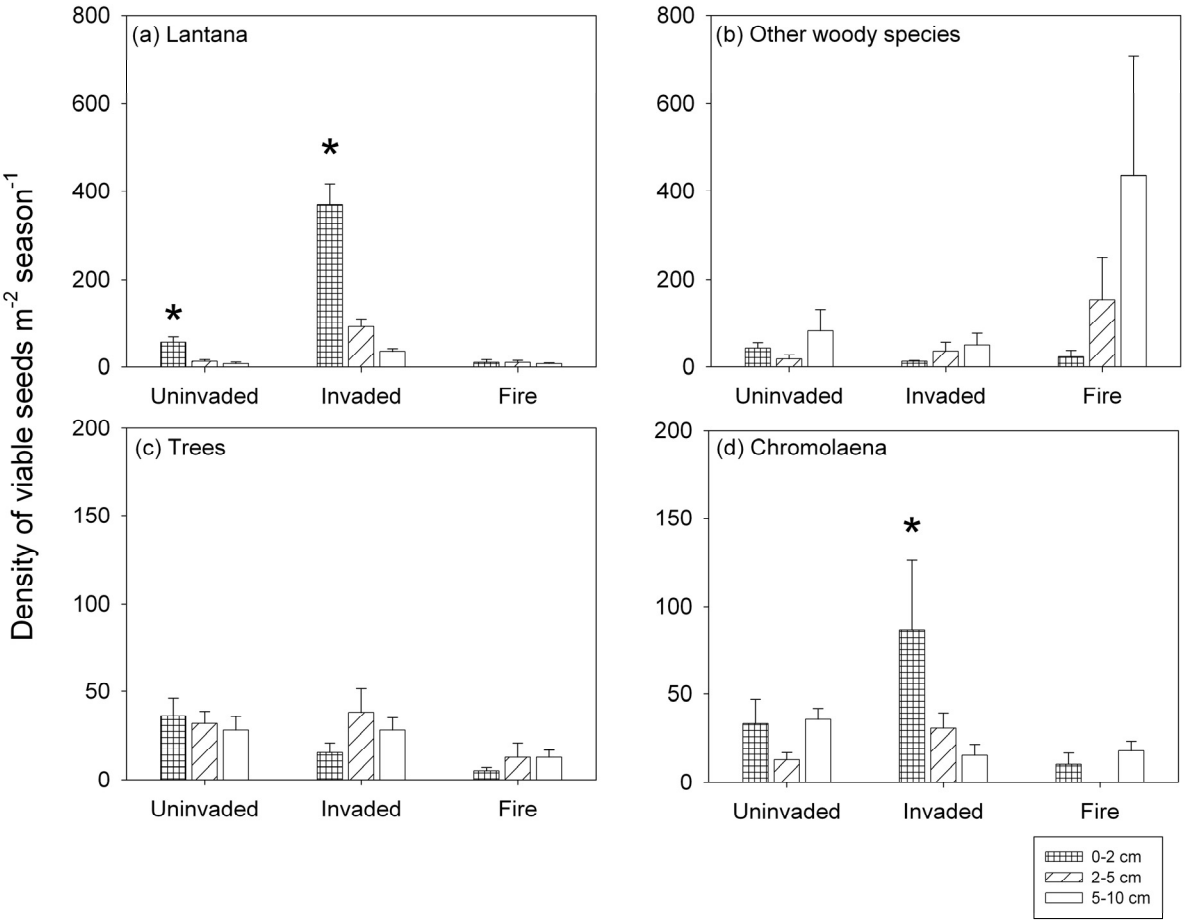

Figure 4.2: Layer differences in the average density of viable seeds present in the soil seed bank of (a) lantana, (b) shrubs and lianas, (c) trees, and (d) Chromolaena in the three different treatments. Output from LME models indicating significant interactions ($p < 0.05$) between treatment and layer within plant categories are shown (*).

Comparison between the soil seed bank and seed rain in the density of viable seeds of lantana, Chromolaena, and the two most abundant trees and other woody species showed that across all plant categories, emergence from the seed bank largely outweighed arrival of viable seeds (Fig. 4.5). Additionally, across the year, the density of viable lantana seeds in the soil outweighed the density of the two most abundant native trees *Oroxylum indicum* and *Trema orientalis*, other woody species *Solanum torvum* and *Cipadessa baccifera*, and the invasive Chromolaena (Fig. 4.5). The density of lantana seeds in soil was at least an order of magnitude higher than soil-held

seeds of the other woody species in February, and June (Fig. 4.5). The disparity between lantana and tree species was stark as well, with the density of viable lantana seeds in soil three orders of magnitude higher than the density of tree seeds in February, and at least quadruple the density of viable tree seeds in June, September and December (Fig. 4.5). The emergence of Chromolaena seeds from soil also exceeded the emergence of *Oroxylum indicum, Trema orientalis*, *Solanum torvum*, and *Cipadessa baccifera* from the soil in June and September (Fig. 4.5).

In addition to being the most dominant species in the seed bank, lantana was the only species in BRT with persistent seeds (sensu Garwood 1989), since lantana seeds emerged from the soil throughout the year, and with emergence from soil far outweighing seed arrival (Fig. 4.5f). Chromolaena seeds, on the other hand, were difficult to classify into any of the three syndromes defined by Garwood (1989), since emergence from soil appeared to be seasonal, and was not proportional to seed arrival (Fig. 4.5e). Of the native shrubs, *Cipadessa baccifera* was difficult to categorize, and could best be classified as a pseudo-persistent species, because the density of germinable seeds from soil through the year appeared to be equal to the quantum of seeds arriving through the year, albeit with a lag between seed arrival and emergence from soil (Fig. 4.5a). However, it must be noted that *C. baccifera* seeds did not emerge from the soil at all in February. The shrub *Solanum torvum* was also difficult to classify, because emergence was seasonal, and was not in proportion with seed arrival (Fig. 4.5b). The tree *Oroxylum indicum* could possibly be classified as a persistent species because its seeds emerged from soil almost through the year, with emergence from soil across all seasons except February (Fig. 4.5c). However, the other tree species *Trema orientalis* was difficult to categorize because although its seeds appeared to germinate from soil seasonally, it was not in proportion with seed arrival (Fig. 4.5d).

Table 4.3: Results from linear mixed-effects models to explain the variation of emergence of seeds from the soil seed bank as a response to random (block and sites over time) and fixed effects (treatment, layer, and time).

Plant category	Random effects	Fixed effects	d.f.	F-value	p-value
Lantana	SD_{block}= 20.85	Treatment	2, 8	6.62	0.02
	$SD_{time/plots}$= 66.63	Time	3, 156	1.59	0.19
	Residual variation= 95.44	Layer	2, 156	29.02	<.0001
		Treatment:Layer	4, 156	18.92	<.0001
Other woody species	SD_{block}= 52.57	Treatment	2, 8	0.88	0.45
	$SD_{time/plots}$= 125.23	Time	3, 156	3.41	0.02
	Residual variation= 618.99	Layer	2, 156	1.04	0.36
		Treatment:Layer	4, 156	0.60	0.67
Trees	SD_{block}= 14.34	Treatment	2, 8	0.99	0.41
	$SD_{time/plots}$= 20.94	Time	3, 156	1.52	0.19
	Residual variation= 46.11	Layer	2, 156	0.51	0.60
		Treatment:Layer	4, 156	0.48	0.75
Chromolaena	SD_{block}= 10.59	Treatment	2, 8	2.66	0.13
	$SD_{time/plots}$= 14.04	Time	3, 156	8.52	<.0001
	Residual variation= 63.27	Layer	2, 156	3.08	0.05
		Treatment:Layer	4, 156	2.30	0.06

Table 4.4: Results from linear mixed-effects models to explain the variation of seed arrival as a response to random (block and sites over time) and fixed effects (treatment and time).

Plant category	Random effects	Fixed effects	d.f.	F-value	p-value
Lantana	SD_{block}= 2.55	Treatment	2, 8	6.39	0.02
	$SD_{time/plots}$= 7.99	Time	3, 42	1.99	0.13
	Residual variation= 145.10				
Other woody species	SD_{block}= 40.57	Treatment	2, 8	0.61	0.57
	$SD_{time/plots}$= 0.09	Time	3, 42	2.31	0.09
	Residual variation= 739.48				
Trees	SD_{block}= 4.22	Treatment	2, 8	1.08	0.38
	$SD_{time/plots}$= 8.15	Time	3, 42	3.99	0.01
	Residual variation= 76.49				
Chromolaena	SD_{block}= 3.77	Treatment	2, 8	2.57	0.14
	$SD_{time/plots}$= 8.40	Time	3, 42	5.74	0.002
	Residual variation= 131.07				

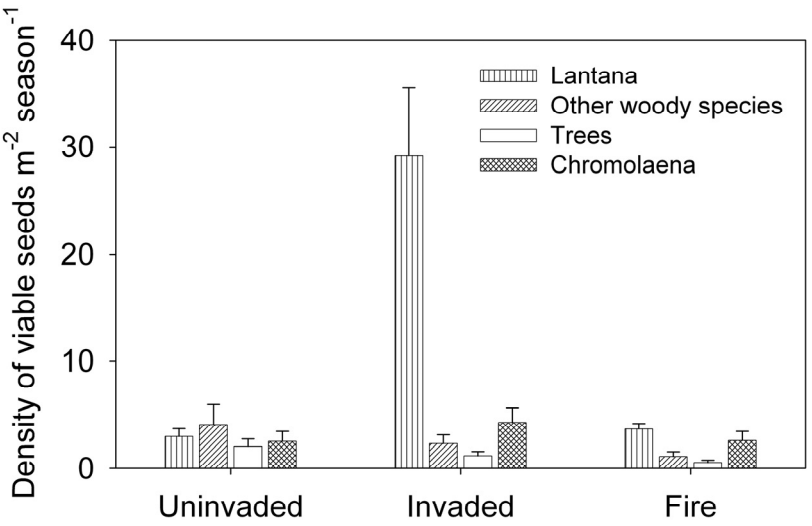

Figure 4.3: Variation in the mean seed arrival of lantana, shrubs and lianas, trees, and Chromolaena across the different treatments, averaged over seasons.

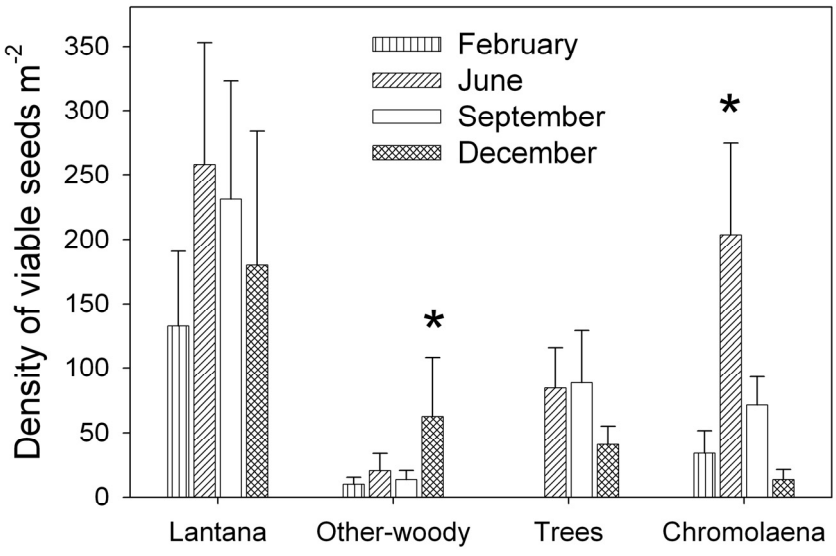

Figure 4.4: Seasonal variation in the soil seed bank density of (a) lantana, (b) other woody species, (c) trees, and (d) Chromolaena across all treatments. Model output from LMEs that showed significant interactions ($p < 0.05$) between seed arrival and season within plant categories are indicated (*).

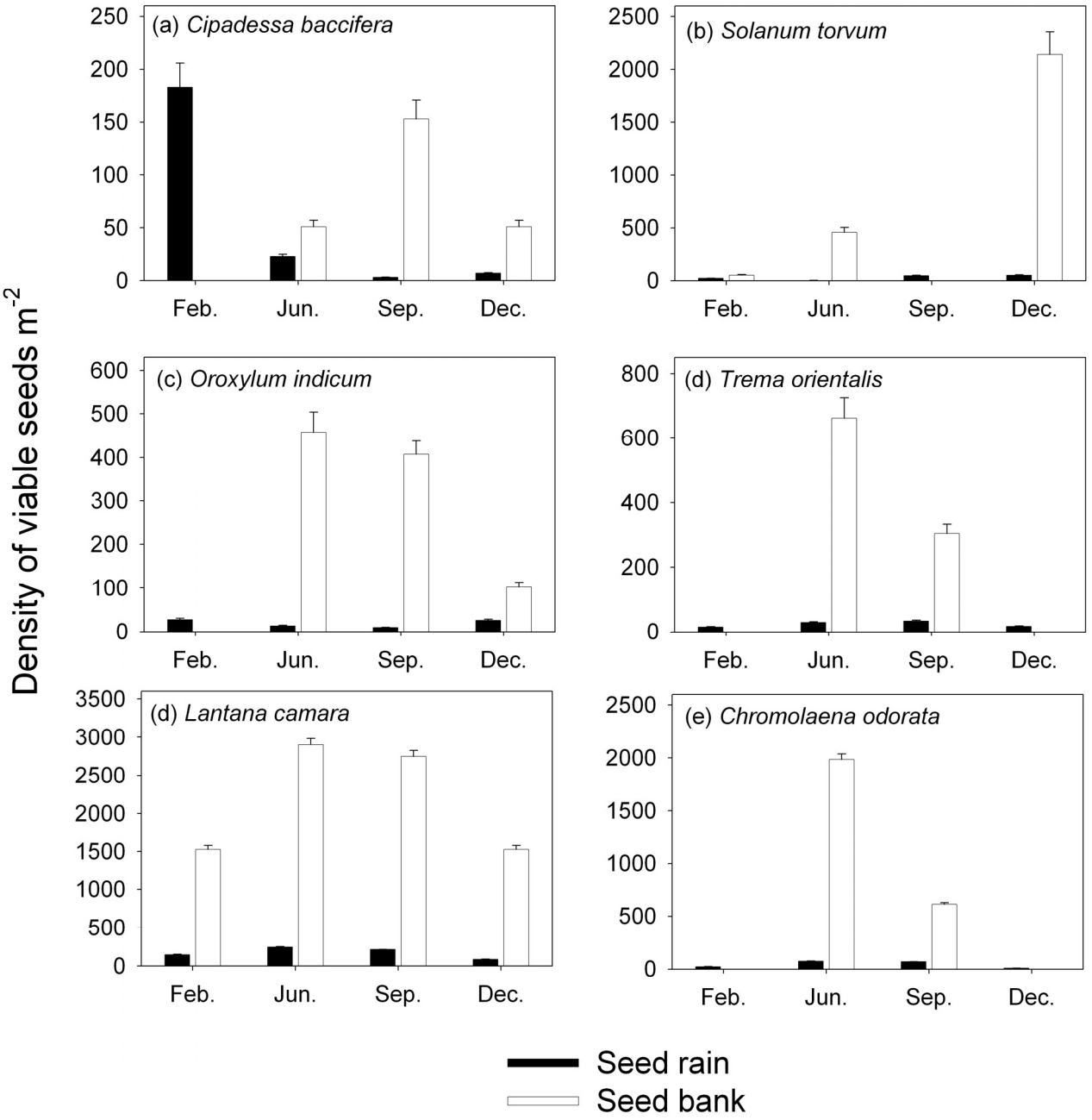

Figure 4.5: Comparison between the density of viable seeds present in the soil seed bank and seed rain for the most dominant other woody species (a & b), the most dominant tree species (c & d), Chromolaena (e), and lantana (f), across the different seasons of sampling in BRT. Note differences in y-axis scale across panels.

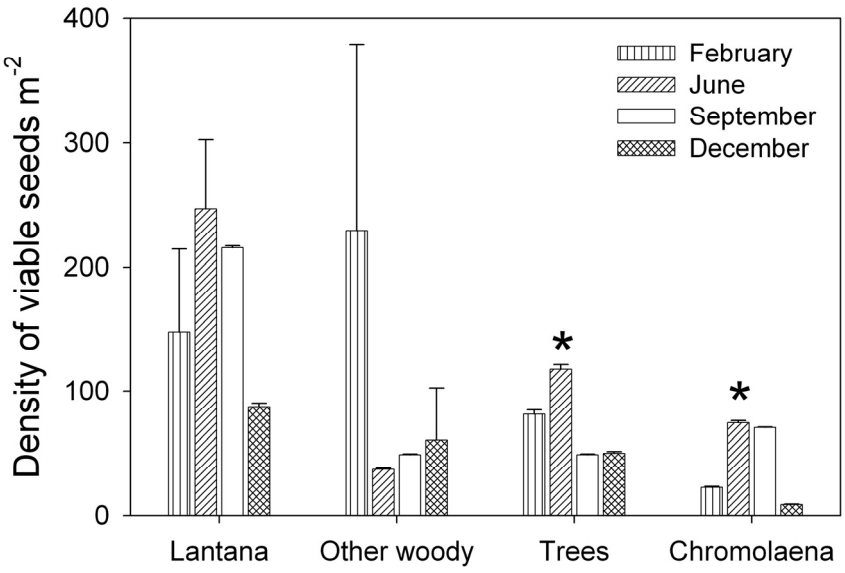

Figure 4.6: Seasonal variation in total seed arrival of (a) lantana, (b) other woody species, (c) trees, and (d) Chromolaena across all treatments. Model output from LMEs that showed significant interactions ($p < 0.05$) between seed arrival and season within plant categories are indicated (*).

Discussion

The role of seed arrival and soil seed banks in tropical forest regeneration

Plant regeneration is governed by the number of individuals surviving through many critical life-stages like seed arrival, survival in the soil seed bank, germination, and seedling recruitment (Chambers and MacMahon 1994). Above ground vegetation thus depends on the interaction between each of these crucial life-stages. However, making the link between seeds held below-ground and vegetation aboveground is problematic. In tropical dry forests, the composition of seeds stored in soil and the composition of overstory vegetation are very often dissimilar (Tekle and Bekele 2000, Thompson 2000, Crawford and Young 1998, Drake 1998, Skoglund 1992, but see Vila and Gemino 2007). Findings from this study also suggest that there is little similarity between the composition of seeds in soil and overstory vegetation. Several tree species that dominate the overstory in BRT, such as *Anogeissus latifolia*, *Terminalia crenulata*, *Pterocarpus marsupium*, and *Syzygium cuminii*, were either completely absent from the seed rain and the soil seed bank, or were present in very low densities. Similarly, a few other woody species, such as *Randia dumetorum*, and *Maesa indica*, which dominate the understory in BRT, were also either completely absent or present at very low densities in seed arrival and soil seed bank samples.

There are many factors that could give rise to differences in the composition between seeds stored below-ground and above-ground vegetation. First, there could be local dispersal limitation that affects seed arrival into suitable microsites (Dalling *et al*. 2002, Nathan and Muller-Landau 2000). Dispersal limitations have been reported in the dry forests of Hawaii (Denslow *et al*. 2006), Panama (Hubbell 2006), and Costa Rica (Holl *et al*. 2000). Dispersal limitations often arise due to post-dispersal seed mortality caused by predatory insects and rodents (Cabin and Marshall 2000). Be that as it may, there is no information on post-dispersal seed predators or on the effects of seed predation on the dispersal dynamics of plants in BRT. Additionally, dispersal limitations are also caused by infrequent or sporadic fruiting, both over space, and over time (Denslow *et al*. 2006). There is some indication that dominant species in BRT, such as *Pterocarpus marsupium*, *Syzygium cuminii*, and *Randia dumetorum* have had infrequent fruiting over the past 5 years, when compared to fruiting 10 years ago (Setty and Bawa. unpublished

data). Infrequent fruiting has been reported for other tree species that are dominant in tropical dry forests elsewhere in India, e.g., *Diospyros melanoxylon* and *Terminalia tomentosa* (Singh and Kushwaha 2006).

Second, dissimilarity between the composition of seeds in soil and aboveground vegetation may be related to the ability of seeds to enter the soil seed bank. Entry into the soil would be more problematic for seeds (or fruit) with large surface/volume ratios relative to small, compact seeds or fruit (Bakker *et al*. 1996). The dissimilarity in below-ground composition and above-ground vegetation in BRT could thus be explained by difference in fruit/seed size. Many of the canopy dominants in BRT, such as *Terminalia crenulata*, *Randia dumetorum*, *Syzygium cuminii* have large fruit/seeds (Murali 1997), and results from this study indicate that they were present at very low density in the soil. However, there is no information on whether large-fruited species form seedling banks in BRT as reported elsewhere (e.g., Comita and Hubbell 2009). Seed and fruit sizes could also be a determinant of persistence, with small seeds thought to be capable of a higher persistence than large seeds (Leishman *et al*. 2000) and is consistent with results obtained in this study. Two large-seeded species which are present in the overstory in BRT, *Pterocarpus marsupium* and *Diospyros melanoxylon*, were completely absent from the soil seed bank, possibly due to low persistence in soil.

Third, in addition to dispersal and physical limitations, seed dormancy could also play a role in determining dissimilar below-ground and aboveground vegetation composition. Seed dormancy is a bet-hedging strategy used by many plant species to tide over unpredictable environments and stochastic rainfall trends (Baskin and Baskin 1998). Additionally, there is evidence to suggest that a large proportion of tropical dry forest species produce seeds that are dormant, and require scarification or chemical treatment to break physical or physiological dormancy (Khurana and Singh 2001, Baskin and Baskin 1998). I used the germination method (in which samples were watered regularly) to infer density of viable seeds either arriving or present in soil. This method probably has limitations, and is likely to underestimate the density of dormant seeds. Most tree and other woody species from the soil seed bank samples in this study germinated during rains (i.e., largely between June and September), the same period during which peak germination occurs *in situ* (Hiremath *et al*. unpublished manuscript). The absence or minuscule levels of

germination during other sampling instances (February, December) indicate that seed dormancy was probably unbroken during these periods. Additionally, germination cues, such as drought are often required for some species to germinate (Baskin and Baskin 1998). It is possible that seeds present in the samples either had a low probability of germination or did not germinate at all due to regular watering of both seed arrival and soil seed bank samples. Estimates of species composition would thus underestimate total species because certain species could have remained undetected, while others would have been detected, albeit at low densities. Future studies of seed arrival and the soil seed bank could explicitly include drought as an additional treatment. Additionally, elutriation of soil samples could be attempted (Gross 1990). However, in tropical dry forest systems, obtaining better estimates of species composition and viable seed density of the soil seed bank (including species that produce dormant seeds) could be possible by using physical or acid scarification (Khurana and Singh 2001). Alternatively, flotation or sieving of samples could yield more robust estimates of total seed density (Bakker *et al*. 1996). Separately conducted seed-burial experiments (e.g. Vivian-Smith and Panetta 2009) could then be used to arrive at estimates of both seed dormancy and viability of species of interest.

Lastly, the dissimilarity between the composition of seeds stored and above-ground vegetation may be a result of insufficient sampling of the soil seed bank. Instead of using soil cores to sample seed banks, other methods, such as the excavation of blocks of soil to a particular depth (e.g., 20 cm x 20 cm, 3 cm depth; Kennard *et al*. 2002) could be employed. Alternatively, using a soil core with a larger diameter (e.g. > 10 cm, Dalling *et al*. 1997) could also be explored.

Native tree species had seasonal seed arrival, but aseasonal emergence from the soil seed bank. Native shrub and liana species however, did not have seasonal seed arrival but had seasonal emergence from the soil. Tropical dry forest species have a fairly predictable fruiting phenology, with fleshy-fruit maturation during early summer, and wind-dispersed fruit maturation during late-summer (Vieira and Scariot 2006, Murali and Sukumar 1994, Murphy and Lugo 1986). Seed arrival patterns of dominant wind-dispersed tree species and other woody species in BRT, such as *Terminalia crenulata*, *Anogeissus latifolia*, *Pterocarpus marsupium*, and animal-dispersed species like *Randia dumetorum* and *Cipadessa baccifera* are consistent with this pattern. However, due to seed dormancy inherent in many species of tropical dry forests, seed

germination typically occurs during the next year's rainy season. The staggered nature of rainfall in BRT that occurs as a result of two monsoonal events annually could be contributing to aseasonal emergence of tree seeds from soil. However, there was no germination of tree seeds from the soil seed bank in February, while the emergence of seeds of other woody species was also quite low. Additionally, since data from all shrub and liana species were combined for analysis of effects of season, variation inherent within individual species could have been obscured, as evidenced by high standard errors.

The role of seed arrival and soil seed banks as drivers of invasive species success

Results from this study show that the soil seed bank in BRT is largely dominated by persistent seeds of lantana, and was counter to my prediction that seed arrival would be more important than seed persistence as a determinant of lantana success. Results from this study indicate that both seed arrival and seed persistence in soil contribute to the success of lantana in BRT. Throughout the year, and across all treatments, the emergence of lantana from the soil seed bank was much higher (sometimes exceeding 3 orders of magnitude) than the emergence of all tree species and as much as an order of magnitude higher than the density of all other woody species seeds in the soil seed bank. Propagules of lantana dominate the soil seed bank in areas that are heavily invaded by lantana, and provide a potentially effective mechanism to make use of favorable conditions to germinate. A similar pattern has been observed in Australia, where lantana seeds saturate the topmost layer of soil, affording them the opportunity to take advantage of favorable conditions such as rainfall or gap creation to germinate and establish (Vivian-Smith and Panetta 2009). The success of lantana in BRT is also enhanced by the year-round arrival of its seeds, coupled with high soil seed bank density. The enrichment of the lantana soil seed bank in BRT appears to be autochthonous, with invaded areas having much higher lantana seed arrival compared to un-invaded areas. The high density of lantana seeds (both arriving and soil-stored) is cause for concern because recent models that used seed-burial experiments to determine persistence of lantana seeds in soil indicate that propagules of lantana can persist in soil for up to a decade (Vivian-Smith and Panetta 2009). Long persistence of lantana seeds imply that even if adult lantana plants are removed, re-invasion can occur rapidly via seeds stored in soil,

suggesting that repeated plant removal across several years till the soil seed bank is exhausted will be required to eradicate lantana from BRT.

My prediction that Chromolaena success in BRT would be driven by its persistent seeds rather than seed arrival is difficult to accept or reject based on results from this study. Although invaded sites were selected based on high lantana density, and not on high Chromolaena density, Chromolaena was present in sites invaded by lantana. Experimental studies on the persistence of Chromolaena seeds indicate that the vast majority of their seeds rarely persist beyond one year, although a small subset of seeds remain viable (Witkowski and Wilson 2001). Notwithstanding reduced viability of Chromolaena seeds over time, results from this study show that barring the early-dry season in December, the density of Chromolaena seeds emerging from soil exceeds that of native shrubs and lianas. The higher density of Chromolaena seeds vis-à-vis native shrubs and lianas indicates that Chromolaena could potentially re-invade or re-establish in areas that have been exposed to disturbance (Bazzaz and Pickett 1980).

Management implications

In BRT, current management activities to control invasive species like lantana are restricted to lantana removal along road-sides, and in a few other areas like plantations and tourism zones. Recent studies from BRT have indicated that lantana invasion has negative effects on the diversity, evenness and size-class distributions of native species (Sundaram and Hiremath, manuscript submitted). Results from the current study indicate that lantana forms large, persistent seed banks, implying that removal activities would have to be continued for a period far beyond eradicating lantana above-ground, as reported elsewhere (Vivian-Smith and Panetta 2009). However, removal activities may not alone be sufficient to prevent re-invasion by lantana, and the option of using fire to destroy seeds of lantana in invaded areas could be explored. However, wielding fire as a management tool for the control of invasive species could have unwanted negative effects on native species both above- and below-ground. Studies from tropical dry forests elsewhere in India indicate that an increasing frequency of fire has negative effects on the diversity and population structure of trees (Saha and Howe 2003). Results from this study partly support my prediction that fires would have a negative effect on seeds stored in

the topmost layer of soil for all species. Although my results indicate that fires kill lantana seeds held below-ground, fire-effects on Chromolaena or native species seed banks were not apparent. However, more research on the effects of fire on the soil seed bank of native species is required before being considered as an option to control lantana.

In addition to intensified efforts to control the persistence of lantana in BRT, Chromolaena invasions in BRT would also have to be targeted. There is no evidence for the increased spread of Chromolaena over the past 11 years (Murali and Setty 2001, Sundaram and Hiremath, unpublished data). Additionally, there is evidence from South Africa that a self-thinning mechanism is inherent within adult populations of Chromolaena, with plants in stand ages > 7 y rapidly declining in their seed output and survivability (Witkowski and Wilson 2001). However, there is information from other areas to suggest that subsequent to the removal of one invasive, the probability of arrival or establishment of another or few other invasives increases (Buckley *et al*. 2004). Therefore, it would be prudent to adopt a whole-ecosystem approach, and work towards the removal of all invasive species in the landscape (Buckley *et al*. 2004).

References

Anonymous. 1996. Map of Karnataka soils. National Bureau of Soil Survey and Land-Use Planning, Indian Council for Agriculture Research, Nagpur.

Bakker, J. P., P. Poschlod, R. J. Strykstra, R. M. Bekker, and K. Thompson. 1996. Seed banks and seed dispersal: important topics in restoration ecology. Acta Botanical Neerlands **45**:461-490.

Baskin, C. C., and J. M. Baskin. 1998. Seeds: Ecology, biogeography, and evolution of dormancy and germination. Academic Press, San Diego, USA.

Bazzaz, F. A., and S. T. A. Pickett. 1980. Physiological ecology of tropical succession: a comparative review. Annual Review of Ecology and Systematics **11**:287-310.

Bhatt, D., and A. Kumar. 2001. Foraging ecology of red-vented bulbul *Pycnonotus cafer*, in Haridwar, India. Forktail **17**:109-110.

Buckley, Y. M., S. Anderson, C. P. Catterall, R. T. Corlett, T. Engel, C. R. Gosper, R. Nathan, D. M. Richardson, M. Setter, and O. Spiegel. 2006. Management of plant invasions mediated by frugivore interactions. Journal of Applied Ecology **43**:848-857.

Buckley, Y. M., M. Rees, Q. Paynter, and W. M. Lonsdale. 2004. Modelling integrated weed management of an invasive shrub in tropical Australia. Journal of Applied Ecology **41**:547-560.

Cabin, R. J., and D. L. Marshall. 2000. The demographic role of soil seed banks. I. Spatial and temporal comparisons of below- and above-ground populations of the desert mustard *Lesquerella fendleri*. Journal of Ecology **88**:283-292.

Chambers, J. C., and J. A. MacMahon. 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. Annual Review of Ecology and Systematics **25**.
Colautti, R. I., I. A. Grigorovich, and H. J. MacIsaac. 2006. Propagule pressure: a null model for biological invasions. Biological Invasions **8**:1023-1037.
Comita, L. S., and S. P. Hubbell. 2009. Local neighborhood and species' shade tolerance influence survival in a diverse seedling bank. Ecology **90**:328-334.
Crawford, E. R., and D. R. Young. 1998. Spatial/temporal variations in shrub thicket soil seed banks on an Atlantic Coast Barrier Island. . American Journal of Botany **85**:1739-1744.
Crawley, M. J. 2007. The R Book. Wiley, New Jersey.
Cronk, Q. C. B., and J. L. Fuller. 1995. Plant invaders. Chapman and Hall, London.
Dalling, J. W., H. C. Muller Landau, S. J. Wright, and S. P. Hubbell. 2002. Role of dispersal in the recruitment limitation of neotropical pioneer species. Journal of Ecology **90**:714-727.
Dalling, J. W., M. D. Swaine, and N. C. Garwood. 1994. Effect of soil depth on seedling emergence in tropical soil seed-bank investigations. Functional Ecology **9**:119-121.
Dalling, J. W., M. D. Swaine, and N. C. Garwood. 1997. Soil seed bank community dynamics in seasonally moist lowland tropical forest, Panama. Journal of Tropical Ecology **13**:659-680.
D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics **23**:63-87.
Day, M. D., C. J. Wiley, J. Playford, and M. P. Zalucki. 2003. Lantana: current management status and future prospects. Australian Centre for International Agriculture Research, Canberra, Australia.
Denslow, J. S., A. L. Uowolo, and R. F. Hughes. 2006. Limitations to seedling establishment in mesic Hawaiian forest. Oecologia **148**:118-128.
Development Core Team, R. 2009. R: A language and environment for statistical computing. *in*. R Foundation for Statistical Computing, Vienna, Austria.
Drake, D. R. 1998. Relationships among the seed rain, seed bank and vegetation of a Hawaiian forest. Journal of Vegetation Science **9**:103-112.
Epp, G. A. 1987. The seed bank of Eupatorium odoratum along a successional gradient in a tropical rain forest in Ghana. Journal of Tropical Ecology **3**:139-149.
Fine, P. V. A. 2002. The invasibility of tropical forests by exotic plants. Journal of Tropical Ecology **18**:687-705.
Forget, P.-M., and T. Milleron. 1991. Evidence for secondary seed dispersal by rodents in Panama. Oecologia **87**:596-599.
Ganesan, R., and R. S. Setty. 2004. Regeneration of *amla*, an important non-timber forest product from southern India. Conservation and Society **2**:365-375.
Garwood, N. C. 1989. Tropical seed banks: a review. Ecology of soil seed banks. Academic Press, London:149-209.
Gross, K. L. 1990. A comparison of methods for estimating seed numbers in the soil. Journal of Ecology **78**:1079-1093.
Hiremath, A. J., and B. Sundaram. 2005. The fire-lantana cycle hypothesis in Indian forests. Conservation and Society **3**:26-42.
Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology **6**:324-337.

Kammathy, R. V., A. S. Rao, and R. S. Rao. 1967. A contribution towards a flora of Biligirirangan Hills. Mysore State Bulletin: Botanical Survey of India **9**.
Keeley, J. E., M. Baer-Keeley, and C. J. Fotheringham. 2005. Alien plant dynamics following fire in Mediterranean-climate California shrublands. Ecological Applications **15**:2109-2125.
Kennard, D. K., K. Gould, F. E. Putz, T. S. Fredericksen, and F. Morales. 2002. Effect of disturbance intensity on regeneration mechanisms in a tropical dry forest. Forest Ecology and Management **162**:197-208.
Kery, M., and J. S. Hatfield. 2003. Normality of Raw Data in General Linear Models: the Most Widespread Myth in Statistics. Bulletin of the Ecological Society of America **84**:92-94.
Khurana, E., and J. S. Singh. 2001. Ecology of seed and seedling growth for conservation and restoration of tropical dry forest: a review. Environmental Conservation **28**:39-52.
Kotanen, P. M. 1997. Effects of Experiemental Soil Disturbance on Revegetation By Natives and Exotics in Coastal California Meadows. Journal of Applied Ecology **34**:631-644.
Leishman, M. R., I. J. Wright, A. T. Moles, and M. Westoby. 2000. The evolutionary ecology of seed size. Seeds: the ecology of regeneration in plant communities **2**:31-57.
Lonsdale, W. M., K. L. S. Harley, and J. D. Gillett. 1988. Seed bank dynamics in *Mimosa pigra*, an invasive tropical shrub. Journal of Applied Ecology **25**:963-976.
Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications **10**:689-710.
Murali, K. S. 1997. Patterns of Seed Size, Germination and Seed Viability of Tropical Tree Species in Southern India. Biotropica **29**:271-279.
Murali, K. S., and R. S. Setty. 2001. Effect of weeds Lantana camara and Chromelina odorata growth on the species diversity, regeneration and stem density of tree and shrub layer in BRT sanctuary. Current Science **80**:675-678.
Murali, K. S., R. S. Setty, K. N. Ganeshaiah, and U. S. R. 1998. Does forest type classification reflect spatial dynamics of vegetation? An analysis using GIS techniques. Current Science **75**:220-227.
Murali, K. S., and R. Sukumar. 1994. Reproductive phenology of a tropical dry forest in Mudumalai, southern India. Journal of Ecology **82**:759-767.
Murphy, P. G., and A. E. Lugo. 1986. Ecology of tropical dry forest. Annual Review of Ecology and Systematics **17**:67-88.
Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology & Evolution **15**:278-285.
Pinheiro, J. C., and D. M. Bates. 2000. Mixed-Effects Models in S and S-Plus. Springer-Verlag, Berlin.
Ranganathan, C. R. 1934. Working plan, Kollegal Forest Division. Government of India, Madras.
Rejmanek, M. 1996. A theory of plant invasiveness: the first sketch. Biological Conservation **78**:171-181.
Rejmanek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? Ecology **77**:1655-1661.
Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. McCauley, P. O'Neil, I. M. Parker, J. N.

Thompson, and S. G. Weller. 2001. The population biology of invasive species. Annual Review of Ecology and Systematics **32**:305-332.
Sharma, G. P., A. S. Raghubanshi, and J. S. Singh. 2005. *Lantana* invasion: an overview. Weed Biology and Management **5**:157-165.
Singh, K. P., and C. P. Kushwaha. 2006. Diversity of flowering and fruiting phenology of trees in a tropical deciduous forest in India. Annals of Botany **97**:265.
Skoglund, J. 1992. The role of seed banks in vegetation dynamics and restoration of dry tropical ecosystems. Journal of Vegetation Science **3**:357-360.
Swarbrick, J. T., B. W. Willson, and M. A. Hannan-Jones. 1998. Lantana camara L. . Pages 119-136 *in* F. D. Panetta, R. H. Groves, and R. C. H. Shepherd, editors. The biology of Australian weeds. R.G. & F.G. Richardson, Melbourne.
Tekle, K., and T. Bekele. 2000. The Role of Soil Seed Banks in the Rehabilitation of Degraded Hillslopes in Southern Wello, Ethiopia1. Biotropica **32**:23-32.
Theoharides, K. A., and J. S. Dukes. 2007. Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. New Phytologist **176**:256-273.
Thompson, K. 2000. The functional ecology of soil seed banks. Pages 215-236 *in* M. Fenner, editor. The ecology of regeneration in plant communities. CABI Publishing, New York.
Thompson, K., and J. P. Grime. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. The Journal of Ecology **67**:893-921.
Vieira, D. L. M., and A. Scariot. 2006. Principles of natural regeneration of tropical dry forests for restoration. Restoration Ecology **14**:11-20.
Vila, M., and I. Gimeno. 2007. Does invasion by an alien plant species affect the soil seed bank? Journal of Vegetation Science **18**:423-430.
Vivian-Smith, G., and F. D. Panetta. 2009. Lantana (*Lantana camara*) seed bank dynamics: seedling emergence and seed survival. Invasive Plant Science and Management **2**:141-150.
Witkowski, E. T. F., and M. Wilson. 2001. Changes in density, biomass, seed production and soil seed banks of the non-native invasive plant, *Chromolaena odorata*, along a 15 year chronosequence. Plant Ecology **152**:13-27.
Zachariades, C., M. Day, R. Muniappan, and G. V. P. Reddy. 2009. *Chromolaena odorata* (L.) King and Robinson (Asteraceae). Pages 130-162 *in* R. Muniappan, G. V. P. Reddy, and A. Raman, editors. Biological control of tropical weeds using arthropods. Cambridge University Press, Cambridge.

Chapter 5: Traditional Soliga knowledge on the ecology and impacts of the invasive *Lantana camara*

Introduction

The explicit inclusion of traditional ecological knowledge (TEK) within the ambit of ecological research on biological invasions could expand the horizons of the field by providing different perspectives on how forest-dwellers view and deal with biological invasions (e.g., Shackleton *et al*. 2007, Neogi *et al*. 1989). Most forest-dwelling people have historically been hunter-gatherers (Hart and Hart 1986, Bahuchet *et al*. 1991, Patin *et al*. 2009), and some continue to be hunter-gatherers (Fortier 2009, Peluso *et al*. 1995). Indigenous people use the natural areas where they live in various ways, e.g., for hunting animals, collecting non-timber forest products (NTFP), collecting fuel-wood, and gathering medicinal plants (McNeely 2004, Bird-David 1992, Guha and Gadgil 1989). Many of these activities, such as fuel wood collection, ensue on a daily basis. Some others, such as the collection of NTFP, may be seasonal. Either way, indigenous people interact in varied ways with large landscapes during the course of their lives. Additionally, many indigenous communities, particularly those who practice slash-and-burn agriculture, do not lead sedentary lives and sometimes come into contact with a large part of the landscape that they live in during the course of their lives. Based on their observations over time, indigenous people may have knowledge and insights about invasive species, and could thus improve our understanding of the spread, effects, and mechanisms of success of invasives.

The context of TEK in forest management has been explored from practical and political standpoints. Firstly, researchers have drawn from TEK sources in 'practical ways' (Berkes *et al*. 1995). Research on knowledge systems related to botany and zoology present in indigenous societies, including forest-dwelling societies, (e.g., Sears *et al*. 2007, Shackleton *et al*. 2007, Shrivastava and Heinen 2005, Basset *et al*. 2004, Bhargava 1983) have led to improvements in our understanding of natural resource management in peopled landscapes, e.g., whale conservation in Alaska (Huntington *et al*. 2000), fire management in agro-pastoral systems in Bolivia (McDaniel *et al*. 2005), or management of NTFP resources in India (Setty *et al*. 2008).

These studies suggest that the incorporation of TEK systems with Western knowledge systems could lead to a sustainable long-term management regime. Indeed, TEK systems have been equated with adaptive management systems as "traditional systems had certain similarities to adaptive management with its emphasis on feedback learning, and its treatment of uncertainty and unpredictability intrinsic to all ecosystems" (Berkes *et al*. 2000). On the other hand, some researchers have explicitly explored the political ecology underlying knowledge systems, both traditional and scientific. In a world where the state has hegemony over natural areas — 86% of all forests and wooded areas in the world are controlled by Central governments (Agrawal *et al*. 2008), studies that urge researchers and managers to incorporate TEK in their way of thinking (the 'practical' context) could be considered as indirect ways to legitimize the use of natural resources by local communities within a power structure that is largely exclusive in its management regime. Political ecologists directly acknowledge the power structure inherent in natural resource management, and situate TEK within it, arguing that the state of the art of TEK is moot considering the current political milieu. Recognizing the political nature of natural resource management, Agrawal *et al*. (2008) argue that irrespective of knowledge about TEK, a greater role for community and market actors in forest governance, and deeper attention to the factors that lead to effective governance beyond ownership patterns, is necessary to address future forest governance challenges. Additionally, Agrawal (1995), arguing from a human rights perspective, suggests that instead of seeking to address our understanding of the dichotomy between TEK and scientific knowledge, we must "work towards greater autonomy for indigenous peoples." Nevertheless, approaches that seek a common ground by discussing complementarity and differences between TEK and scientific knowledge within their own epistemologies could only enrich our overall knowledge of the dynamics of human impacts on natural landscapes and vice-versa.

Invasive species are foremost amongst the many threats to biodiversity. Invasive species are defined as non-native species that cause negative impacts in recipient systems (Colautti and MacIsaac 2004). The negative effects of invasive species are seen at the level of ecosystems, and at the level of native biological communities. At the ecosystem level invasive species have been found to increase flammability (Nunez and Simberloff 2005), alter nutrient cycling (Funk and Vitousek 2007), and affect hydrology (Le Maitre *et al*. 2002). At the level of biological

communities invasive species can out-compete native species, thus resulting in loss of biodiversity over time (Strayer *et al*. 2006). Additionally, invasive species can disrupt native species regeneration and thus negatively affect diversity, population structure, and physical structure of invaded habitats (Kennard *et al*. 2002, Gooden *et al*. 2009).

Due to their largely negative ecosystem effects, invasive species affect society both directly and indirectly. The direct societal effects of invasive species can take the form of reduced livelihoods for forest-dependent communities resulting from the loss or reduction in the density of species that are otherwise consumed or sold (Jones *et al*. 2009, Chapin *et al*. 2000). The indirect societal effects of invasive species can take the form of a reduction in the supply of ecosystem services to communities, e.g., water (Pejchar and Mooney 2009, Le Maitre *et al*. 2002). As a result, many countries now allocate substantial financial resources for the control and eradication of invasive species (Lovell *et al*. 2006, Perrings *et al*. 2002, Zavaleta 2000), with some countries like the United States spending up to USD 120 billion annually to control or mitigate the negative effects of invasive species (Pimentel *et al*. 2005).

Given the many deleterious effects of invasive species, ecological monitoring has been recognized as an important tool to track the spread and effects of invasive species worldwide (Delaney *et al*. 2008, Ricciardi *et al*. 2000, Blossey 1999). Ecological monitoring helps track the response of native biological communities to invasions and could also help to identify those habitats that are most vulnerable to being invaded (Sutton *et al*. 2007). Data for tracking biological invasions can come directly (e.g., from long-term monitoring plots), or by using indirect methods such as comparing the accrual of known invasive species within floras over time. However, examples of systematic long-term monitoring approaches for the study of invasive species and recipient native communities are rare. There are several reasons for this, including the high costs of implementation (Basset *et al*. 2004, but see Bogich *et al*. 2008). Additionally, in some developing countries, the intrinsic value of ecological monitoring has not been widely appreciated (Perrings *et al*. 2002). Furthermore, the lack of ecological monitoring projects often results due to the absence of requisite institutions who would otherwise oversee their design and implementation. Lastly, ecological monitoring projects that are recent in their

genesis cannot shed light on the spread of invasion species that may have begun decades or centuries ago.

But there are other ways to overcome the lack of long-term information regarding invasive species, e.g., through historical forest cover or vegetation maps and aerial photographs (Von Holle and Motzkin 2007, Civille *et al*. 2005), or through the compilation of anecdotal information appearing in news articles or popular science writings, or travel writings (Coates 2006, Hansen and Clavinger 2005, Crosby 2004). Additionally, records kept by amateur naturalists could also be used to track the trajectory of biological invasions (Silvertown 2009). However, one aspect that has been hitherto under-researched, but can provide valuable information, is examining how local and indigenous communities inhabiting and using forest ecosystems perceive biological invasions.

Lantana camara (hereafter, lantana) is one of the most widely distributed invasive species in India. Having arrived via multiple introductions during the early part of the 19th century, lantana is now commonly seen in seasonally dry tropical forests, agricultural fallows, grazing lands, and along roads and railway lines in most parts of India (Sharma *et al*. 2005). Anecdotal information about the invasive nature of lantana, including its spread and effects on timber species, began to appear in the literature during the early 20th century (Tireman 1916, Iyengar 1933), i.e., within approximately a century after its arrival. These anecdotal reports are fairly preliminary in nature and consist largely of observations made by forestry officials, but are immensely valuable to trace the trajectory of lantana invasion in India. However, in some parts of India, it is possible to build-up a more detailed picture of lantana invasion. For example, in the Biligiri Rangaswamy Temple Wildlife Sanctuary (hereafter, BRT) in South India, we know that lantana was first reported in 1934 (Ranganathan 1934). Preliminary conversations with the resident Soliga community indicated that the rapid spread of lantana began occurring during the 1970s, possibly due to the occurrence of forest fires that created an empty understory for lantana to occupy (Hiremath and Sundaram 2005). Additionally, because lantana is resistant to fire and can resprout in response to being burnt, Hiremath and Sundaram (2005) hypothesized that lantana invasion could be encouraged by fire occurrence, while frequent fires, in turn, would be encouraged by lantana – a positive feedback. Vegetation in BRT was first inventoried in 1997

and indicated that lantana was restricted in its spatial extent and density (Murali and Setty 2001). This inventory was repeated by Sundaram and Hiremath (manuscript submitted) in 2008, and indicated that lantana had not only increased in its spatial extent, but also in its density, and was accompanied by significant negative effects on native biodiversity. However, given that systematic monitoring of lantana began only in 1997, sourcing information from the Soliga could provide slightly more long-term insights into the lantana invasion process.

The objectives of this study are to examine the perceptions of the indigenous Soliga community on lantana invasion, its management, and its impacts on forest process and structure in the BRT wildlife sanctuary, a protected area of the Western Ghats in peninsular India. Responses are discussed in relation to current scientific understanding of processes regulating lantana spread, and management. This study is an attempt to seek a convergence of TEK and scientific knowledge to enrich our understanding of lantana invasion and its impacts on forest structure and functioning, with the potential to improve ecosystem management.

Methods

Study area

I conducted this study in the BRT Wildlife Sanctuary (hereafter, BRT), located in the Western Ghats mountain range in Karnataka State, India. The sanctuary covers an area of 540 km^2, and is located between 77° – 77° 16′ E, and 11° 47′ – 12° 09′ N. The BRT terrain is hilly, with elevation ranging from 600-1800 m above sea level. The sanctuary receives rainfall from both the southwest monsoon (June-September) and the northeast monsoon (October-December), with a pronounced dry period between January and March. Further details of rainfall, temperature, and soil are given in Sundaram and Hiremath (manuscript submitted).

The BRT sanctuary is part of the Western Ghats biodiversity hotspot (Myers, 2003; Mittermeier *et al*., 2004) in Karnataka State, India, and was notified as a wildlife sanctuary in 1973 (Barve *et al*., 2005). The area is rich in biodiversity, with at least 1400 species of higher plants (Ramesh, 1989; Kammathy *et al*., 1967). The main vegetation types in BRT are scrub-savanna, dry

deciduous forests, moist deciduous forests, riparian semi-evergreen forests, evergreen forests, and the shola-grassland mosaic, a forest type endemic to the Western Ghats. Seasonally dry forests comprising the scrub-savanna, and dry deciduous and moist deciduous forests, constitute approximately 90% of the study area (Ganesan and Setty, 2004) and are now extensively invaded by lantana.

The BRT has a long history of management and use. Prior to the declaration of BRT as a wildlife sanctuary, resident Soligas practiced shifting agriculture. They also hunted game and gathered wild tubers, fruits, and honey to supplement their diet. Additionally, prior to the area being declared a wildlife sanctuary, the forest department managed areas within the present-day BRT for timber, bamboo, and grass resources (Sundaram *et al*. manuscript submitted). In 1973 BRT was declared a wildlife sanctuary and came under the purview of the Wildlife Protection Act (Barve *et al*. 2005). Thereafter, the Soliga practice of shifting agriculture was banned, as was hunting (Setty *et al*. 2008). The extraction of timber, bamboo, and grass by the Forest Department was also suspended. However, Soliga usufruct rights for the collection of NTFP (e.g., honey, lichens, and *Phyllanthus* spp. or 'amla' fruits) were fraught with equivocal administrative deliberation that allowed, disallowed, or regulated the collection of NTFP from 1973 onward. The collection of NTFP in BRT from 1973-2004 was an activity permitted by the forest department (Shaanker *et al*. 2004) in accordance with the provisions of the Wildlife (Protection) Act (Government of India 1972). The Act was amended in 2003 to modify use of NTFP to *bona fide* (subsistence-only) use of NTFP. However, before the amendment of the Act could be implemented, and due to a case filed in the Supreme Court of India being heard at the same time that asked for the strict enforcement of the Wildlife (Protection) Act 1972, a total ban on the collection of NTFP came into effect between 2005 and 2008. Thereafter, only the collection of amla fruits was allowed in 2009, while both amla and honey collection was permitted in 2010. However, on paper, the ban on collecting NTFP still stands. Additionally, as mandated by the Wildlife Protection Act, fire prevention was initiated within BRT, and the setting of forest fires was declared illegal (Madegowda 2009). Forest fires continue to occur in BRT, albeit on an infrequent basis (Sundaram *et al*. unpublished manuscript).

Lantana camara

Lantana camara is a woody straggling shrub native to Central and South America. Lantana was introduced to India on multiple occasions (Cronk and Fuller, 1995; Sharma *et al*., 2005), although its earliest documented introduction dates back to 1809 (Cronk and Fuller, 1995). Within about a century of its introduction, there were reports of lantana's invasiveness from different parts of the country, ranging from Coorg in the wet forests of the Western Ghats, to Salem in the arid lowlands of Tamil Nadu in South India (Tireman 1916, Iyengar 1933, Anon. 1942).

Information regarding the exact year of arrival of lantana in BRT is unavailable. Forest working plans mention the presence of lantana in BRT as early as 1934 (Ranganathan, 1934), although interviews with the Soliga people, who have lived in BRT for centuries, suggest that the spread of lantana began during the 1970s. The first study to record the presence and density of lantana was conducted by Murali and Setty (2001) in 1997. Using a systematic sampling approach, Murali and Setty (2001) overlaid a 2 km x 2 km grid on the BRT map, yielding a total of 134 grid cells. They then inventoried all stems ≥ 1 cm DBH (diameter at breast height), regardless of whether they were of native species or of lantana, from a 5 m x 80 m plot placed at the centre of each grid cell. Results from their study showed that lantana was present at low densities, and only in ~ 40% of all plots inventoried in 1997 (Murali and Setty 2001; Fig. 5.1). By the time the same plots were re-visited in 2008, lantana distribution had changed drastically. Lantana was present in ~80% of all plots and its density had increased four-fold from what it was in 1997 (Sundaram and Hiremath, manuscript submitted). Investigations into the mechanisms underlying lantana invasion in BRT suggest that propagule pressure (i.e., the colonizing pressure exerted by lantana seeds arriving via dispersal) and the high density of lantana seeds in soil vis-à-vis seeds of native species have played important roles in enhancing lantana's success (Sundaram *et al*. manuscript submitted, Sundaram and Hiremath, manuscript submitted).

The Soliga

The Soliga (literally, 'children of the bamboo') are a tribal people largely concentrated in the Chamrajnagar, Kollegal, Yelandur, and Gundlupet talukas (provinces) of Karnataka. Soligas are genetically related to other tribal groups in the region, such as the Jenu Kuruba and Kadu Kuruba (Kumar 2008). The Soligas speak a language called Soliganudi, which has been classified as a Dravidian language closely related to Kannada and Tamil. The Soliga language is a spoken one, and has no script.

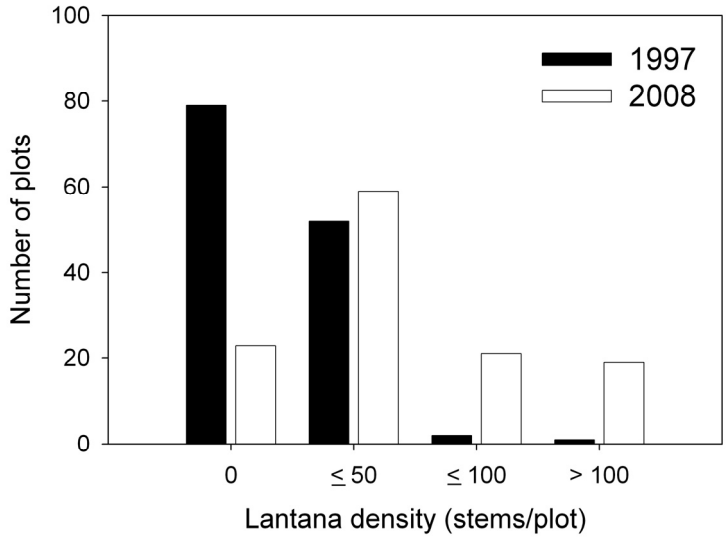

Figure 5.1: Numbers of lantana stems per 400 m^2 plot encountered in 1997 and in 2008. In 1997 134 plots were sampled by Murali and Setty (2001); by 2008, 12 of these plots had been converted to other land uses, and so only 122 plots were sampled by Sundaram and Hiremath (manuscript submitted).

After BRT was declared a wildlife sanctuary in 1972, Soliga lifestyles changed significantly. The Soliga practice of shifting cultivation was banned. Most Soligas living in the forest interior were sedentarized in settlements called 'podus.' After sanctuary notification some Soligas received titles to plots of cultivable land ranging in size from 0.5 ha to 2 ha. Landed Soligas now make a living from cultivating rain-fed crops of finger miller, maize, and vegetables. However, prior to

2004, a large proportion (50%; Hegde *et al*. 1996) of their income was generated through the sale of NTFP such as honey and *P. emblica* fruits. Today there are 62 Soliga settlements either within or in close proximity to BRT and the population of Soligas in BRT is approximately 16000 (Madegowda 2009). In addition to income from cultivation and NTFP collection, some Soligas also augment their income by seeking seasonal employment in coffee plantations in BRT during the coffee picking season, or by working for the Karnataka Forest Department to clear and maintain forest roads within BRT.

Interview schedule

I used an interview schedule to gather information on various aspects of lantana invasion, including time of spread, patterns of spread, reasons for spread, effects on native trees, forest structure, and effects of lantana on their livelihoods. Interview schedules were an appropriate instrument to generate such qualitative information. In order to build a list of interviewees, village elders from 5 podus were consulted. Elders were given details about the objectives of the study, and were asked to provide names of potential interviewees who would fit in one or more of three broad *a priori* categories: (a) other village elders, (b) non-timber forest product collectors, and (c) fuel-wood gatherers. These categories were chosen in order to maximize the proportion of interviewees who had long-term knowledge of the forest (village elders), or who accessed the forest on a regular basis (NTFP collectors, fuel-wood collectors). In order to maximize the spatial representation of respondents, elders were also requested to provide details of potential interviewees from across as many podus as their knowledge would permit.

Names of 55 potential interviewees were provided by the elders. Of the 55 potential interviewees, the responses of a total of 47 people were recorded between July and October 2008. Respondents belonged to 17 podus all across BRT. Prior informed consent was obtained from each respondent after explaining the aims and objectives of the study. Interviews were conducted in Kannada. A digital voice recorder was used to record data. All interviews were then transcribed and translated into English. After transcribing all interviews, individual responses to each conversation topic (e.g., natural history of lantana invasion) were collated in a single file,

along with corresponding details like respondent age, and respondent location. Similar responses were then grouped together to calculate summary statistics.

The age of all respondents varied from 35-65 years, with a mean age of 44 years. All 47 respondents were male. Although attempts were made to interview women, it was not possible to do so. Soliga society is largely male-dominated. Both people who conducted interviews in this study were male, and interviewing women was not possible. It is therefore likely that information presented in this study represents an incomplete perspective of lantana invasion in BRT. The mean duration of interviews varied from 45 minutes to 96 minutes, and was on average 55 minutes in duration.

Ecological data

Soliga responses regarding lantana invasion were juxtaposed with relevant ecological field data. Field data relevant to three different components of lantana invasion was collected. The three components were the long-term change in the basal area of lantana, the long-term change in the basal area of native species, and the long-term change in the density of important tree species (both NTFP species and canopy dominants) in BRT. The first two components (change in basal area of lantana and of native species) are related to changes in forest structure, while the third (changes in the density of important tree species, including NTFP species) are related to the effects of lantana on Soliga livelihoods.

Baseline data for all three components came from a study conducted by Murali and Setty (2001). Basal area of native species in each plot was calculated by summing the cross-sectional area of all stems occurring within the plot, for 1997 and for 2008. A *t* test was then used to check for differences in the basal area of native species in 1997 and 2008. Basal area of lantana was calculated the same way. A *t* test was then used to check for differences in the basal area of lantana between 1997 and 2008. Statistical analyses were performed using R 2.9.0. (R Development Core Team 2009).

Change in the density of important tree species, including NTFP species, in BRT between 1997 and 2008 was estimated using data from Murali and Setty (2001) and data collected by me. Studies indicate that the five most economically important NTFP species in BRT are *Phyllanthus emblica* and P. *indofischieri* (collectively known as *amla*; Indian gooseberry), *Acacia sinuata* (*seege*; soap-nut), *Sapindus laurifolius* (*antuwala*; soap-berry), *Terminalia bellerica* (*taare*; belliric myrobalan), and *Terminalia chebula* (*arale*; black myrobalan) (Hegde *et al*. 1996, Setty *et al*. 2008). The change in the average number of stems per plot of each of these important NTFP species was calculated for plots in which they occurred in 1997; no individuals of these species were found in any additional plots in 2008. Using similar methods, the change in density of important canopy dominants in BRT such as *Anogeissus latifolia*, *Terminalia crenulata*, *Dalbergia latifolia*, *Pterocarpus marsupium*, and *Kydia calycina* was also calculated.

Results

Natural history of lantana invasion in BRT (origin, spread, and mechanisms of spread)

More than half the respondents (26/47; 55 %) were not aware of lantana's geographical origins. Respondents who expressed knowledge about lantana's origins (21/47; 45 %) said that it was from 'abroad.'

A large majority of respondents believed that lantana's rapid spread has occurred over the past 15 years (Fig. 5.2). However, about a fifth of the respondents felt that the spread of lantana began occurring 30 years ago (Fig. 5.2). All respondents who felt that lantana spread began 30 years ago were from podus located in the forest interior (Banglipodu, Bhutani, Boodipadaga, Kanneri Colony, Bedguli, Seegebetta) relative to other podus. It may be that lantana was introduced as a hedge plant in coffee plantations located in the BRT interior before making an appearance in the plains, thus influencing their response. Additionally, respondents who felt that lantana spread began 30 years ago were on average older (mean 53.2 ± 2.5 years) than all other respondents (48.4 ± 3.4 years).

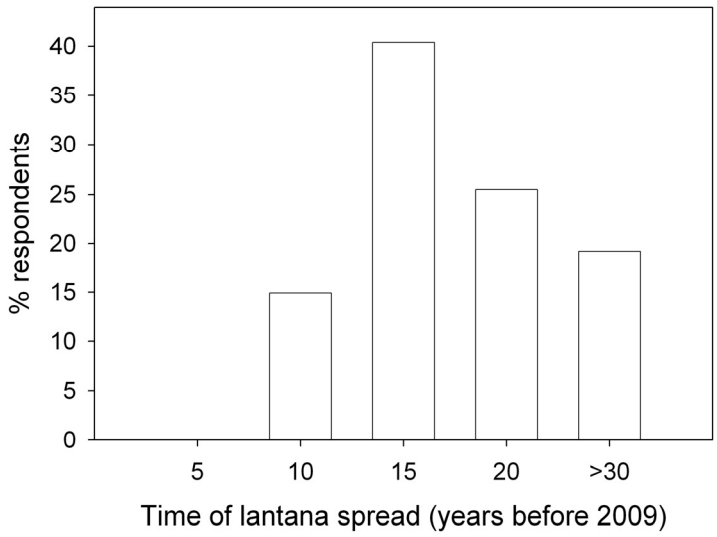

Figure 5.2: Distribution of the responses (n= 47) related to the time of lantana spread in BRT.

The Soligas largely attributed the rapid spread of lantana in BRT to three factors. The first factor was a function of lantana's biology—its prolific fruit production and wide dispersal. A large proportion of respondents (37/47; 79 %) believed that birds, and mammals like chital, sambar, civet, pig, and sloth bear are responsible for the spread of lantana in BRT. The copious fruiting of lantana provided food that was easy to gather for these animals, with lantana gaining dispersal advantages.

The second factor underlying lantana's rapid spread through BRT, according to the Soliga, was the change in fire regimes in BRT over the past 25 years (after BRT was declared a wildlife sanctuary). Half the respondents (24/47; 51%) believed that the spread of lantana in BRT was due to the decrease in fire frequency. The decrease in fire frequency in BRT occurred due to fire prevention measures being put in place by the Forest Department after 1973, when the BRT wildlife sanctuary was created. The Soliga believe that regular fires suppressed lantana because fires killed young lantana plants as well as lantana seeds present on the soil surface. One more reason put forward was that the soils dry up after a fire occurs and prevents lantana establishment because dry soils are not preferred by lantana. All respondents who said that the decrease in fire

frequency was a major reason for the spread of lantana also believed that native species remain unaffected by forest fires, because native species have been exposed to forest fires for a long time.

On the other hand, 19/47 people (40 %) believed that lantana was benefitted by an increase in fire frequency. One of the reasons mentioned was that lantana resprouts readily in response to fire. The other reason put forward was that dense lantana leads to the occurrence of intense fires, and that native species present in the midst of dense lantana are killed by fire, leading to a decrease in the abundance of native species over time.

Responses to the fire question seemed to be influenced by age of the respondent. Respondents who believed that a decrease in fire frequency led to an increased spread of lantana were on average older (mean 55.4 ± 4.5 years) than respondents who believed that lantana was benefited by an increase in fire frequency (mean 43.5 ± 5.2 years). Four respondents did not have an opinion on fire as a factor underlying lantana spread.

Although respondents had differing thoughts on the link between forest fires and lantana invasion, almost all respondents (45/47; 96 %) believed that early-dry season forest fires (‘*tharagu benki*;’ litter fires) were important to maintain what they called the ‘health’ of the forest. Burning the understory was likened to cleansing, like bathing or shaving for humans. Many said that a clean and clear understory was necessary for a healthy forest. They said that fires that occurred during the early dry season (January, February) did not harm saplings of native species, because only the litter was burnt. Additionally, because the fire passed through an area quickly, the time of exposure of each plant to fire was minimized. Furthermore, ash from a fire was considered good fertilizer for native species. However, almost all respondents (45/47; 96 %) believed that it was not possible to return to the early dry season fire regime now due to extensive lantana invasion. Due to the thick growth of lantana, fires would no longer be restricted to the forest floor, and may become destructive canopy fires. Many (23/47; 49 %) cited recent large fires that occurred in 2007, where entire trees burnt down. Fires in heavily lantana invaded areas would be catastrophic to all trees in the area, they said.

The third factor to which the Soliga attributed the spread of lantana in BRT was historical over-extraction of grass and bamboo resources. Prior to BRT being declared a wildlife sanctuary, grass and bamboo extraction was common in many parts of the sanctuary. More than half the respondents (24/47; 51%) believed that bamboo and grass were over-extracted from BRT, with bamboo being extracted before it could seed. The empty spaces left behind after grass and bamboo extraction were quickly occupied by lantana. Once lantana had established, bamboo seedlings were shaded out, resulting in the gradual reduction of bamboo over time. Similarly, the regeneration of light-demanding grasses was also affected by the increase in lantana density, leading to their gradual decline. However, (18/47; 38%) respondents did not believe bamboo and grass extraction to be a driver of lantana spread, and fell back upon the seed dispersal argument for their explanation of lantana spread. Five respondents did not have an opinion.

In addition to illustrating patterns of lantana spread, the Soligas described the effects of lantana invasion on the regeneration of native species as further contributions to lantana success in BRT. These reasons included seed germination limitations, and reduced seedling survival of native species under lantana. A large proportion of respondents (41/47; 87 %) believed that lantana success was enhanced because seeds of native species do not germinate on the thick layer of leaf litter that accumulates under lantana. Lantana leaf litter prevents seeds of native species from reaching the soil, thus affecting native species regeneration. A majority of respondents (41/47; 87 %) also believed that even if a native species seed did germinate, seedlings could not survive long without touching soil, especially when there was a thick layer of lantana leaf litter between the newly germinated seedling and the soil. Additionally, 41/47 people (87 %) believed that a lantana canopy limited seedling survivorship of native species because access to light is cut off by lantana. The same respondents also said that lantana seeds are unaffected by lantana leaf litter because they possess fast growing roots that touch the soil before seeds desiccated and died.

Forest change due to lantana invasion (changes in forest composition and structure)

A majority of respondents believed that subsequent to lantana invasion the forests in BRT had become degraded in terms of their species composition. Most respondents talked about the deciduous forests of BRT having a grassy understory prior to lantana invasion. Many respondents (42/47; 89 %) believed that the quantity of grass and bamboo has reduced in BRT due to lantana invasion.

In addition to the loss of bamboo and grass resources, many respondents (40/47; 85%) believed that the density of common tree species such as *Anogeissus latifolia*, *Terminalia crenulata*, *Dalbergia latifolia*, *Pterocarpus marsupium*, *Kydia calycina*, had reduced drastically as a result of lantana invasion. Ecological data about the change in the density of species indicates that drastic reductions in density have occurred for *Anogeissus latifolia* and *Kydia calycina*, while the density of the other species have more or less remained similar (Table 5.1).

A large majority of respondents (40/47; 85%) believed that there have been structural changes in the lantana-invaded forests of BRT particularly due to the reduction in the density of saplings. People said that there are no young trees now, only old ones. Many respondents (40/47; 85%) feared that once the old trees die, there will be nothing but lantana left in the forests of BRT.

The basal area of native species showed a reduction from 1997 (mean basal area= 29.22 ± 2.25 m^2/ha) to 2008 (mean basal area= 26.68 ± 2.16 m^2/ha; Fig. 5.3). However these differences were not statistically significant ($t= 0.81$, $p= 0.42$). On the other hand, the basal area of lantana showed a tremendous increase from 1997 (mean basal area= 0.08 ± 0.02 m^2/ha) to 2008 (mean basal area= 0.52 ± 0.08; Fig. 5.3). The difference in the basal area occupied by lantana stems in 1997 and 2008 was statistically significant ($t= 5.60$, $p<0.0001$).

Table 5.1: The density (± 1 s.e.) of important NTFP species and canopy trees in 1997 and 2008.

	1997		2008	
Species	**Mean density (stems/ha)**	**Number of plots present**	**Mean density (stems/ha)**	**Number of plots present**
NTFP species				
Acacia sinuata	110.0 ± 38.9	20	57.1 ± 15.2	7
Phyllanthus emblica	162.2 ± 23.7	74	154.2 ± 46.4	42
Sapindus laurifolius	25.0 ± 0.0	2	75.0 ± 0.0	1
Terminalia bellerica	32.1 ± 7.1	7	28.9 ± 2.6	13
Terminalia chebula	83.7 ± 13.7	26	53.9 ± 10.5	13
Canopy dominants				
Anogeissus latifolia	985.3 ± 117.9	90	350.6 ± 48.6	88
Terminalia crenulata	117.1 ± 15.6	57	94.0 ± 13.7	62
Dalbergia latifolia	66.7 ± 14.9	24	70.0 ± 12.4	25
Pterocarpus marsupium	48.7 ± 7.1	37	63.7 ± 9.3	31
Kydia calycina	203.6 ± 39.4	28	72.7 ± 31.7	11

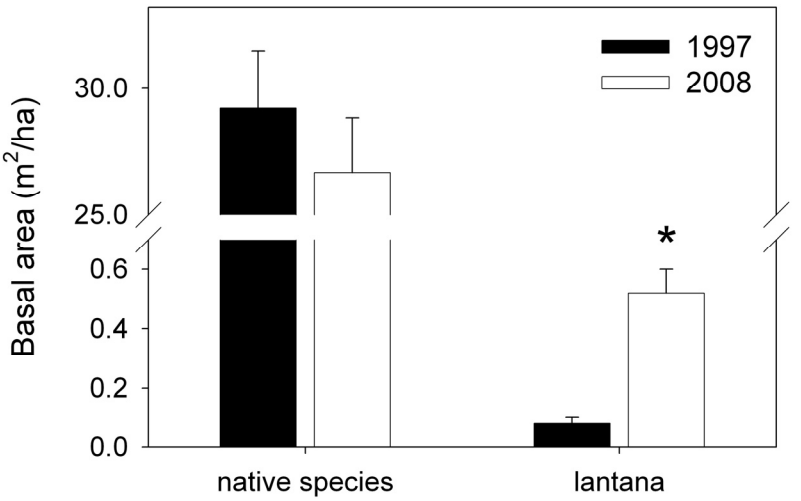

Figure 5.3: The differences between mean basal area per plot of native species and of lantana in 1997 and 2008. Significant differences in the average values as identified by a *t* test are labeled with *. Error bars signify 1 standard deviation from the average basal area.

In addition to the effects of lantana invasion on vegetation dynamics and structure, respondents also said that lantana invasion has negative effects on animal communities in BRT. A large proportion of respondents (42/47; 89 %) believed that herbivores are suffering due to lantana invasion. Lantana is largely unpalatable to wild herbivores. Since there is very little grass and bamboo left in BRT now, many animals are in an unhealthy condition and resort to crop-raiding to augment their diet.

Lantana invasion and Soliga livelihoods

All respondents believed that lantana was making their daily lives more difficult. Lantana growth over forest paths impeded the collection of fuel-wood and other NTFP. All respondents said that as a result of thick lantana growth on paths, they have either stopped or greatly minimized efforts at trying to maintain their forest paths. All respondents said that the visibility inside the forest

now is minimal due to lantana invasion. Due to reduced visibility, their encounters with dangerous animals such as elephants and bears now are much more than in the past. Additionally, all respondents said that it is now exceedingly difficult for them to search for edible tubers due to the thick growth of lantana. Lantana invasion in the forest was also leading to increased crop raiding by animals such as wild pigs, all respondents said.

In addition to physically impeding their access to the forest, all respondents also said that the density of important NTFP species such as amla, soap-nut, soap-berry, belliric and black myrobalan have reduced. Field data indicated that the total number of stems ≥ 1 cm DBH of *Acacia sinuata* and *Terminalia chebula* had indeed reduced from 1997 to 2008 (Table 5.1). Not only did these species occur in fewer plots in 2008 than in 1997, they occurred in lower densities as well. Except for *Terminalia bellerica*, the occurrence of all the other NTFP species showed a reduction over time, i.e., the number of plots in which these species were encountered in 2008 was less than the number of plots in which they were observed in 1997 (Table 5.1).

Discussion

A Soliga theory of lantana invasion

Adaptability or 'feedback learning' according to Berkes *et al*. (2000), is an intrinsic part of TEK systems. Berkes *et al*. (2000) add that the development of world views that underlie the accumulation of TEK over time shape management regimes that deal with multiple species (e.g., in fisheries; Huntington *et al*. 2000), landscape patchiness (e.g., fires; McDaniel *et al*. 2005), and ecological surprises (e.g., fluctuation in the production of NTFP; Setty *et al*. 2008). The Soliga view of their forest has no doubt helped them develop an adaptive theory of lantana invasion, a theory constituted by specific thoughts related to lantana natural history, the mechanisms of lantana success, and the ecological impacts of lantana on native plants and animal communities. For example, the Soliga believe that the large quantum of fruit that lantana produces, combined with widespread dispersal by birds and mammals contributes to lantana's success. Similarly, while Soligas differ on how long ago lantana invasions began occurring, based on whether they

live in the forest interior or closer to the periphery, most agree that the rapid spread of lantana has been a recent (< 30 years) rather than a historical phenomenon. There were some people (9/47), however, who believed that the maximum spread of lantana occurred > 30 years ago. The opinion of these respondents may be related to their being older than the other respondents. Older respondents are likely to have seen lantana in the forests of BRT in the 1970s or even in the 1960s. Younger respondents on the other hand, probably mention lantana increase as mostly occurring during the past 3 decades because they were too young to recollect lantana, or any other species for that matter, during the 1970s or 1980s, when they were children.

Studies elsewhere have shown that TEK systems evolve typically based on multiple factors, rather than singular factors. For example, McDaniel *et al*. (2005) found that Chiquitano Indians took into account multiple factors influencing their use of fire as a management tool in savannas in Bolivia. These multiple factors related to fire behavior and effects of fire included wind direction, relative humidity, soil moisture, and the trade-off between fire intensity and soil fertility (McDaniel *et al*. 2005). Similarly, whilst describing the reasons for lantana spread, the Soliga invoke multiple causation, and cite the lack of dispersal limitation for lantana, fire frequency, and historical extraction of bamboo and grasses as reasons. However, there seems to be an intimate link between the occurrence of forest fires, the change in fire regimes, and lantana invasion for the Soliga. It also appears that the Soliga view of fire is not a static one, but one that has evolved with a changing landscape and changing management practices. On the one hand, opinion is split on whether fires benefit or inhibit the spread of lantana, with older Soligas standing up for the use of fire as a management tool, a tool that was wielded on a regular basis prior to the creation of the protected area, but also a time when lantana density was lower than what is it is today. Younger Soligas, on the other hand, who hold that an increase in fire frequency benefits lantana, and is therefore bad for the forest, may be making a correlation between intense fires in lantana dominated areas with damage to native trees. Alternatively, younger Soligas would not have seen the forests of BRT with a grassy understory and bamboo because the BRT forests were extensively invaded by lantana by the time they reached adulthood. Be that as it may, the Soliga people are clear that a return to historical fire regimes is out of the question due to the present state of lantana invasion in BRT. Fires, if they occur now, would indeed be destructive, due to the accumulation of lantana biomass, resulting in more

intense fires. The Soliga perception of fire as a management tool is similar to how the Kraho, an indigenous people native to the Brazilian savanna, use and perceives fires. Mistry *et al*. (2005) found that the Kraho use of fire in a savanna landscape was dynamic and nuanced. The Kraho refer to fires as being 'good and bad at the same time' (Mistry *et al*. 2005). Depending on the purpose of the fire, the timing of the fires changed. For example, fires to protect swidden agriculture were lit during April each year, while fires to induce the fresh growth of grass for livestock were lit during May (Mistry *et al*. 2005).

Revisiting the lantana-fire-cycle hypothesis

Information on the link between forest fires and lantana invasion has been enriched by Soliga knowledge, and could potentially challenge existing views of fire prevention — views held by biologists and managers alike. The Indian Forest Act of 1927 stated that the setting of fire in any reserved forest was an offense punishable by the levying of fines, or the suspension of rights such as grazing or firewood collection (Government of India 1927). However, the no-fire rule could not be strictly enforced due to logistical difficulties. Fires, particularly in the dry forests of India, continued to occur, either to promote a new flush of grass for livestock, or sometimes as acts of retaliation or protest against restrictive state policies regarding fires (Hiremath and Sundaram 2005). Recent research indicates that the frequency of forest fires has been on the increase in the Western Ghats over the past two decades (Kodandapani *et al*. 2004). The increase in fire frequency was attributed to habitat fragmentation and intense human pressures (Kodandapani *et al*. 2004). Theoretical studies, based on existing information about increasing fire frequency and the response of lantana to fire, proposed that lantana could be benefitted by an increase in fire frequency (e.g. Sharma *et al*. 2005, Hiremath and Sundaram 2005). Adult lantana plants are not killed by fire, and resprout in response to fires (Day *et al*. 2003). Fires that may occur in lantana-invaded areas are likely to burn hotter, thereby affecting native species. Over time, the mortality of native tree species that cannot withstand the effects of fire, coupled with resprouting lantana creates a feedback loop that benefits lantana (the 'lantana-fire-cycle hypothesis'; Hiremath and Sundaram 2005).

Results from this study suggest that the lantana-fire-cycle hypothesis may indeed be valid, but its validity is specific to a certain phase of the lantana invasion trajectory. Invasive species typically go through three phases — arrival, establishment, and spread (Sakai *et al*. 2001). On the basis of this study, it is possible that frequent early-dry-season fires could have potentially kept lantana in check between the 1930s (1934 is the earliest record of lantana in BRT) and 1970s (fire prevention was strengthened in 1973, coinciding with BRT becoming a wildlife sanctuary), i.e., the period between lantana's arrival in BRT, but before it had become widespread. Therefore, the lantana-fire-cycle hypothesis probably does not apply during the arrival and establishment phases of lantana from 1934-1973. After 1973, either due to strict fire prevention, or because lantana progressed to the next phase of the invasion trajectory (i.e., the spread phase), or both, infrequent fires that occurred in densely invaded areas probably burnt hotter, to the detriment of native species, but to lantana's advantage, resulting in its rapid spread. Results from this study indicate that older respondents believed that fires could have kept lantana in check before its rapid spread. But younger Soligas, on the other hand, who had probably not seen a BRT forest devoid of dense lantana, did not know what effect fires could have had in a low lantana density situation, and believed that fires could benefit lantana. The development of the lantana-fire-cycle hypothesis by Hiremath and Sundaram (2005) is similar to the way younger Soligas viewed the relationship between forest fires and lantana, since the hypothesis was proposed based on observation of lantana and fire between 2000 and 2003, by which time lantana was already widespread.

Complementarity and variation between Traditional and scientific knowledge on lantana ecology and impact

By comparing results from this study (which examines Soliga TEK) with results from other studies on lantana in BRT (that use 'scientific' approaches), it is possible to examine the levels of concordance between them, as well as the limits of that concordance. Overall, there were very high levels of concordance between Soliga TEK and studies that used scientific approaches to study lantana invasions in BRT. Murali and Setty (1998), in their landscape-level study of lantana and native species, demonstrated that the density of lantana in BRT was quite low, with an average density of 362.5 ± 87.5 stems per hectare. Sundaram and Hiremath (unpublished

manuscript) revisited sites established by Murali and Setty (1998) in 2008, and found that there had been a tremendous increase in lantana presence and abundance over the 11 year period, with lantana density in 2008 averaging 1652.5 ± 255.0 stems per hectare — a 4-fold change. Results from Sundaram and Hiremath (unpublished manuscript) establish that the maximal spread of lantana occurred between 1997 and 2008. A large number of respondents in this study (37/47; 79 %) said that maximum lantana spread has occurred over the past 20 years. Consistent with the Soliga view, Sundaram and Hiremath (unpublished manuscript) also report that lantana is now the most dominant species in the deciduous forests of BRT, and has displaced canopy dominants such as *Anogeissus latifolia* and *Randia dumetorum* in terms of relative abundance.

The Soliga mention of propagule pressure as an important factor underlying the spread of lantana is concordant with scientific studies as well. Sundaram *et al*. (unpublished manuscript) examined the role played by disturbance in influencing the local arrival and establishment of lantana. They report that the degree to which lantana is present in surrounding areas or the 'lantana neighborhood' (which can be regarded as a measure of lantana propagule pressure) greatly influenced lantana presence over time. Furthermore, Sundaram and Hiremath (unpublished manuscript) studied the effect of lantana invasion on seed arrival and soil seed bank dynamics of both lantana and native species in BRT. Comparing seed arrival and soil storage in areas with and without lantana, they reported that soils in lantana-invaded sites were saturated with lantana seeds vis-à-vis native species.

Lastly, Soliga references to other factors that underlie lantana success are also concordant with existing studies. The Soliga perception of the present status of the forests of BRT, sans regenerating individuals of native species, is concordant with results reported by Sundaram and Hiremath (unpublished manuscript). Some factors, such as the lack of dispersal limitation for lantana, are direct. Others such as the reduced ability of seeds of native species to germinate under lantana, and the low survivorship of seedlings of native species under lantana, are indirect, and probably have a positive feedback in encouraging further lantana spread and establishment.

The conservation implications of drawing from both local knowledge sources and scientific sources are manifold. Drawing from local knowledge and scientific sources has challenged and

helped refine existing hypotheses, such as the lantana-fire-cycle hypothesis. It becomes apparent from this study that documenting the Soliga view on lantana invasions has also helped provide insights into the potential role of fire in the dynamics of these forests. Indeed Soliga's local knowledge base has been tapped by other studies, particularly those on non-timber forest products such as *Phyllanthus emblica* and *P. indofischieri* (Rist *et al*. 2010, Setty *et al*. 2008). Setty *et al*. (2008) found high levels of agreement between Soliga estimates and scientific monitoring estimates of *Phyllanthus* yield. However, Rist *et al*. (2010) found that Soliga TEK about mistletoe infections of NTFP species in BRT provided both concordant and discordant information when examined side-by-side with ecological data. For example, Soliga TEK and scientific data indicated that the forest types affected by a mistletoe hemiparasite and the seasonal fruiting patterns of mistletoe were concordant. However, Soliga TEK on how mistletoe fruits were dispersed and the degree of susceptibility of species to being infected by mistletoe differed from conclusions drawn from scientific approaches (Rist *et al*. 2001). Be that as it may, Soliga knowledge on other ecological issues, such as decline in honey bee populations and human-wildlife conflict are now being explored in detail, and appear to complement existing ecological information (Nitin Rai and R. Siddappa Setty, personal communication).

Progressive legislation in India, such as the recent Recognition of Forest Rights Act (Government of India 2006) recognizes co-management as a viable management alternative in peopled ecosystems, and may provide a legal framework for evolving adaptive management systems for lantana-invaded forests. Participatory and inter-disciplinary research involving indigenous people, scientists and park managers has been recognized as a priority for achieving biodiversity conservation and livelihood protection in human-dominated landscapes (Chazdon *et al*. 2009). This study shows that examining the Soliga perception about lantana invasion and the management of invaded areas has improved our understanding of the invasion process and its management. The potential for involving the Soliga in co-management of BRT should be therefore be explored further. The growing body of research on Soliga knowledge of several aspects of BRT as a landscape could technically lead to the formulation of adaptive management approaches that address the restoration of the lantana-invaded landscape.

References

Agrawal, A., Chhatre, A. & Hardin, R. (2008) Changing governance of the world's forests. *Science*, **320**, 1460.

Agrawal, A. (1995) Dismantling the divide between indigenous and scientific knowledge. *Development and change*, **26**, 413-439.

Anonymous (1942) Control of lantana in Madras. *Nature*, **150**, 399-400.

Bahuchet, S., McKey, D. & de Garine, I. (1991) Wild yams revisited: Is independence from agriculture possible for rain forest hunter-gatherers? *Human Ecology*, **19**, 213-243.

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

Basset, Y., Novotny, V., Miller, S.E., Weiblen, G.D., Missa, O. & Stewart, A.J.A. (2004) Conservation and biological monitoring of tropical forests: the role of parataxonomists. *Journal of Applied Ecology*, **41**, 163-174.

Berkes, F., Colding, J. & Folke, C. (2000) Rediscovery of traditional ecological knowledge as adaptive management. *Ecological applications*, **10**, 1251-1262.

Berkes, F., Folke, C. & Gadgil, M. (1995) *Traditional ecological knowledge, biodiversity, resilience and sustainability*. Beijer International Institute of Ecological Economics.

Bhargava, N. (1983) Ethnobotanical studies of the tribes of Andaman and Nicobar Islands, India. I. Onge. *Economic Botany*, **37**, 110-119.

Bird-David, N. (1992) Beyond 'The Hunting and Gathering Mode of Subsistence': Culture-Sensitive Observations on the Nayaka and Other Modern Hunter-Gatherers. *Man*, **27**, 19-44.

Blossey, B. (1999) Before, during and after: the need for long-term monitoring in invasive plant species management. *Biological Invasions*, **1**, 301-311.

Bogich, T.L., Liebhold, A.M. & Shea, K. (2008) To sample or eradicate? A cost minimization model for monitoring and managing an invasive species. *Journal of Applied Ecology*, **45**, 1134-1142.

Chapin III, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E. & Hobbie, S.E. (2000) Consequences of changing biodiversity. *Nature*, **405**, 234-242.

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

Civille, J.C., Sayce, K., Smith, S.D. & Strong, D.R. (2005) Reconstructing a century of Spartina alterniflora invasion with historical records and contemporary remote sensing. *Ecoscience*, **12**, 330-338.

Coates, P. (2006) Strangers on the land: American perceptions of immigrant and invasive species. University of California Press , Berkeley and Los Angeles.

Colautti, R.I. & MacIsaac, H.J. (2004) A neutral terminology to define'invasive'species. *Diversity and Distributions*, **10**, 135-141.

Cronk, Q.C.B. & Fuller, J.L. (1995) *Plant invaders.* Chapman and Hall, London.

Crosby, A.W. (2004) *Ecological imperialism: the biological expansion of Europe, 900-1900*. Cambridge Univ Pr.

Day, M.D., Wiley, C.J., Playford, J. & Zalucki, M.P. (2003) *Lantana: current management status and future prospects.* Australian Centre for International Agriculture Research, Canberra, Australia.

Delaney, D.G., Sperling, C.D., Adams, C.S. & Leung, B. (2008) Marine invasive species: validation of citizen science and implications for national monitoring networks. *Biological Invasions*, **10**, 117-128.

Fortier, J. (2009) The Ethnography of South Asian Foragers. *Annual Review of Anthropology*, **38**, 99.

Funk, J.L. & Vitousek, P.M. (2007) Resource-use efficiency and plant invasion in low-resource systems. *Nature*, **446**, 1079-1081.

Ganesan, R. & Setty, R.S. (2004) Regeneration of *amla*, an important non-timber forest product from southern India. *Conservation and Society*, **2**, 365-375.

Gooden, B., French, K. & Turner, P.J. (2009) Invasion and management of a woody plant, *Lantana camara* L., alters vegetation diversity within wet sclerophyll forest in southeastern Australia. *Forest Ecology and Management*, **257**, 960-967.

Government of India 1927. Indian Forest Act. Government of India Press, New Delhi. Also available from http://envfor.nic.in/legis/forest/forest4.html.

Government of India 1972. The Wildlife (Protection) Act. Government of India Press, New Delhi. Also available from http://envfor.nic.in/legis/wildlife/wildlife1c1.pdf.

Government of India 2006. Scheduled tribes and other traditional forest dwellers (recognition of forest rights) Act 2006. Ministry of Tribal Affairs, New Delhi. Also available from http://tribal.nic.in/writereaddata/mainlinkFile/File1033.pdf.

Guha, R. & Gadgil, M. (1989) State forestry and social conflict in British India. *Past & Present*, **123**, 141.

Hansen, M.J. & Clevenger, A.P. (2005) The influence of disturbance and habitat on the presence of non-native plant species along transport corridors. *Biological conservation*, **125**, 249-259.

Hart, T. & Hart, J. (1986) The ecological basis of hunter-gatherer subsistence in African Rain Forests: The Mbuti of Eastern Zaire. *Human Ecology*, **14**, 29-55.

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.

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

Huntington, H.P. (2000) Using traditional ecological knowledge in science: methods and applications. *Ecological Applications*, **10**, 1270-1274.

Iyengar, A.V.V. (1933) The problem of the lantana. *Current Science*, **1**, 266-269.

Jones, J.P.G., Rasamy, J.R., Harvey, A., Toon, A., Oidtmann, B., Randrianarison, M.H., Raminosoa, N. & Ravoahangimalala, O.R. (2009) The perfect invader: a parthenogenic crayfish poses a new threat to Madagascar's freshwater biodiversity. *Biological Invasions*, **11**, 1475-1482.

Kammathy, R.V., Rao, A.S. & Rao, R.S. (1967) A contribution towards a flora of Biligirirangan Hills. *Mysore State Bulletin: Botanical Survey of India*, **9**

Kennard, D.K., Gould, K., Putz, F.E., Fredericksen, T.S. & Morales, F. (2002) Effect of disturbance intensity on regeneration mechanisms in a tropical dry forest. *Forest Ecology and Management*, **162**, 197-208.

Kodandapani, N., Cochrane, M.A. & Sukumar, R. (2004) Conservation threat of increasing fire frequencies in the Western Ghats, India. *Conservation Biology*, **18**, 1553-1561.
Kumar, S. (2008) Genetic Profile of Jenu Kuruba, Betta Kuruba and Soliga Tribes of Southern Karnataka and Their Phylogenetic Relationships. *Anthropologist*, **10**, 11-20.
Le Maitre, D.C., Van Wilgen, B.W., Gelderblom, C.M., Bailey, C., Chapman, R.A. & Nel, J.A. (2002) Invasive alien trees and water resources in South Africa: case studies of the costs and benefits of management. *Forest Ecology and Management*, **160**, 143-159.
Lovell, S.J., Stone, S.F. & Fernandez, L. (2006) The economic impacts of aquatic invasive species: a review of the literature. *Agricultural and Resource Economics Review*, **35**, 195-208.
Madegowda, C. (2009) Traditional Knowledge and Conservation. *Economic & Political Weekly*, **44**, 21-65.
McDaniel, J., Kennard, D. & Fuentes, A. (2005) Smokey the Tapir: traditional fire knowledge and fire prevention campaigns in lowland Bolivia. *Society & Natural Resources*, **18**, 921-931.
McNeely, J.A. (2004) Nature vs. nurture: managing relationships between forests, agroforestry and wild biodiversity. *Agroforestry systems*, **61**, 155-165.
Mistry, J., A. Berardi, V. Andrade, T. Kraho, P. Kraho, and O. Leonardos. 2005. Indigenous Fire Management in the cerrado of Brazil: The Case of the Kraho of Tocantıns. Human Ecology **33**:365-386.
Mittermeier, R.A., Robles-Gil, P., Hoffman, M., Pilgrim, J.D., Brooks, T.M., Mittermeier, C.G., Lamoreux, J.L. & Fonseca, G. (2004) *Hotspots revisited: Earth's biologically richest and most endangered terrestrial ecoregions.* . CEMEX, Mexico City.
Murali, K.S. & Setty, R.S. (2001) Effect of weeds Lantana camara and Chromelina odorata growth on the species diversity, regeneration and stem density of tree and shrub layer in BRT sanctuary. *Current Science*, **80**, 675-678.
Myers, N. (2003) Biodiversity hotspots revisited. *Bioscience*, **53**, 916-917.
Neogi, B., Prasad, M.N.V. & Rao, R.R. (1989) Ethnobotany of some weeds of Khasi and Garo hills, Meghalaya, Northeastern India. *Economic Botany*, **43**, 471-479.
Nuñez, M.A. & Simberloff, D. (2005) Invasive species and the cultural keystone species concept. *Ecology and Society*, **10**, r4.
Patin, E., Laval, G., Barreiro, L.B., Salas, A., Semino, O., Santachiara-Benerecetti, S., Kidd, K.K., Kidd, J.R., Van Der Veen, L. & Hombert, J.M. (2009) Inferring the demographic history of African farmers and pygmy hunter-gatherers using a multilocus resequencing data set. *PLoS Genet*, **5**, e1000448.
Pejchar, L. & Mooney, H.A. (2009) Invasive species, ecosystem services and human well-being. *Trends in Ecology & Evolution*, **24**, 497-504.
Peluso, N.L., Vandergeest, P. & Potter, L. (1995) Social Aspects of Forestry in Southeast Asia: A Review of Postwar Trends in the Scholarly Literature. *Journal of Southeast Asian Studies*, **26**
Perrings, C., Williamson, M., Barbier, E.B., Delfino, D., Dalmazzone, S., Shogren, J., Simmons, P. & Watkinson, A. (2002) Biological invasion risks and the public good: an economic perspective. *Conservation Ecology*, **6**, 1.
Pimentel, D., Zuniga, R. & Morrison, D. (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, **52**, 273-288.

R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Ramesh, B.R. (1989) *Flora of Biligirirangan Hills.* Madras University, Chennai.
Ranganathan, C.R. (1934) *Working plan, Kollegal Forest Division.* Government of India, Madras.
Ricciardi, A., Steiner, W.W.M., Mack, R.N. & Simberloff, D. (2000) Toward a global information system for invasive species. *BioScience*, **50**, 239-244.
Rist, L., Shaanker, R.U., Milner-Gulland, E.J. & Ghazoul, J. The Use of Traditional Ecological Knowledge in Forest Management: an Example from India. *Ecology and Society*, **15**, 3.
Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N. & Weller, S.G. (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics*, **32**, 305-332.
Sears, R., Padoch, C. & Pinedo-Vasquez, M. (2007) Amazon Forestry Tranformed: Integrating Knowledge for Smallholder Timber Managemet in Eastern Brazil. *Human Ecology*, **35**, 697-707.
Setty, R.S., Bawa, K., Ticktin, T. & Gowda, C.M. (1996) Evaluation of a Participatory Resource Monitoring System for Nontimber Forest Products: the Case of Amla (Phyllanthus spp.) Fruit Harvest by Soligas in South India. *Ecology and Society*, **13**, 19.
Shaanker, R. U., K. N. Ganeshaiah, S. Krishnan, R. Ramya, C. Meera, N. A. Aravind, A. Kumar, D. Rao, G. Vanaraj, and J. Ramachandra. 2004. 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.
Shackleton, C.M., McGarry, D., Fourie, S., Gambiza, J., Shackleton, S.E. & Fabricius, C. (2007) Assessing the effects of invasive alien species on rural livelihoods: case examples and a framework from South Africa. *Human Ecology*, **35**, 113-127.
Sharma, G.P., Raghubanshi, A.S. & Singh, J.S. (2005) *Lantana* invasion: an overview. *Weed Biology and Management*, **5**, 157-165.
Shrivastava, R.J. & Heinen, J.T. (2005) Migration and home gardens in the Brahmaputra Valley, Assam, India. *Journal of Ecological Anthropology*, **9**, 20-34.
Silvertown, J. (2009) A new dawn for citizen science. *Trends in Ecology & Evolution*, **24**, 467-471.
Strayer, D.L., Eviner, V.T., Jeschke, J.M. & Pace, M.L. (2006) Understanding the long-term effects of species invasions. *Trends in Ecology and Evolution*, **21**, 645-651.
Sutton, J.R., Stohlgren, T.J. & Beck, K.G. (2007) Predicting yellow toadflax infestations in the Flat Tops Wilderness of Colorado. *Biological Invasions*, **9**, 783-793.
Tireman, H. (1916) Lantana in the forests of Coorg. *Indian Forester*, **42**, 384-392.
Von Holle, B. & Motzkin, G. (2007) Historical land use and environmental determinants of nonnative plant distribution in coastal southern New England. *Biological Conservation*, **136**, 33-43.
Zavaleta, E. (2000) The economic value of controlling an invasive shrub. *Ambio*, **29**, 462-467.

Chapter 6: Synthesis

According to Baker (1965), and 'ideal' invader is typified by fast growing species that flower early, produce large quantities of fruit that are dispersed widely, and are efficient competitors. Lantana appears to be an 'ideal' invader (sensu Baker 1965) of tropical dry forests. Lantana's pathway to success probably begins with high seed output and the widespread dispersal of lantana propagules, thus leading to propagule pressure (sensu Colautti et al. 2006). Propagule pressure has been recognized as one of the major factors influencing invasive species success. Lantana propagule pressure seems to operate in two stages — first as seed arrival in uninvaded sites, and second as high seed input in sites already invaded. Propagule pressure originating from sites already invaded by lantana substantially explained lantana arrival in uninvaded sites (Chapter 3). Lantana seed arrival into previously uninvaded sites occurs due to transport of seeds by bird or mammalian dispersers. On the other hand, young age to reproduction and prolific seed output by lantana contributes to autochthonous input (Chapter 4).

The prolific fruiting of lantana has implications for native plant-animal interactions. Invasive species have been reported to alter or disrupt seed dispersal mutualisms between native dispersers of plants elsewhere (Traveset and Richardson 2006). Preliminary information from BRT suggests that seed dispersers are disproportionately consuming lantana fruit, which may be interfering with dispersal of fruits of native species (Monika Kaushik, unpublished manuscript). Thus, over the long-term, lantana invasions could lead to native species becoming dispersal limited. On the other hand, the high input and soil storage of lantana seeds in areas already invaded implies that seeds of lantana are always available to make use of favorable regeneration opportunities.

In addition to propagule pressure, the next milestone on lantana's pathway to success is related to how native tree communities seem to be responding to lantana invasion. Seedlings and saplings of native species are shaded out by the thick growth of lantana (Chapter 5). For native trees, the loss of a large proportion of the regenerating size classes is likely to manifest over time into serious population bottlenecks. There is evidence that the density of recruiting stems has already been impacted due to lantana invasion (Chapter 2). The thick growth of lantana is likely to affect

adult tree populations as well. Adult trees are known to be affected negatively by forest fires that occur in lantana-invaded areas, due to the formation of ladder fuels, and because fires in dense lantana burn hotter (Tireman 1916). Adult tree mortality, combined with a paucity of recruiting stems, is likely to negatively affect future forest structure and dynamics. Meanwhile, lantana density is likely to increase further, due to the reduction of overstory canopies that would follow adult tree mortality, as reported elsewhere, e.g., in Australia (Duggin and Gentle 1998).

Studies on lantana invasions in Australia show that ecosystem invasibility increases with an increase in disturbances such as fire, understory clearing, or canopy removal (Duggin and Gentle 1998). Factors that influence lantana success (e.g., propagule pressure) acting alongside legacy effects of historical habitat modification (e.g., plantations, slash-and-burn agriculture) lead to an increase in ecosystem invasibility (Chapter 3). Thus characteristics of the disturbance regime, such as historical habitat modification, combined with factors that enhance lantana invasibility, such as propagule pressure, combine to increase ecosystem invasibility.

However, examining information about the role played by other disturbance, such as fire, indicates that fire's role is more nuanced than considered earlier. Information on the link between forest fires and lantana invasion has been enriched by both traditional ecological knowledge and scientific knowledge, and could potentially challenge existing views of fire prevention — views held by biologists and managers alike. Fires, particularly in the dry forests of India, are set for a variety of reasons (promoting grass growth, collecting NTFP), and are sometimes difficult to prevent or control. The frequency of forest fires in Western Ghats is also on the increase (Kodandapani et al. 2004). Theoretical studies have proposed that lantana could be benefitted by an increase in fire frequency since adult lantana plants resprout in response to fires. Fires that may occur in lantana-invaded areas are likely to burn hotter, thereby affecting native species. Over time, the mortality of native tree species that are not adapted to fire, coupled with resprouting lantana, creates a feedback loop that benefits lantana (the 'lantana-fire-cycle hypothesis'; Hiremath and Sundaram 2005). Collating information about lantana invasions from traditional and scientific studies suggests that the validity of the lantana-fire-cycle hypothesis may be specific to a certain phase of the lantana invasion trajectory (Chapter 5). After the arrival of lantana, but prior to it attaining the density at which it is present today, fires could have kept

lantana in check. However, a combination of fire prevention in conjunction with increasing lantana density, have led to a situation where fires could negatively affect native species, if allowed to occur in areas densely invaded by lantana. This creates a contradictory situation where the use of fire could potentially be used to control lantana, but using fire would be detrimental to native species. As a way out, reducing lantana density, followed by experimental studies on the effects of fire on native communities could provide additional information if fires are to be used to control lantana.

Thus, tabling traditional ecological knowledge with scientific knowledge from multiple aspects of lantana invasions has helped refine our views on the role of fire as an influence on lantana invasions. The stage is set for future research that involves indigenous communities, researchers, and forest managers. Collaborative and adaptive research could help in the formulation of projects to first prioritize reducing lantana density, and then returning to historical fire regimes on an experimental scale.

Lantana invasion has implications for the conservation of the Western Ghats biodiversity hotspot. A large part of the Western Ghats comprises seasonally dry tropical forests (~ 40 %; Wikramanayake et al. 1999). A large part of this 40 % is probably already invaded by lantana, and areas presently uninvaded could be considered vulnerable to lantana invasion in the near future. Several protected areas within the Western Ghats are important for the conservation of large mammal assemblages (Walston et al. 2010). Lantana could have a negative impact on large mammal populations in the Western Ghats due to habitat loss created due to both the rapid spread of lantana, and due to the negative effects of lantana on native flora and habitat structure. Additionally, lantana invasions could also disrupt trophic interactions. Prasad (2010) demonstrated that the reduced access to forage in lantana could negatively affect ungulate populations. Tropical dry forests of the Western Ghats additionally provide essential ecosystem services (e.g., NTFP and hydrological cycling). It is therefore imperative to prioritize the management of lantana in the Western Ghats.

References

Baker, H. G. 1965. Characteristics and modes of origin of weeds. Pages 147-169 *in* H. G. Baker and C. L. Stebbins, editors. The genetics of colonizing species. Academic Press, New York.

Colautti, R. I., I. A. Grigorovich, and H. J. MacIsaac. 2006. Propagule pressure: a null model for biological invasions. Biological Invasions **8**:1023-1037.

Duggin, J. A., and C. B. Gentle. 1998. Experimental evidence on the importance of disturbance intensity for invasion of *Lantana camara* L. in dry rainforest-open forest ecotones in north-eastern NSW, Australia. Forest Ecology and Management **109**:279-292.

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

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

Prasad, A. E. Effects of an Exotic Plant Invasion on Native Understory Plants in a Tropical Dry Forest. Conservation Biology **24**:747-757.

Tireman, H. 1916. Lantana in the forests of Coorg. Indian Forester **42**:384-392.

Traveset, A., and D. M. Richardson. 2006. Biological invasions as disruptors of plant reproductive mutualisms. Trends in Ecology & Evolution **21**:208-216.

Walston, J., J. G. Robinson, E. L. Bennett, U. Breitenmoser, G. A. B. da Fonseca, J. Goodrich, M. Gumal, L. Hunter, A. Johnson, and K. U. Karanth. 2010. Bringing the Tiger Back from the Brink—The Six Percent Solution. PLoS Biology **8**:493-506.

Wikramanayake, E. D., E. Dinerstein, J. G. Robinson, K. U. Karanth, A. Rabinowitz, D. Olson, T. Matthew, P. Hedao, M. Conner, and G. Hemley. 1999. Where can tigers live in the future? A framework for identifying high-priority areas for the conservation of tigers in the wild. Pages 255–272 *in* J. Seidensticker, S. Christie, and P. Jackson, editors. Riding the tiger: tiger conservation in human dominated landscapes. Cambridge University Press, Cambridge.