

博士論文

ミャンマーにおける外来植物のリスク評価

Ecological risk assessment of alien plant invasion in Myanmar

国立大学法人横浜国立大学大学院

環境情報学府

ティリアウン

THIRI AUNG

2015年9月

Doctoral Thesis

Ecological risk assessment of alien plant invasion in Myanmar

ミャンマーにおける外来植物のリスク評価

THIRI AUNG

ティリアウン

Supervisor: Professor Fumito Koike

Graduate School of Environment and Information Sciences
Yokohama National University

A thesis submitted in fulfillment of the requirements for the
Degree of Doctor of Environmental Sciences

September 2015

Acknowledgements

First of all, I would like to thank my supervisor Professor Fumito Koike for his excellent guidance and support throughout this research work. I acknowledge the Global COE (Centers of Excellence) program and Leadership Program in Sustainable Living with Environmental Risk (SLER), Yokohama National University, for funding the intensive vegetation surveys in Myanmar. I sincerely thank the local staff of the Forest Department and the Dry Zone Greening Department within the Ministry of Environmental Conservation and Forestry, Myanmar for their supports during the vegetation surveys and for providing the departmental plantation records.

I am also grateful to all my fellow colleagues from Koike Laboratory, Yokohama National University, for their companionship, advice and assistance that made this dissertation realistic. I would like to show my gratitude to my family for giving me love and courage to accomplish this task.

Last but not the least, I would like to express thanks to my husband, Wei Phyo Oo (Graduate School of Environment and Information Sciences, Yokohama National University) for his permission to use his vegetation data and always gives me strength and encouragement throughout this challenging period.

Table of Contents

ABSTRACT	2
CHAPTER 1: INTRODUCTION	3
CHAPTER 2: IDENTIFICATION OF INVASION STATUS USING A HABITAT INVASIBILITY ASSESSMENT MODEL: THE CASE OF <i>PROSOPIS</i> SPECIES IN THE CENTRAL DRY ZONE OF MYANMAR.....	10
CHAPTER 3 PREDICTING POTENTIAL INVASION RISK OF NEWLY INTRODUCED ALIEN WOODY PLANTS IN CENTRAL DRY ZONE, MYANMAR	35
CHAPTER 4: GENERAL DISCUSSION	52

Abstract

Biological invasion of alien species will likely be an increasingly important driver of future ecosystem disturbance and degradation, loss of biodiversity, and even global climate change. To deal with the problem of biological invasion by alien species, we need to understand which species invade, which habitats are invaded and based on this knowledge; we need to consider how we can manage their invasions.

In this study, there are two major parts which are discussed in chapter 2 and 3. In the first part (Chapter 2), we explained the habitat invasibility to *Prosopis* species introduced for land rehabilitation of the central dry zone of Myanmar by the invasibility assessment model which integrates both mesoscale environmental variables and native plant communities. We assessed current invasion status by vegetation survey and invasibility assessment model. The areas free from *Prosopis* expansion and the areas where many invulnerable habitats had not yet been invaded were identified. Quarantine between infested and uninfested areas; and conservation and appropriate management of less-invasive forest communities were recommended.

In the second part (Chapter 3), we attempted to evaluate potential invasion risk of newly added alien plant species in the dry zone of central Myanmar by plant trait analysis. We used logistic regression to predict the species occurrence for each community based on plant traits. We proposed that the probability that a locally new alien plant will invade into each type of community can be predicted by the plant trait analysis. Prediction models based on plant traits were significant for all community types. Prediction of potential invasion risks of alien species was possible; however, predictability was quite low. Key traits in the tropical dry zone of Myanmar were quite different from those of climax forests in other part of the world; we need to consider such difference to formulate a risk assessment system for the tropical dry zone of Myanmar.

Chapter 1: Introduction

Review on invasive alien species research in tropical dry forest region

Alien species have been one of the main factors threatening global biodiversity (Keane, Crawley 2002; Vitousek et al. 1996) and will likely be an increasingly important driver of future ecosystem disturbance and degradation, loss of biodiversity, and even global climate change (Mack et al. 2000; Vitousek et al. 1997).

Biological invasion of alien animals and plants has been gaining scientific attention since 1958 with the publication of “The ecology of invasions by animals and plants” by Charles Elton. Many concepts and theories of biological invasion have been developed. Some are organism-focused and relate to species invasiveness, others are ecosystem-centered and deal with determinants of the invasibility of communities, habitats and regions; and some theories have taken an overarching approach to plant invasions by integrating the concepts of species invasiveness and community invasibility (Richardson, Pyšek 2006).

Three major questions addressed by the SCOPE program in the 1980s (Which species invade, which habitats are invaded and how we can manage invasions) (Drake 1989) pointed out the importance of species invasiveness and the invasibility of recipient communities to be considered for the research application solving the problem of biological invasion.

Risk assessment system such as weed risk assessment (WRA) considered both species invasiveness (e.g. biological traits) and habitat invasibility (e.g. environmental suitability between native and introduced habitats) (Pheloung et al. 1999, Daehler et al. 2004). We need to understand the biological traits of introduced species that can cause species invasive in a particular region and the ecosystem susceptibility of introduced region. Understanding biological traits of native species are also important as they could, in some ways, represent the habitat susceptibility of a region (e.g. biotic resistance).

Tropical dry forests (TDF) are defined as forests having a distinct dry season lasting several months with little or no precipitation and represent one of the most desired habitats in the tropics for human settlements and exploitation (Murphy and Lugo 1986). Much of the dry tropical forest ecosystem has been converted to agricultural land uses over the past several centuries (Powers et al. 2009). Less than 0.1% of the dry forests (Pacific Mesoamerican, Australia, Southeast Asia, Africa, and South America) are protected, and TDF are among the most endangered and degraded of all ecosystems in the world (Murphy and Lugo 1986, Bullock et al. 1995). These ecosystems contain highly diverse and unique species assemblages, failure to preserve and restore dry forests will clearly result in significant biodiversity losses. Comparing

with other ecosystems, TDF also has little attention from research and conservation society (Sánchez-Azofeifa et al. 2005). Little is known about this tropical forest type including its vegetation regeneration (Khurana, Singh 2001) and the impact of invasive species on its ecosystem dynamic (Litton et al. 2006).

There have been few studies on the impact of invasive species on the tropical dry forest ecosystem. Invasion of alien fire-promoting grasses (*Pennisetum setaceum*) was a hazard to seedling germination, establishment and growth of forest species (Cabin et al. 2002) and to the carbon pools and tree population structure (Litton et al. 2006) in dry forest ecosystem of Hawaii. Invasive species (including *Prosopis* species) have caused disasters that affected the environment (biodiversity loss, water shortage, reduced income and reduced food security etc.) and socio-economic wellbeing of local communities (including death of livestock, disease) inhabiting in dry forests and rangelands of East Africa (Obiri, F. 2011). The problem of biological invasions may have been accelerating in the dry forest ecosystems but few have been scientifically acknowledged compared to other ecosystems of the world.

Invasive alien species (IAS) research for the tropical dry forest ecosystem were mainly observed for America, Australia and Hawaii. Some research have been done in dry forests of India but mainly on few species such as the invasion and impact of *Lantana camara* on species richness, diversity and population structure of native community (Sundaram, Hiremath 2012), impact of *Lantana camara* on soil nitrogen pools and processes (Sharma, Raghubanshi 2009), environmental correlates of *Lantana* invasion (Ramaswami and Sukumar 2013), and the impact of *Prosopis juliflora* in dry lands of India devaluing grasslands and threatening birds and fodder production (<http://www.fao.org/docrep/006/ad321e/ad321e04.html>).

Only few documents reported about alien species in tropical dry ecosystem of Southeast Asia region. A regional report on IAS in South-Southeast Asia was developed as a workshop proceeding initiated by Global Invasive Species Programme (GISP 2003) although Myanmar was not listed in the report. The report mainly provided the information of IAS in the region; lists of IAS, their source regions and naturalized habitats in introduced countries, their invasion status and general impacts; and the departmental policies and legal instruments for the management of IAS. FAO (2013) also compiled the list of invasive alien plants in Asia-Pacific region from the Global Invasive Species Database and the information on habitat, threat and damage caused, and the management measures collected from authentic websites, research papers, books and workshop proceedings. Literatures relating to IAS are generally in the format of departmental reports and workshop proceedings. More scientific research on IAS impacts, invasion status and underlying causes of the invasion problems (invasive traits and susceptibility of introduced

region) should be conducted to understand the extent and risk of biological invasion in the region. Although the region contains a large area of dry forest ecosystem with rich biodiversity such as lower Mekong dry forest eco-region, lack of literatures acknowledged the biological invasion in the region does not necessarily imply that the region has no biological invasion.

Myanmar National Biodiversity Strategy and Action Plan as a follow up to Convention on Biological Diversity (CBD) recognized the threat of IAS on Myanmar's biodiversity and stated the limited research and database of IAS in Myanmar (Ministry of Environmental Conservation and Forestry, Myanmar 2011). As biological invasion is one of the main drivers of biodiversity losses, we need to improve our basic ecological understanding of biological invasions in tropical dry forest ecosystem and enhance our ability to reverse or mitigate their often devastating effects.

As a significant step forward to protect vulnerable dry forest ecosystem in Myanmar from the invasion risk of IAS, in my doctoral study, I attempted to assess the ecological risk of alien plant invasion in the dry zone of central Myanmar. The first part of the study (Chapter 2) discussed the approach to assess the invasion risk of notorious *Prosopis* species based on the concept of habitat invasibility considering both environmental factors and the presence of native plant communities. The second part of the study (Chapter 3) discussed the prediction models to evaluate the potential invasion risk of newly introduced alien plant species based on plant biological traits.

Terminology

Alien plants

Plant taxa in a given area whose presence there is due to intentional or accidental introduction as a result of human activity (synonyms: exotic plants, non-native plants; non-indigenous plants).

Naturalized plants

Alien plants that reproduce consistently (cf. *casual alien plants*) and sustain populations over many life cycles without direct intervention by humans (or in spite of human intervention); they often recruit offspring freely, usually close to adult plants, and do not necessarily invade natural, semi-natural or human-made ecosystems.

Invasive plants

Naturalized plants that produce reproductive offspring, often in very large numbers, at considerable distances from parent plants (approximate scales: > 100 m; < 50 years for taxa

spreading by seeds and other propagules; $> 6 \text{ m}^3$ years for taxa spreading by roots, rhizomes, stolons, or creeping stems), and thus have the potential to spread over a considerable area.

Weeds

Plants (not necessarily alien) that grow in sites where they are not wanted and which usually have detectable economic or environmental effects (synonyms: plant pests, harmful species; problem plants).

Terminologies relating to invasion ecology applied in the manuscript are according to Richardson et al. (2000).

References

- Bullock SH, Mooney HA, Medina E (1995) *Seasonally Dry Tropical Forests*. Cambridge University Press
- Cabin RJ, Weller SG, Lorence DH, et al. (2002) Effects of Light, Alien Grass, and Native Species Additions on Hawaiian Dry Forest Restoration. *Ecological Applications* 12:1595-1610
- Daehler CC, Denslow JS, Ansari S, et al. (2004) A Risk-Assessment System for Screening Out Invasive Pest Plants from Hawaii and Other Pacific Islands Un Sistema de Evaluación de Riesgo para Seleccionar Plantas Invasoras Nocivas de Hawai'i y Otras Islas del Pacífico. *Conservation Biology* 18:360-368
- Drake JA, International Council of Scientific Unions. Scientific Committee on Problems of the Biological invasions: a global perspective (1989) Published on behalf of the Scientific Committee on Problems of the Environment of the International Council of Scientific Unions by Wiley
- Global Invasive Species Programme (2004) *Tropical Asia invaded: The growing danger of invasive alien species*
- Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution* 17:164-170
- Khurana E, Singh JS (2001) Ecology of seed and seedling growth for conservation and restoration of tropical dry forest : a review. *Environmental Conservation* 28:39-52
- Litton CM, Sandquist DR, 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
- Mack RN, Simberloff D, Lonsdale WM, et al. (2000) Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* 10:689-710

Murphy PG, Lugo AE (1986) Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* 17: 67-88

Ministry of Environmental Conservation and Forestry (2011) National Biodiversity Strategy and Action Plan Myanmar. Nay Pyi Taw, Myanmar. Retrieved May 25, 2014, from <https://www.cbd.int/doc/world/mm/mm-nbsap-01-en.pdf>

Obiri FJ (2011) Invasive plant species and their disaster-effects in dry tropical forests and rangelands of Kenya and Tanzania. *Journal of disaster risk studies* 3 (2):417-428

Pallewatta, N, Reaser J.K and Gutierrez AT (eds.) (2003) Invasive Alien Species in South-Southeast Asia: National Reports & Directory of Resources. Global Invasive Species Programme, Cape Town, South Africa

Pheloung PC, Williams PA, Halloy SR (1999) A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. *Journal of Environmental Management* 57:239-251

Powers JS, Becknell JM, Irving J, et al. (2009) Diversity and structure of regenerating tropical dry forests in Costa Rica: Geographic patterns and environmental drivers. *Forest Ecology and Management* 258:959-970

Ramaswami G, Sukumar R (2013) Long-Term Environmental Correlates of Invasion by *Lantana camara* (Verbenaceae) in a Seasonally Dry Tropical Forest. *PLoS ONE* 8(10): e76995. doi:10.1371/journal.pone.0076995

Richardson DM, Pyšek P (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography* 30:409-431

Richardson DM, Pyšek P, Rejmánek M, et al. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6:93-107

Sankaran KV, Suresh TA (2013) Invasive alien plants in the forests of Asia and the Pacific. Food and Agricultural Organization of the United Nations, Regional office for Asia and the Pacific,

Bangkok, Thailand

Sharma GP, Raghubanshi AS (2009) Lantana invasion alters soil nitrogen pools and processes in the tropical dry deciduous forest of India. *Applied Soil Ecology* 42:134-140

Sundaram B, Hiremath A (2012) Lantana camara invasion in a heterogeneous landscape: patterns of spread and correlation with changes in native vegetation. *Biological Invasions* 14:1127-1141

Sánchez-Azofeifa GA, Quesada M, Rodríguez JP, et al. (2005) Research Priorities for Neotropical Dry Forests1. *Biotropica* 37:477-485

Tewari JC, Pasiecznik NM, Harsh LN, Harris PJC (1993) Prosopis speices in the arid and semi-arid zones of India. Proceedings of a conference held at the Central Arid Zone Research Institute, Jodhpur, Pajasthan, India. Nov 21-23. Last accessed : <http://www.fao.org/docrep/006/ad321e/ad321e00.htm>

Vitousek PM, D'Antonio C, Loope LL, et al. (1997) Introduced species: a significant component of human-caused global change. 21:16-Jan

Vitousek PM, Dantonio CM, Loope LL, et al. (1996) Biological invasions as global environmental change. *American Scientist* 84:468-478

Chapter 2: Identification of invasion status using a habitat invasibility assessment model: the case of *Prosopis* species in the central dry zone of Myanmar

(This chapter was published in the Journal of Arid Environments, Volume 120, Page 87-94)

Abstract

In arid regions, land restoration projects that use alien plants often cause damage to ecosystems and the livelihoods of local people. Management of these invasive alien species is difficult without knowledge of the habitat invasibility of the regions where it has been introduced and the species' invasion status (absent, invading, or saturated). We developed a habitat invasibility assessment model that integrates the local plant community and mesoscale environments by controlling the effect of propagule pressure, to determine the habitat risk posed by *Prosopis* (mesquite) species introduced for land rehabilitation in the central dry zone of Myanmar (Burma). Current invasion status was assessed based on a vegetation survey and the invasibility assessment model. Habitats with dry and hot climatic conditions were suitable for *Prosopis* invasion. Tree patches in human-dominated landscapes showed higher invasibility to *Prosopis* than remnant forests. Large-scale geographic range expansion (≥ 10 -km radii) had already been completed. However, at a smaller scale there were some sites lacking *Prosopis* and sites with a propagule deficit close to heavily invaded areas in suitable habitats, indicating that local invasion was in progress. These results suggest that ecological and economic damage caused by *Prosopis* will continue to increase unless propagule control measures are initiated.

Keywords *Prosopis*, habitat invasibility, invasion status, local plant community, mesoscale environment, dry zone, Myanmar

Introduction

Invasion by alien species causes damage to biodiversity, ecosystem processes (Vitousek 1990; Vitousek et al. 1997), local economies, and peoples' livelihoods worldwide (Pimentel et al. 2001; Milton and Dean 2010). The intentional introduction of alien woody species for restoration projects in arid ecosystems has led to widespread biological invasions (D'Antonio and Meyerson 2002; Low 2012). These invasions are often detected too late, making eradication unfeasible (Milton and Dean 2010).

Habitat risk (invasibility) is the susceptibility of a region to the establishment of invasive alien species (Burke and Grime 1996). Assessments of habitat invasibility and current geographic distribution of invasive species are important for developing management plans. Large-scale climatic patterns determine the potential distribution range of an invasive species (Guisan and Thuiller 2005; Wilson et al. 2007), whereas biotic interactions and local disturbance represented by local vegetation are key factors for the susceptibility of a site to invasion (Lonsdale 1999; Rejmánek et al. 2012). Such potentially suitable sites are usually distributed as patches in regional landscapes (Hanski 1998; Komuro and Koike 2005; Koike 2006). After its arrival in the first habitat patch, an invasive species will gradually occupy all the suitable habitat patches in a region through the metapopulation process (Komuro and Koike 2005; Koike 2006). Three stages are recognized in the invasion process: (1) the prior-to-establishment stage, in which no population occurs regionally; (2) the invading stage, in which the number of occupied patches is increasing; and (3) the steady or saturated stage, in which all suitable patches in the region have been occupied.

Taxa of the genus *Prosopis* (mesquites; Fabaceae) are native to Africa, Asia, and North and South America (Gallaher and Merlin 2010), and they have been widely introduced and become invasive, particularly in subtropical areas and the semi-arid tropics (Landeras et al. 2006). *Prosopis* species were introduced into the semi-arid and arid central dry zone of Myanmar in the 1950s by the Agriculture and Rural Development Corporation for the purpose of land restoration (Ministry of Environmental Conservation and Forestry 2011). Of the 44 species within the genus (Burkhart 1976), two species and one variety have been recorded in Myanmar: *Prosopis juliflora* (Sw.) DC., native to Central and South America; its variety *Prosopis juliflora* var. *glandulosa* (Torrey) Cockerell; and *Prosopis spicigera* L. (syn. *P. cineraria*), native to the Indian subcontinent and western Asia (Lace and Hundley 1987). Among these taxa, the *P. juliflora* complex from the Americas (section *Algarobia*) has become widely naturalized in Myanmar. Species of this complex can interbreed and produce hybrid populations, which makes it difficult to identify species (Pasicznik et al. 2001; Landeras et al. 2006). Thus, to avoid confusion among

species, we simply identified plants to the genus level in our study.

Previous studies on *Prosopis* suggested that they possess many biological traits that can facilitate rapid invasion in dry regions, including high seed production, long seed viability in the dung of livestock, good resprouting ability, fast coppice growth (Shiferaw et al. 2004), resistance to browsing and drought (Troup 1921), and high water-use efficiency (Felker et al. 1983). *Prosopis* spreads naturally from land-rehabilitation sites through seed dispersal by stream flow and in the dung of livestock feeding on *Prosopis* pods (Sawal et al. 2004; Jadeja et al. 2013). *Prosopis* is still being planted for restoration of much degraded lands and degraded mountain ranges in the central dry zone of Myanmar (2013 plantation records of the Forest Department and the Dry Zone Greening Department). However, *Prosopis* invasions are known to induce many negative social, economic, and environmental impacts globally (Pasiiecznik et al. 2001; Shackleton et al. 2014), including impacts on hydrological, energy, and nutrient cycling (Goslee et al. 2003); native biodiversity and soil properties (El-Keblawy and Abdelfatah 2014); and farm lands and grazing lands (Haregeweyn et al. 2013). *Prosopis* thorns impose health risks, as local people and domestic livestock are often cut or stabbed by large *Prosopis* thorns (Haregeweyn et al. 2013), although these plants are used for fodder, firewood, and wood products in arid environments when other resources are not available (Pasiiecznik et al. 2001; Wise et al. 2012). Local people and foresters in the central dry zone of Myanmar have recognized the invasive potential of *Prosopis*, but the spatial processes underlying these invasions remain unclear. This lack of information makes it difficult to plan management activities.

In this study, we developed a habitat invasibility assessment model that integrates the local plant community types and mesoscale environmental variables assuming the sufficiently high propagule pressure, to determine areas in the central dry zone of Myanmar that are potentially invasible by *Prosopis*. Based on the habitat invasibility assessment model and a vegetation survey, we mapped the spatial zones of invasion status, which will help to guide the management of *Prosopis* within the region.

Materials and Methods

Study area

The central dry zone of Myanmar is a rain-shadow lowland around the Irrawaddy River and accounts for approximately 12% of the country's land area. It is situated between two higher regions, the Shan Plateau to the east and the Rakhine Yoma mountain range and Chin Hills to the west (latitudes 18°49' to 23°43'N, longitudes 94°19' to 96°32'E). The annual rainfall in the dry zone ranges from 500 to 1000 mm across the area. The mean daily temperature ranges from 9°C

(January) to 44°C (April and May). The area is characterized by many endemic species (National Commission for Environmental Affairs 2009), such as *Tectona hamiltoniana* Wall., one of the dominant tree species in the central dry zone of Myanmar (Stamp 1925).

Vegetation survey and plant community types

Unpublished raw data from an intensive vegetation survey (Wei Phyo Oo and Koike, unpublished) conducted during February and March 2011 in the lower Sagaing, Mandalay, and Magway Divisions were used to identify *Prosopis* invasion status in a 100 km × 100 km area (square in Fig. 1). We used Google Earth 2011 and Forest Department 1:50000 maps produced in 2003 (Survey Department, Ministry of Environmental Conservation and Forestry) to look for woody vegetation to be surveyed. To capture all possible woody plant communities in all accessible areas, we divided the area into 5-km grids and allocated at least one sample plot in different vegetation types occurring in each grid. Additional vegetation surveys were done during September and October 2011 in order to include various mesoscale environments, including higher elevation hills within the dry zone (Fig. 1). We recorded the presence or absence of all plant species in sample plots of 15 m × 15 m (1399 plots in total).

Wei and Koike (unpublished) produced a detailed classification and described the woody vegetation in a similar area, but we focused on invasion by *Prosopis*. We removed *Prosopis* from the vegetation dataset to obtain species composition before *Prosopis* invasion (Fig. 2). We then used the vegetation classification before *Prosopis* invasion (the dataset without *Prosopis*) to detect the vegetation effect on habitat invasibility. Plant community types were classified on the basis of species presence/absence data using the two-way indicator species analysis TWINSpan (Hill 1979) in PC-ORD ver. 4 (McCune and Mefford 1999). The chi-squared test was used to identify highly significant differences between large community types. Only vegetation assemblages that were significantly different at the 99% confidence level and represented in more than five plots were accepted as a community. In order to obtain a coarse classification of vegetation, the community divisions were stopped after the fifth level, even if further divisions were statistically significant in this research. We calculated the frequency of *Prosopis* (%) occurring in these plant community types as the number of plots in which *Prosopis* occurs divided by the total number of plots examined in the community. We used the average number of other species per plot as the species richness in the communities.

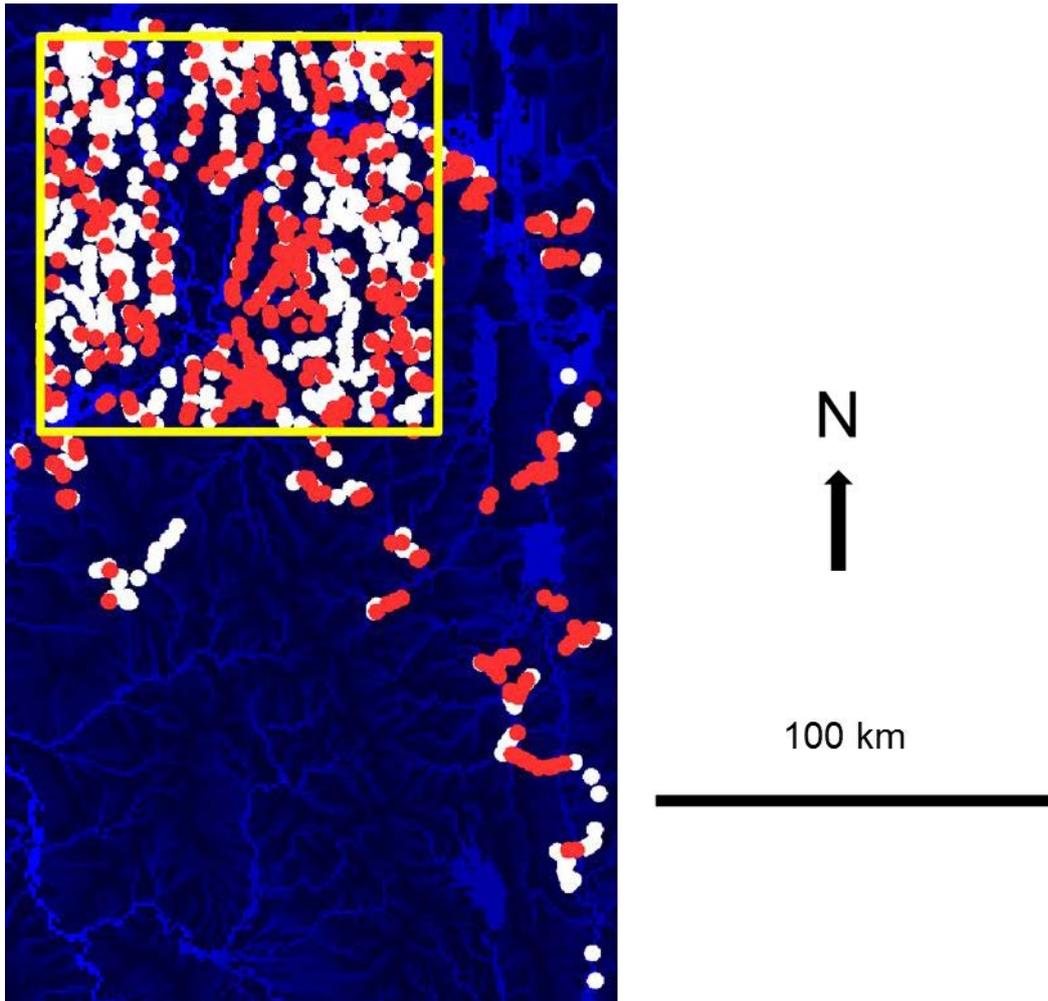


Fig. 1. *Prosopis* presence (red circles) and absence (open circles) in the vegetation survey plots in the central dry zone of Myanmar. The square marks the intensively surveyed 100 km \times 100 km area. Background catchment area shows rivers and flood plains as brighter blue, and mountains and ridges as a dark color.

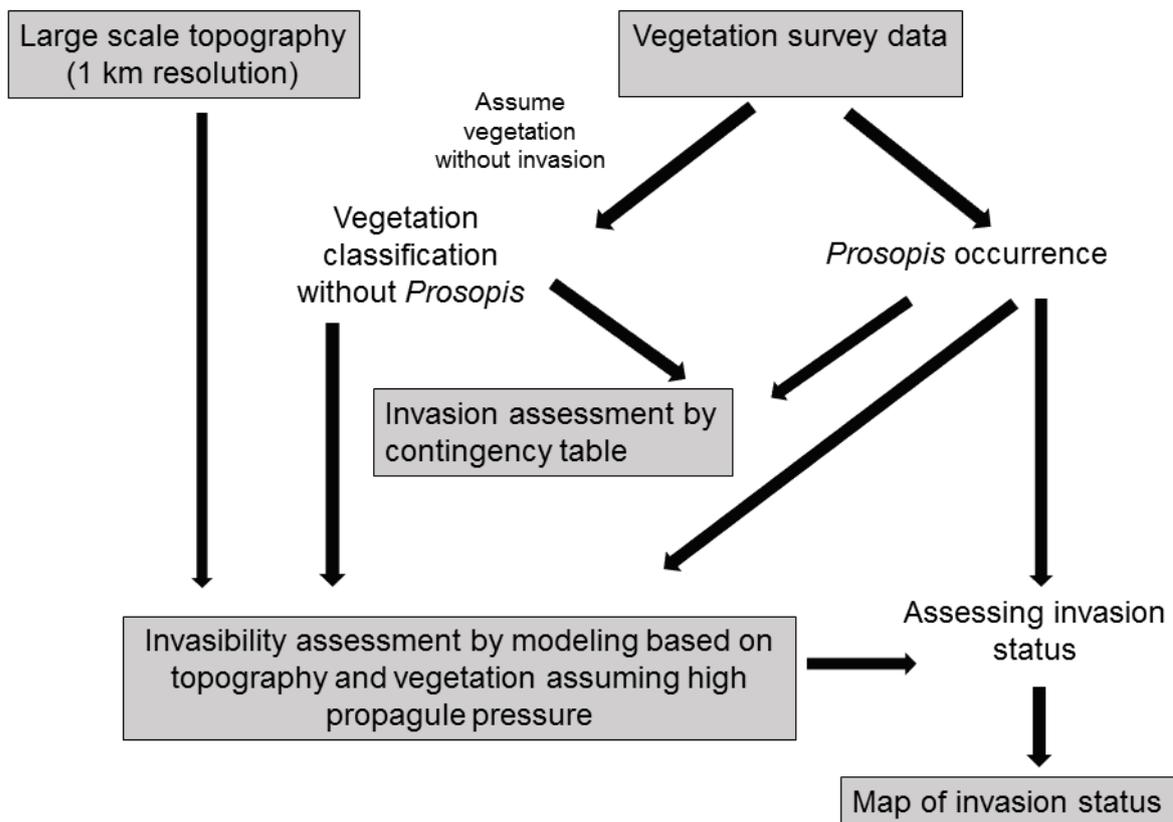


Fig. 2. Study approach for habitat invasibility assessment and invasion status identification.

Habitat invasibility assessment model

The invasibility of sites can be quantified in various ways, such as the probability of establishment and survival per arriving propagule at the site or the increase in biomass or percentage cover of the invaders in the site over a specified period given a defined propagule pressure (Davis et al. 2000). We quantified habitat invasibility as the occurrence probability of *Prosopis* under the sufficiently high propagule supply.

Large-scale climatic patterns and local environments should be considered simultaneously in order to predict the habitat invasibility of a site (Rejmánek et al. 2012). We assumed that the resident plant community represents many local environmental factors as the biotic interactions, local disturbance, human management, and soil. Mesoscale topography was considered to represent the climatic differences between cool-wet highlands and dry-hot lowlands within the dry zone (Stamp 1930). Actual climate data were not used because few meteorological stations are present in this region (Hijmans et al. 2005). Environmental variables (elevation, slope, watershed catchment area, and solar radiation as a function of slope orientation) were derived

from a 1-km-mesh digital elevation model (GTOPO30) using the Minna de GIS software (Koike 2013). The presence of *Prosopis* in the vegetation survey within 5 km around the focal site was considered as the propagule pressure.

Logistic regression analysis using a generalized linear model in R ver. 2.13.0 (R Development Core Team 2011) was performed to develop the invasibility assessment model. The response variable was the occurrence of *Prosopis* (presence or absence), and the predictor variables were the plant community type, environmental variables, and occurrence of a nearby *Prosopis* source population. The best-fit model with the smallest Akaike information criterion (AIC) value (Akaike 1974) was selected by using a backward stepwise algorithm. A smaller AIC value represents a better fit of the model to the observed occurrence data. Δ AIC, the difference in AIC after removing the focal variable from the best-fit model, was calculated to evaluate the actual contribution of a given variable.

The result of logistic regression was represented as:

$$Y = \frac{1}{1 + e^{-(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_n X_n + \alpha_1 + \alpha_2)}} \quad \text{Eq. 1}$$

where Y is the predicted probability of occurrence of *Prosopis*, X_n are the predictor variables (quantitative environmental variables of elevation, solar radiation, ground surface slope, and specific catchment area), β_n are parameters estimated by the regression, β_0 is the intercept, α_1 represents the effect of the local plant community type, and α_2 represents that of the *Prosopis* source population within 5 km. A different α_1 value was assigned to each community type in the regression procedure. The α_1 value was fixed as zero for one plant community type to eliminate redundancy of $\beta_0 + \alpha_1$, thus α_1 values for other community types represent the deviation from that community. The α_2 value was fixed as zero for the absence of a *Prosopis* source population within 5 km. In the assessment of habitat invasibility, we assumed the occurrence of a nearby source population to be present for all sites (i.e. $\alpha_2 \neq 0$ in Eq. 1), in order to obtain the potential occurrence probability under the sufficiently high propagule supply. By this assumption, we also controlled the effect of propagule pressure in our invasibility assessment model

Analysis of invasion status

Understanding the stages of the invasion process is the key to formulating management activities, although quantitative methods to detect these stages have not yet developed. In this study, we examined the stages of *Prosopis* invasion by using the actual presence/absence data from the vegetation survey sites (Fig. 1), and the habitat invasibility of the site. Habitat invasibility was

the predicted occurrence probability based on the invasibility assessment model assuming a high propagule pressure (i.e. assuming the presence of a nearby *Prosopis* source population, $\alpha_2 \neq 0$ in Eq. 1) We identified four zones of invasion status: zone 0, unsuitable habitat for *Prosopis*; zone 1, *Prosopis* population is absent in potentially suitable habitats; zone 2, many habitats have not yet been invaded due to a propagule deficit, even though there are *Prosopis* populations regionally; and zone 3, most habitats are invaded or saturated.

Invasive species occasionally spread to far distant sites in the manner of “leaping flames”, and then gradually spread to the surrounding areas from the invaded sites (Shigesada and Kawasaki 1997). Uninvaded suitable patches can remain even when the whole area is considered to be invaded due to occurrence of the invasive species in several habitats. Thus the spatial scale at which the occurrence of an invasive species is examined can affect the results of a geographic range expansion analysis. We examined and compared plots within circles at different spatial scales (radii of 5, 10, 20, and 40 km) to account for spatial scale biases when assessing *Prosopis* geographic distribution ranges. We located circle centers at regular grid points (5-km distance) covering the intensively surveyed area of 100 km \times 100 km. This spatial analysis was performed in the Minna de GIS software (Koike 2013).

To identify the unsuitable habitat for *Prosopis* (zone 0), we evaluated the arithmetic mean of the expected probability that *Prosopis* occurs at the survey plot within the circular area, assuming a high propagule pressure ($\alpha_2 \neq 0$ in Eq. 1). A given circular area was identified as zone 0 if the arithmetic mean of the expected probability was less than 0.1 (Table 1).

To identify the area where *Prosopis* population is absent in potentially suitable habitats (zone 1), we looked for sites lacking *Prosopis* by examining the vegetation survey data within the circles. To exclude unsuitable sites and to account only for the vacant suitable habitats, the probability that *Prosopis* occurs in at least one plot within the focal j th circle, S_j , was evaluated as:

$$S_j = 1 - \prod_{i=1}^k (1 - Y_i) \quad \text{Eq. 2}$$

where k is the number of plots within the circle and Y_i is the expected probability of occurrence according to the habitat invasibility assessment model in the i th site within the circle, assuming a high propagule pressure ($\alpha_2 \neq 0$ in Eq. 1). A given circular area was identified as zone 1 if *Prosopis* was absent in all surveyed plots in the circle, and if the region is sufficiently suitable, $S_j > 0.95$ (5% significance level; Table 1). By considering this probability S_j , we excluded those areas where *Prosopis* was absent solely due to the unsuitable habitat or an insufficient number of examined sites.

To identify the area of propagule deficit (zone 2), we detected the sites where vacant habitat patches still exist even if a local *Prosopis* population is present. The true occurrence probability, p , at a site can be determined by occurrence / (occurrence + absence). Likelihood, L , for absence data was defined as the probability that a given p causes an absence datum, and the likelihood function is $L = 1 - p$ in our case (Fig. 3). Although any value of p can cause *Prosopis* absence at a given plot through stochasticity, L is large if p is close to 0.0 and small if p is close to 1.0. The true occurrence probability, p , is affected by two factors: habitat suitability, Y_i , and the propagule pressure. If Y_i for a vacant plot is close to 1.0, the plot is suitable for *Prosopis*, hence the propagule deficit should be the reason for the absence. If Y_i is close to 0.0, the plot is unsuitable for *Prosopis*. The point midway between these two cases is the median of the likelihood distribution along p (Fig. 3), and the area below the line $L = 1 - p$ is equivalent in both sides (Table 1).

In order to detect a propagule deficit in each plot, we calculated the accumulated likelihood, Q_i , from the median to the model estimates (shaded area in Fig. 3):

$$Q_i = \frac{\int_{\text{median}}^{Y_i} L dp}{\int_0^1 L dp} \quad \text{Eq. 3}$$

where Y_i is the estimated value for p according to the invasibility assessment model, assuming a high propagule pressure ($\alpha_2 \neq 0$ in Eq. 1). Q_i is positive when Y_i is larger than the median (i.e., the site is vacant due to propagule deficit). The Q_i value was calculated for each vegetation survey plot where *Prosopis* was absent, and the average Q_i in neighboring plots within each circle was calculated and analyzed by using a t -test. If the average Q_i was significantly larger than zero, we determined that *Prosopis* was able to invade the currently vacant habitats but was absent due to a propagule deficit, and the area was identified as zone 2.

To identify the area where most habitats are invaded or saturated (zone 3), the observed number of plots with *Prosopis* should be sufficiently close to saturation, in our case in more than the half of the expected number of plots predicted by the invasibility assessment model assuming a high propagule pressure ($\alpha_2 \neq 0$ in Eq. 1; Table 1). We applied a binomial test, and an area was considered to be zone 3 when the significance level was <0.05 . These thresholds can be adjusted depending on the target species and the management objectives.

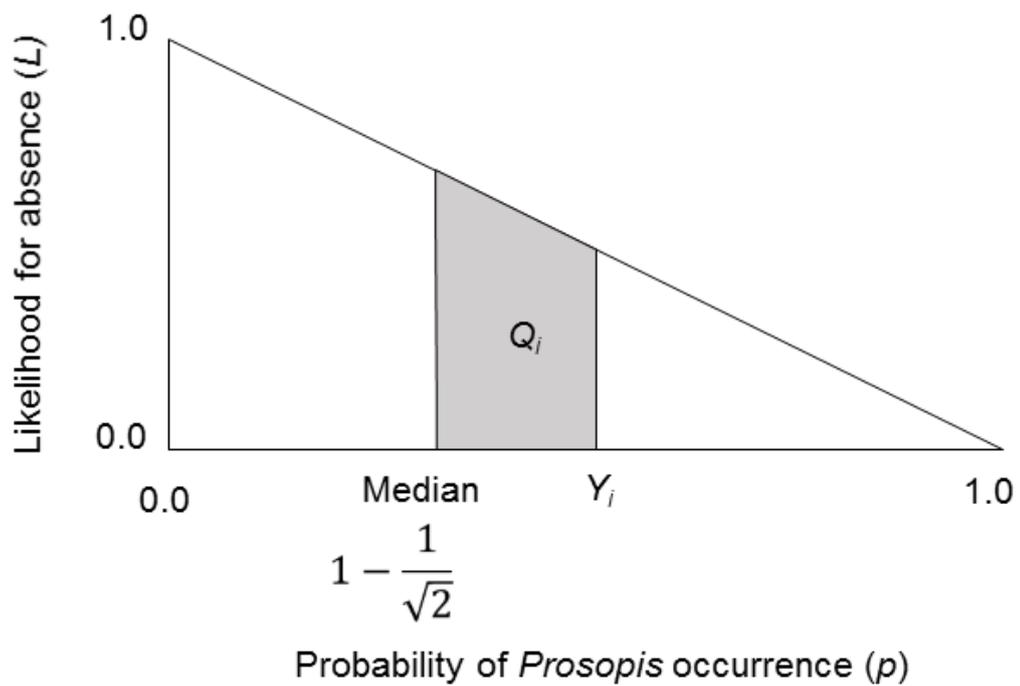


Fig.3. The approach used to detect the propagule deficit. The likelihood distribution (triangular area below $L = 1 - p$ in this case) was of “absence” data in the vegetation survey. If the potential occurrence (Y_i) is larger than the median the plot is suitable for *Prosopis* and a propagule deficit should be the reason for the absence. The shaded area (Q_i) represents the magnitude of the deviation between the expected and observed occurrence.

Table 1. Identification of *Prosopis* invasion status in the central dry zone of Myanmar. Predicted invasibility was estimated based on large-scale environment and local vegetation type assuming a high propagule pressure.

Regional invasion status	Description	Methods of detection
Unsuitable area (Zone 0)	Unsuitable habitat for <i>Prosopis</i> due to environment or biological community	Predicted invasibility < 0.1 as arithmetic mean of sites in the focal region
Suitable but <i>Prosopis</i> not yet arrived (Zone 1)	No <i>Prosopis</i> population is found in the suitable habitats	Not Zone 0 AND <i>Prosopis</i> is absent in all sites studied AND Predicted probability that <i>Prosopis</i> occurs in at least one site >0.95 due to the presence of suitable habitat
Area with many propagule-deficit sites (Zone 2)	Spatial invasion process is ongoing Propagule-deficit sites remain in the suitable habitats even if a local <i>Prosopis</i> population is present	Not Zone 0 AND <i>Prosopis</i> occurs in at least one site studied AND At sites lacking <i>Prosopis</i> , (the predicted invasibility) > (the median probability value expected to cause “absence” based on the likelihood distribution), at the significance level of 0.05
Heavily invaded area (Zone 3)	<i>Prosopis</i> exists in more than 50% of potential habitats	Not Zone 0 AND Number of <i>Prosopis</i> present sites > expected number of present sites/2, at the significance level of 0.05

Results

Plant community types and *Prosopis* frequency

We recorded 360 plant species in 1399 sample plots. *Prosopis* was present in 427 plots. TWINSpan classified vegetation within 1361 plots (i.e., the dataset without *Prosopis*) into six statistically significant ($P < 0.01$) plant communities (Fig. 4). We detected three forest communities, Semi-indaing forests (Type A), Dahat-Tham forests (*Tectona-Terminalia* association) dominated by the endemic *T. hamiltoniana* (Type B), Shar-Dahat Thorn forests (*Acacia-Tectona* association) (Type C), and three woody communities in the human-dominated landscape: agricultural hedgerow community (Type D), *Combretum* hedgerows (Type E), and a woody community in rural residential areas (Type F). The names of community types were given according to Stamp's vegetation classification except Types D and F (Table 2). The Semi-indaing forests and Dahat-Tham forests were found mainly in the remnant forest areas; and Shar-Dahat Thorn forests were widely distributed in the open forest landscape.

Prosopis frequency was lower in the forest areas and coppice tree patches (2.56% in Type A and 6.48% in Type B), where the average number of species was higher (10.33 in Type A and 10.19 in Type B) than the other communities (Table 2). *Prosopis* frequency was highest in *Combretum* hedgerows (71.88%), followed by the agricultural hedgerow community (48.48%), rural residential community (39.29%), and Shar-Dahat Thorn forests (36.08%).

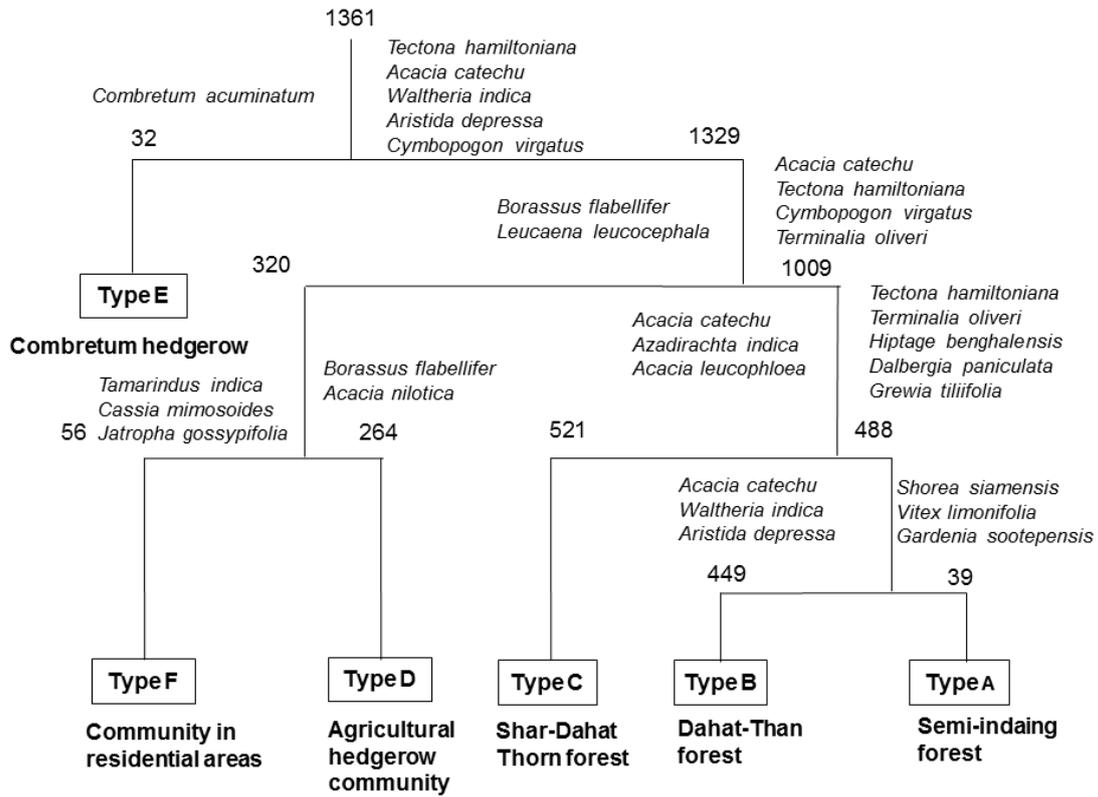


Fig.4. Dendrogram showing the TWINSpan classification of plant communities (without *Prosopis* data) with their indicator species. Significant differences between plant communities were verified by a chi-squared test at the 99% confidence level. The community division was stopped after the fifth level to obtain a coarse classification. Indicator species of each division branch and the number of sample sites are shown.

Table 2. Detected community types before *Prosopis* invasion (without *Prosopis* data) and frequency of *Prosopis*

Community	Community name [†]	Total plots	Average number of species	Frequency of <i>Prosopis</i> (%)	Community description, management, and human use
Type A	Semi-Indaing forest	39	10.33	2.56	Remnant forest areas, conservation areas.
Type B	Dahat-Tham forest (<i>Tectona hamiltoniana</i> – <i>Terminalia oliveri</i> forest)	449	10.19	6.46	Remnant forest areas, coppice tree patches.
Type C	Shar-Dahat Thorn forest (<i>Acacia catechu</i> – <i>Tectona hamiltoniana</i> association)	521	7.70	36.08	Open forest areas, grazed tree patches.
Type D	Agricultural hedgerow community	264	5.80	48.48	Agricultural hedgerows, roadsides connecting villages.
Type E	<i>Combretum</i> hedgerow	32	2.13	71.88	Thickets on river and stream sides, roadsides, fallow lands, scrub lands, near water ponds and rural residential areas.
Type F	Woody community in rural residential areas	56	2.80	39.29	Rural residential areas.

[†]Nomenclature following Stamp (1925) except Types D and F.

Habitat invasibility assessment model

The results of the logistic regression analysis are summarized in Table 3. Local plant community was the strongest factor ($P<0.01$), followed by the occurrence of a source population within a 5-km radius ($P<0.01$), to predict the habitat invasibility to *Prosopis* invasion. Mesoscale elevation ($P<0.05$) and solar radiation ($P<0.1$) were also significant factors in the logistic regression analysis. At the mesoscale, low elevation was strongly associated with habitat invasibility by *Prosopis* and the drier sites were susceptible to *Prosopis* invasion (Table 3).

The regression parameter α_1 (Eq. 1) was smallest for Semi-indaing forests and small for Dahat-Tham forests. According to a *t*-test combining the community types into two categories, α_1 values for Shar-Dahat thorn forests and the three woody communities in human-dominated landscapes (Types C–F) were larger than those for Types A and B ($P<0.01$), suggesting that these areas have a higher susceptibility to *Prosopis* invasion.

Table 3. The predictor variables and regression parameters of the best-fit logistic regression model (Eq. 1). Δ AIC is the difference in AIC between the best-fit model and the model without the focal variable, representing the importance of the focal variable. All quantitative variables were standardized before the analysis as (value – mean)/standard deviation. A likelihood-ratio test was used to compare the model with and without the focal variable, and *P*-value shows the significance of the difference between those two models.

Variable	Coefficient	Δ AIC
Intercept	–20.87	
Elevation	–0.30	11.43**
Solar radiation	0.23	3.89 ⁺
Local vegetation type		173.89**
Type A	0.00	
Type B	0.78	
Type C	2.80	
Type D	3.17	
Type E	4.34	
Type F	3.17	
<i>Prosopis</i> source population		115.99**
Absent within a 5-km radius	0.00	
Present within a 5-km radius	17.64	

** $P<0.01$, * $P<0.05$, ⁺ $P<0.1$ in likelihood-ratio test

Invasion status

Prosopis was widely distributed in the study area (Fig.1). At the spatial scale of 5-km radius, we detected unsuitable areas (zone 0) at five grid points, located on a hill and ridges in the 100 km × 100 km study area (Fig.5). Suitable areas lacking a *Prosopis* population (zone 1) were also found scattered across the study area. At all spatial scales, the propagule-deficit sites (zone 2) were detected in wide areas (Fig. 5). Heavily invaded sites (zone 3) were found in areas, especially parallel to the Irrawaddy River (center of Fig.5). The southeastern side of the Irrawaddy River was at a more advanced stage of invasion than the northwestern side of the river.

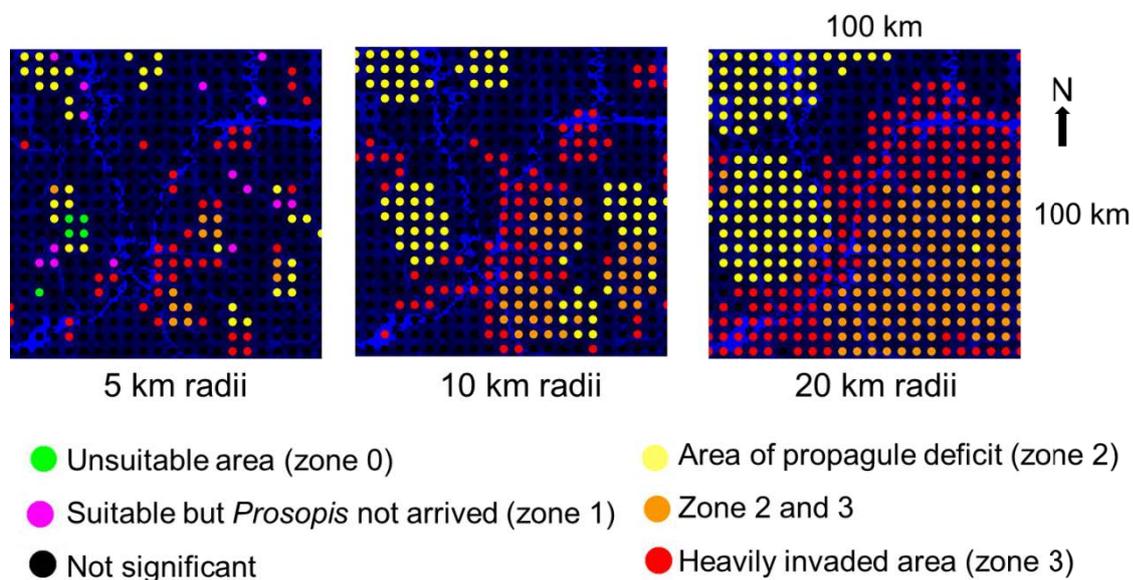


Fig.5. Invasion status of *Prosopis* at our study area in the central dry zone of Myanmar. Unsuitable area for *Prosopis* (zone 0), areas lacking *Prosopis* in suitable habitats (zone 1), areas of *Prosopis* propagule deficit (zone 2), and heavily invaded areas (zone 3) were detected at spatial scales of 5-, 10-, and 20-km radii centered on the grid points at 5-km intervals (dots) in the intensively surveyed 100 km × 100 km area. Background catchment area shows rivers and flood plains as brighter blue, and mountains and ridges as dark color. The bright belt running diagonally from northeast to southwest is the Irrawaddy River.

Discussion

Our analysis pointed out that the choice of a spatial scale is important in assessing the geographic range expansion of a currently spreading alien species. *Prosopis* has already invaded all the regions in our study area in the central dry zone of Myanmar, if we consider large spatial scales. However, areas lacking *Prosopis* existed in suitable habitats at the small spatial scale of a 5-km radius, and many local sites with a propagule deficit remained close to heavily invaded areas (Fig.5). These findings suggest that *Prosopis* invasion will continue to spread gradually, and costs will rise unless adequate management is initiated soon.

Habitat invasibility assessment model

Removing *Prosopis* data from the vegetation classification and evaluating the effect of a nearby *Prosopis* source population allowed us to determine habitat invasibility by controlling the effect of propagule pressure. This is a more direct approach than the approach by Chytrý et al. (2008) assuming a distance from a river and human activities as the proxy of propagule pressure. We did not apply a spatial-spread model for alien species range expansion (unlike the studies by Koike 2006; Fukasawa et al. 2009) because the data on the initial *Prosopis* introduction sites is not available. We used globally available large-scale topography data (1-km mesh GTOPO30) and local vegetation survey data to assess the occurrence probability of the invasive species. Mesoscale topography is a good proxy of mesoscale climate (Hijmans et al. 2005), and local vegetation type is a proxy of biotic interactions, local environment, and local disturbance by human activities. Our approach assessing habitat invasibility of *Prosopis* may be appropriate for developing countries where high-resolution databases of climate and other geographic variables are not available.

Our findings suggest that the direct climatic factors enhancing *Prosopis* invasion in the central dry zone of Myanmar are a dry environment, high temperature represented by low elevation and high solar radiation, as has been reported in other areas of the world (Pasiiecznik et al. 2001). The local plant communities, influenced by local environments, disturbances, and human management, were strongly associated with the habitat invasion risks posed by *Prosopis*, and large ΔAIC showed the large contribution of the effect of plant community type independent of the mesoscale environments and propagule pressure (Table 3).

We cannot differentiate cause from consequence with our observational design; the lower-than-average number of species in the human-dominated communities with higher *Prosopis* frequency could be due either to the tendency of *Prosopis* to become established in

heavily disturbed lands with low plant diversity or either because the presence of *Prosopis* hindered the survival and establishment of other species (van Klinken et al. 2006; El-Keblawy and Abdelfatah 2014). Regardless of the mechanisms, we show that *Prosopis* frequency was negatively correlated with higher native species diversity (Types A and B; Table 2).

Invasion status

Our finding suggests that *Prosopis* is spreading at sites within a small scale (≤ 5 km) in these regions (Fig.5). Because *Prosopis* trees begin to flower at the age of 3–4 years (Orwa et al. 2009), we assume that *Prosopis* populations will gradually spread from the invaded habitat patches to the surrounding uninvaded areas (Fig.5). The costs caused by *Prosopis* will increase in the future due to the newly formed populations at the suitable sites in zones 1 and 2. A greater encroachment of *Prosopis* into the open forest lands, agricultural lands, and residential areas will pose higher threats to the local economy, native ecosystems, and human health (Wise et al. 2012; Haregeweyn et al. 2013).

There were several grid points belonging to both zones 2 and 3, especially at the spatial scale of a 20-km radius. If few vacant suitable sites were found within the heavily invaded area in a circle of large radius, both zones 2 and 3 would be detected by our criteria (Table 1). Such a phenomenon may happen in the late stage of alien species invasion when only a few vacant sites remain or when bare lands are created due to new land development in heavily invaded areas.

Small-scale analysis was suitable for detecting locally uninvaded areas as zone 1 (5-km radius in Fig.5), whereas many survey sites were necessary to obtain statistically significant results (7.9 sites per grid point on average). Large-scale analysis was suitable for assessing the status across a wide area (average 112.0 sites per grid point in the case of a 20-km radius), although any single area tended to include different invasion status, such as zones 2 and 3 (Fig. 5). A suitable spatial scale needs to be determined based on the available survey sites. In this study, we attempted to detect statistically significant zones for *Prosopis* invasion status (i.e., $P < 0.05$ in Table 1), and many sites appeared to be statistically insignificant (Fig.5). The decision to deal with these sites may depend on the management objective. If the objective is eradication, the insignificant data-deficient sites should be considered as high-risk areas (zone 3), whereas these sites can be considered as less important if the objective is simply to reduce *Prosopis* population density.

Management recommendations

Spatial zoning of invasion status based on a habitat invasibility assessment model is useful for planning the management of invasive species (Biggs et al. 2011). Our study suggests that *Prosopis* invasions will continue to increase in the central dry zone of Myanmar unless propagule control measures are initiated soon. Early control of newly established populations should be done to prevent further damage caused by *Prosopis* in the uninvaded suitable zones 1 and 2. Land managers should not initiate new plantings in areas where *Prosopis* is absent in suitable habitats (zone 1) and where uninvaded suitable habitats remain, even if *Prosopis* is regionally present (zone 2). Because *Prosopis* spreads via livestock dung, the movement of livestock from the zones 3 and 2 to the zone 1 needs to be controlled. In unavoidable cases, feeding *Prosopis*-free fodder before moving livestock from highly invaded areas to other areas may reduce new infestations.

Regional and local eradication programs should focus on the newly formed populations in the zone 1 (Moody and Mack 1988; Koike 2006). For the zones 2 and 3, the eradication of *Prosopis* may not be cost-effective and may be practically impossible (Van Auken 2000). In the zones 2 and 3, control through *Prosopis* use as firewood may reduce the damage and delay the spread (Choge and Chikamai 2004). In some areas where native forest resources are not easily accessible, the multipurpose uses of *Prosopis* as fodder and firewood makes the eradication issue controversial (Wise et al. 2012). Social perspectives of local residents need to be considered with regard to the management of the invasive species (Fischer and Charnley 2012). We recommend improving management of the remnant native forests in order to produce better-quality forest resources from native species to help prevent further introduction of *Prosopis*.

References

- Akaike H (1974) A new look at the statistical model identification. *IEEE Transactions. Automatic Control* 19:716-723, <http://dx.doi.org/10.1109/TAC.1974.1100705>
- Bigsby KM, Tobin PC, Sills EO (2011) Anthropogenic drivers of gypsy moth spread. *Biological Invasions* 13:2077-2090, <http://dx.doi.org/10.1007/s10530-011-0027-6>
- Burke MJW, Grime JP (1996) An experimental study of plant community invasibility. *Ecology* 77:776-790, <http://dx.doi.org/10.2307/2265501>
- Burkhart A (1976) A monograph of the genus *Prosopis* (Leguminosae Subfam. Mimosoideae). *Journal of the Arnold Arboretum* 57:219-249
- Choge SK, Clement N, Gitonga M, et al. (2012) Status report on commercialization of *Prosopis* tree resources in Kenya. Nairobi: KEFRI; 2012. Technical report for the KEFRI/KFS Technical Forest Management and Research Liaison Committee
- Chytry M, Jarosik V, Pysek P, et al. (2008) Separating habitat invasibility by alien plants from the actual level of invasion. *Ecology* 89:1541-1553, <http://dx.doi.org/10.1890/07-0682.1>
- D'Antonio C, Meyerson LA (2002) Exotic plant species as problems and solutions in ecological restoration: A synthesis. *Restoration Ecology* 10:703-713, <http://dx.doi.org/10.1046/j.1526-100X.2002.01051.x>
- Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88:528-534, <http://dx.doi.org/10.1046/j.1365-2745.2000.00473.x>
- El-Keblawy A, Abdelfatah MA (2014) Impacts of native and invasive exotic *Prosopis* congeners on soil properties and associated flora in the arid United Arab Emirates. *Journal of Arid Environments* 100:1-8, <http://dx.doi.org/10.1016/j.jaridenv.2013.10.001>
- Felker P, Cannell GH, Osborn JF, et al. (1983) Effects of irrigation on biomass production of

32 *Prosopis* (mesquite) accessions. *Experimental Agriculture* 19:187-198, <http://dx.doi.org/10.1017/S0014479700022638>

Fischer AP, Charnley S (2012) Private forest owners and invasive plants: Risk perception and management. *Invasive Plant Science and Management* 5:375-389, <http://dx.doi.org/10.1614/IPSM-D-12-00005.1>

Fukasawa K, Koike F, Tanaka N, Otsu K (2009) Predicting future invasion of an invasive alien tree in a Japanese oceanic island by process-based statistical models using recent distribution maps. *Ecological Research* 24:965-975, <http://dx.doi.org/10.1007/s11284-009-0595-4>

Gallaher T, Merlin M (2010) Biology and impacts of Pacific island invasive species. 6. *Prosopis pallida* and *Prosopis juliflora* (Algarroba, Mesquite, Kiawe) (Fabaceae). *Pacific Science* 64:489-526, <http://dx.doi.org/10.2984/64.4.489>

Goslee SC, Havstad KM, Peters DPC, et al. (2003) High-resolution images reveal rate and pattern of shrub encroachment over six decades in New Mexico, USA. *Journal of Arid Environments* 54:755-767, <http://dx.doi.org/10.1006/jare.2002.1103>

Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8:993-1009, <http://dx.doi.org/10.1111/j.1461-0248.2005.00792.x>

Hanski I (1998) Metapopulation dynamics. *Nature* 396:41-49, <http://dx.doi.org/10.1038/23876>

Haregeweyn N, Tsunekawa A, Tsubo M, et al. (2013) Analysis of the invasion rate, impacts and control measures of *Prosopis juliflora*: a case study of Amibara District, Eastern Ethiopia. *Environmental Monitoring and Assessment* 185:7527-7542, <http://dx.doi.org/10.1007/s10661-013-3117-3>

Hijmans RJ, Cameron SE, Parra JL, et al. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25:1965-1978, <http://dx.doi.org/10.1002/joc.1276>

Hill MO (1979) TWINSPAN: A Fortran program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Department of Ecology and Systematics, Cornell University, Ithaca

Jadeja S, Prasad S, Quader S, et al. (2013) Antelope mating strategies facilitate invasion of grasslands by a woody weed. *Oikos* 122:1441-1452, <http://dx.doi.org/10.1111/j.1600-0706.2013.00320.x>

Koike F (2006) Prediction of range expansion and optimum strategy for spatial control of feral raccoon using a metapopulation model. In: Koike F, Clout MN, Kawamichi M, De Poorter M, Iwatsuki K (eds) Assessment and control of biological invasion risks. Shoukadoh Book Sellers, Kyoto, Japan and IUCN, Gland, Switzerland, pp. 148-156

Koike F (2013) Minna de GIS: Spatial data analysis system for education, research and environmental assessment by citizens. <http://www13.ocn.ne.jp/~minnagis/>

Komuro T, Koike F (2005) Colonization by woody plants in fragmented habitats of a suburban landscape. *Ecological Applications* 15:662-673, <http://dx.doi.org/10.1890/03-5232>

Lace JH, Hundley HG (1987) List of trees, shrubs, herbs and principal climbers, etc.: Recorded from Burma with vernacular names. Superintendent, Government Printing and Stationery, Rangon, Union of Burma

Landeras G, Alfonso M, Pasiecznik NM, et al. (2006) Identification of *Prosopis juliflora* and *Prosopis pallida* accessions using molecular markers. *Biodiversity and Conservation* 15:1829-1844, <http://dx.doi.org/10.1007/s10531-004-6682-5>

Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology* 80:1522-1536, <http://dx.doi.org/10.2307/176544>

Low T (2012) Australian acacias: Weeds or useful trees? *Biological Invasions* 14:2217-2227, <http://dx.doi.org/10.1007/s10530-012-0243-8>

McCune B, Mefford J (1999) PC-ORD: Multivariate analysis of ecological data. Version 4. MjM Software Design, Glenden Beach, Oregon, U.S.A

Milton SJ, Dean WRJ (2010) Plant invasions in arid areas: special problems and solutions—a South African perspective. *Biological Invasions* 12:3935-3948, <http://dx.doi.org/10.1007/s10530-010-9820-x>

Ministry of Environmental Conservation and Forestry (2011) National biodiversity strategy and action plan Myanmar. Nay Pyi Taw, Myanmar, Retrieved May 25, 2014, from <https://www.cbd.int/doc/world/mm/mm-nbsap-01-en.pdf>

Moody ME, Mack RN (1988) Controlling the spread of plant invasions: The importance of nascent foci. *Journal of Applied Ecology* 25:1009-1021, <http://dx.doi.org/10.2307/2403762>

National Commission for Environmental Affairs (2009) Myanmar: Fourth national report to the United Nations Convention on Biological Diversity. Ministry of Environmental Conservation and Forestry, Nay Pyi Taw, Myanmar, Retrieved June 12, 2014, from <https://www.cbd.int/doc/world/mm/mm-nr-04-en.pdf>

Orwa C, Mutua A, Kindt R, Jamnadass R, Anthony S (2009) Agroforestry Database: a tree reference and selection guide. Version 4.0. World Agroforestry Centre, Nairobi, Kenya.

Pasiecznik NM, Felker PH, Harsh PJC, et al. (2001) The *Prosopis juliflora*–*Prosopis pallida* complex: A monograph. HDRA, Coventry, UK.

Pimentel D, McNair S, Janecka J, et al. (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture Ecosystems and Environment* 84:1-20, [http://dx.doi.org/10.1016/s0167-8809\(00\)00178-x](http://dx.doi.org/10.1016/s0167-8809(00)00178-x)

R Development Core Team (2011) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>

Rejmánek M, Richardson DM, Pyšek P (2012) Plant invasions and invasibility of plant communities. In: van der Maarel E and Franklin J (eds) *Vegetation ecology*, 2nd edn.

Wiley-Blackwell, Chichester, UK, pp. 387-424

Sawal RK, Ratan R, Yadav SBS (2004) Mesquite (*Prosopis juliflora*) pods as a feed resource for livestock: A review. *Asian-Australasian Journal of Animal Sciences* 17:719-725

Shackleton RT, Le Maitre DC, Pasiieczni, NM, Richardson DM (2014) *Prosopis*: A global assessment of the biogeography, benefits, impacts and management of one of the world's worst woody invasive plant taxa. *AOB Plants* 6: plu027, <http://dx.doi.org/10.1093/aobpla/plu027>

Shiferaw H, Teketay D, Nemomissa S, et al. (2004) Some biological characteristics that foster the invasion of *Prosopis juliflora* (Sw.) DC. at Middle Awash Rift Valley Area, north-eastern Ethiopia. *Journal of Arid Environments* 58:135-154, <http://dx.doi.org/10.1016/j.jaridenv.2003.08.011>

Shigesada N, Kawasaki K (1997) *Biological invasions: theory and practice*. Oxford University Press, Oxford, UK

Stamp LD (1925) *The vegetation of Burma from an ecological standpoint*. Thacker, Spink & Company, Calcutta, India

Stamp LD (1930) *Burma: An undeveloped monsoon country*. *Geographical Review* 20:86-109, <http://dx.doi.org/10.2307/209128>

Troup RS (1921) *The silviculture of Indian trees. Volume 2: Leguminosae (Caesalpinieae) to Verbenaceae*. Oxford University Press, Oxford, UK

Van Auken OW (2000) Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics* 31:197-215, <http://dx.doi.org/10.1146/annurev.ecolsys.31.1.197>

van Klinken RD, Graham J, Flack LK (2006) Population ecology of hybrid mesquite (*Prosopis* species) in Western Australia: How does it differ from native range invasions and what are the implications for impacts and management? *Biological Invasions* 8:727-741,

<http://dx.doi.org/10.1007/s10530-005-3427-7>

Vitousek PM (1990) Biological invasions and ecosystem processes: Towards an integration of population biology and ecosystem studies. *Oikos* 57:7-13, <http://dx.doi.org/10.2307/3565731>

Vitousek PM, Dantonio CM, Loope LL, et al. (1997) Introduced species: A significant component of human-caused global change. *New Zealand Journal of Ecology* 21:1-16

Wilson JRU, Richardson DM, Rouget M, et al. (2007) Residence time and potential range: Crucial considerations in modelling plant invasions. *Diversity and Distributions* 13:11-22, <http://dx.doi.org/10.1111/j.1366-9516.2006.00302.x>

Wise RM, van Wilgen BW, Le Maitre DC (2012) Costs, benefits and management options for an invasive alien tree species: The case of mesquite in the Northern Cape, South Africa. *Journal of Arid Environments* 84:80-90, <http://dx.doi.org/10.1016/j.jaridenv.2012.03.001>

Chapter 3 Predicting potential invasion risk of newly introduced alien woody plants in central dry zone, Myanmar

Abstract

This study evaluated potential invasion risk of newly added alien plant species in the dry zone of central Myanmar based on plant traits. Complete trait measurements were available for 36 species and the best fit models predicting the species occurrence for each community were developed by logistic regression. Prediction models by plant traits were significant for all community types. Maximum height and shade tolerance were important key-traits as in other parts of the world while animal palatability was also an important key-trait in tropical dry zone of Myanmar. Specific leaf area was negatively correlated with species occurrence probability due to stressful environment of dry zone. Predictability was generally low in the open forests of tropical dry zone. Agricultural hedgerow with high human disturbance had lowest predictability. Prediction of potential invasion risks of alien species was possible; however, predictability was lower than those in closed forests of temperate areas. Key traits in tropical dry zone of Myanmar were quite different from those of temperate moist regions. Risk assessment system as WRA (weed risk assessment) in Myanmar needs to consider such difference. We need to continue to identify key-traits in order to improve species risk assessment in tropical dry zone.

Keywords biological trait, plant trait analysis, dry zone, Myanmar (Burma), animal palatability, potential invasion risk

Introduction

Understanding where plants grow and why they grow there is the fundamental component of plant ecology. Some ecologists believe the keys to understanding these secrets depends on our understanding of plant functional traits (Laughlin, Laughlin 2013). Although learning about plant functional traits has always been an important component of plant science research (Westoby, Wright 2006), predicting abundance and distribution of species from a regional species pool based on trait-based models of community assembly is gaining growing attention recently. Many implications of applied plant ecology have been developed based on the concept of trait-based community assembly such as restoration ecology, invasion ecology.

The dry zone once had the substantial deciduous forest cover (Stamp 1924; Davis 1964). The dry zone has been largely deforested (0.4 – 1.2 % between 1990- 2000, Leimgruber 2005). Major factors for deforestation and degradation are over-cutting, shifting cultivation, agricultural expansion, development projects such as dam construction and heavy grazing by domestic cattle and goats. The dry zone restoration works was started since 1950s by Agriculture and Rural Development Corporation (ARDC). At present, many dry forests are remained as remnant forests in which firewood cutting, domestic grazing and illegal harvesting are inevitable while few areas are well protected as climax forests. The forests have been currently managed by the conservation effort of the Forest Department and the Dry Zone Greening Department within the Ministry of Environmental Conservation and Forestry and some are well protected by community-based conservation mainly for religious purpose. Forest restoration is ongoing in such conservation area.

To facilitate the restoration process in the dry zone, the Forest Department and the Dry Zone Greening Department are conducting greening projects, such as plantation establishment on degraded and denuded lands, and are protecting and conserving the remaining natural forests. Native and alien plant species that can grow in arid environments are being used in these greening projects (Oo et al. 2006). Many alien species including *Eucalyptus* species, *Leucaena leucocephala*, *Acacia nilotica*, *Acacia auriculiformis*, *Acacia senegalensis* have been introduced and the potential invasion risks of such alien species have not been documented. *Prosopis* species was introduced since ARDC period and has been found to be widely distributed in the central dry zone region.

This study aimed to determine the ecological traits of dry forest species in Myanmar and evaluate potential invasion risk of newly introduced alien woody plants to native plant communities based on their plant biological traits.

Methods

Study area

The majority of people living in the dry zone region depends on agriculture and livestock production. Due to low mean annual rainfall (500 – 1000 mm) the trees and plants are stunted. Lack of proper pasture management has driven the grazing of domestic livestock into the forests where many grass species and leave sprout are abundant. The regeneration and growth of dry forest species have been hindered by the uncontrolled grazing and hence the effect of grazing may be one of the most important factor determining vegetation composition in the central dry zone.

Vegetation survey and community classification

Vegetation survey for community classification was done during dry season (February to March) and growing season (September to October) in 2011. Un-naturalized planted species were removed from the dataset. Six plant communities were observed in the study area; three forest communities (1: Semi-Indaing forest with *Shorea* species; 2: Than-Dahat community; 3: Shar-Dahat community), two communities in agricultural landscapes (4: Agricultural hedgerow community; 5: *Prosopis*-dominated community), and one woody community in rural residential areas (6). The names of community types 1, 2, and 3 were given according to the vegetation classification of Stamp (1924). The detailed procedure for classifying plant communities were discussed in chapter 2.

Plant trait measurements

In this study, we considered the following four plant traits: maximum height (m), shade tolerance, animal palatability and specific leaf area (SLA; $\text{mm}^2 \text{mg}^{-1}$); and evaluated their importance in determining potential invasion risk of newly introduced alien plant species to native plant communities.

Plant trait measurements were done during the growing season (September to November) in 2012 and 2013. Due to the remnant nature of vegetation in the dry zone, we took a large study area (Fig 1, Chapter 2) and observed vegetation in all possible community types which are scattered across the study area. Along a transect line of 1 km ($n=1$), we recorded maximum height, minimum light intensity and grazing traces for five individuals of each species. Leaf specimen from five different trees were taken for each species at each transect to measure SLA. We attempted to observe the four ecological traits of each species at

least at five transect lines if the samples were available. The matrix of sample collection (species trait, transect, individuals) is $(1 \times 5 \times 5)$.

Previous studies suggested the variation of plant traits in various habitat types (Dansereau 1951). In our study, we surveyed species in various community types as possible and analyzed the combined data to get an average trait measurement of species.

Maximum height

The mean height of three tallest individuals was taken as the maximum height of species. In the dry zone area, the trees were heavily cut and the coppice stands are growing in some areas. The maximum height values of trees at some sites are not reasonable and such values were removed before analysis.

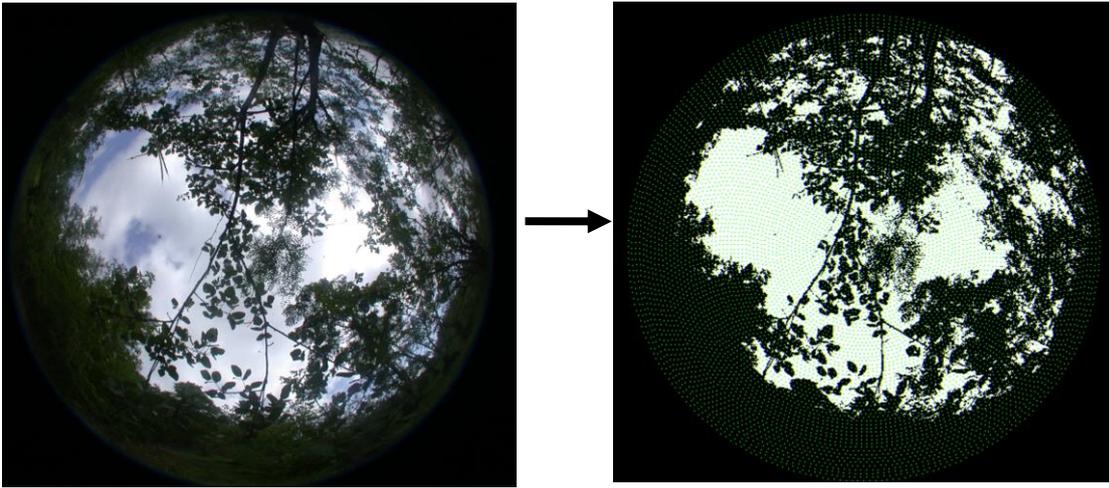
Shade tolerance (-log of Geometric mean of minimum light intensity)

Shade tolerance, minimum light under which a plant can survive, is an important life-history trait that plays a major role in plant community dynamics. Competitive potentials among co-occurring species associated with shade tolerance is critical to predict ecosystem responses to global drivers such as elevated CO₂, climate change and the spread of invasive species (Valladares, Niinemets 2008).

In our study, for higher sampling efficiency, we observed the nearest five seedlings of 15 cm to 1 meter height which were growing under the lowest light condition along the transect line. Hemispherical photographs were taken above the seedlings to measure relative light intensity (%). The relative light intensity values were calculated by automatically continuous analysis of hemispherical photographs (Sora to mori software: Koike 2009) and – log (geometric mean of three minimum light intensities) was taken shade tolerance of species.



Taking hemispherical photographs above seedlings of 15 cm to 1 m height



Sora to mori software converts the image of 24bit-bmp into black and white image by the set threshold value and calculates the relative composition of light (white portion) and shade (dark portion)

Animal palatability

Our survey was done at the end of growing season (September to November) although grazing pressure on vegetation may differ seasonally. We observed grazing traces on seedlings of 15 cm to 1 meter height and on tree stems up to 1 meter height to which animals can easily reach. We observed 5 individuals for each species along a transect line and recorded the presence/absence of grazing traces. We considered only major species in the palatability analysis for reliable results. Major species are those which occurred at least at 5 sites; with at least 3 individuals at each sites and with at least 3 grazed individuals in total for all sites. From the frequency of grazing occurrence, we calculated animal palatability value of species by distance likelihood analysis (Minna de GIS, Koike 2013).



Domestic goats feeding on the natural regeneration of *Acacia nilotica* along roadsides



Domestic sheep grazing on the branches and stem of *Eucalyptus* trees planted along roadsides

Specific leaf area (SLA)

Specific leaf area is the one-sided area of a fresh leaf divided by its oven-dry mass, expressed in $\text{m}^2 \text{kg}^{-1}$ or (correspondingly) $\text{mm}^2 \text{mg}^{-1}$. SLA of a species in many cases has a good positive correlation with its potential relative growth rate. Lower values tend to correspond with relatively high investments in leaf defenses and long leaf lifespan. Species in resource-rich environments tend to have larger SLA than those in environments with resource stress, although some shade-tolerant woodland under-storey species are known to have remarkably large SLA as well (Cornelissen et al. 2003).

Five leaf samples were taken from five individual trees of each species. The leaves were oven-dried at 70 degree Celsius for three days. Leaf area and leaf dry mass measurement were done according to (Cornelissen et al. 2003).

Prediction of species composition based on logistic regression

Logistic regression using a generalized linear model (GLM in R v.2.15.2 software; R Development Core Team 2012) was performed to predict the species composition of plant communities from plant traits; that is, the probability that a given species will appear in a given community on the basis of its traits. The response variable was the occurrence probability of species, and the predictor variables were maximum height, shade tolerance, animal palatability and SLA of species. The best fit model with the smallest Akaike information criterion (AIC; Akaike 1974) value was selected by a backward stepwise algorithm. A smaller AIC value represents a better fit of the model to the observed occurrence data. The result of logistic regression was represented as:

$$Y = \frac{1}{1 + e^{-(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_n X_n)}} \quad \text{Eq.4}$$

where Y is the predicted probability of occurrence of species, X_n are the predictor variables (four traits), and β_n are regression coefficients. Delta AIC is the difference in AIC between the best fit model and the model without the specific variable, and it represents the importance of the focal variable.

Result

We observed 108 transect lines (n=108) in total.

Plant trait measurements

Maximum height was recorded for 151 species. Maximum heights of dominant tree species vary from 4.46 to 15 meter. Minimum light intensity was measured for 133 species. The minimum light intensity of species ranges between 27.44 ± 9.29 (mean \pm SD). Frequency distributions of minimum light intensity for the most important characteristic species (20 % occurring species) in each community type are shown as below.

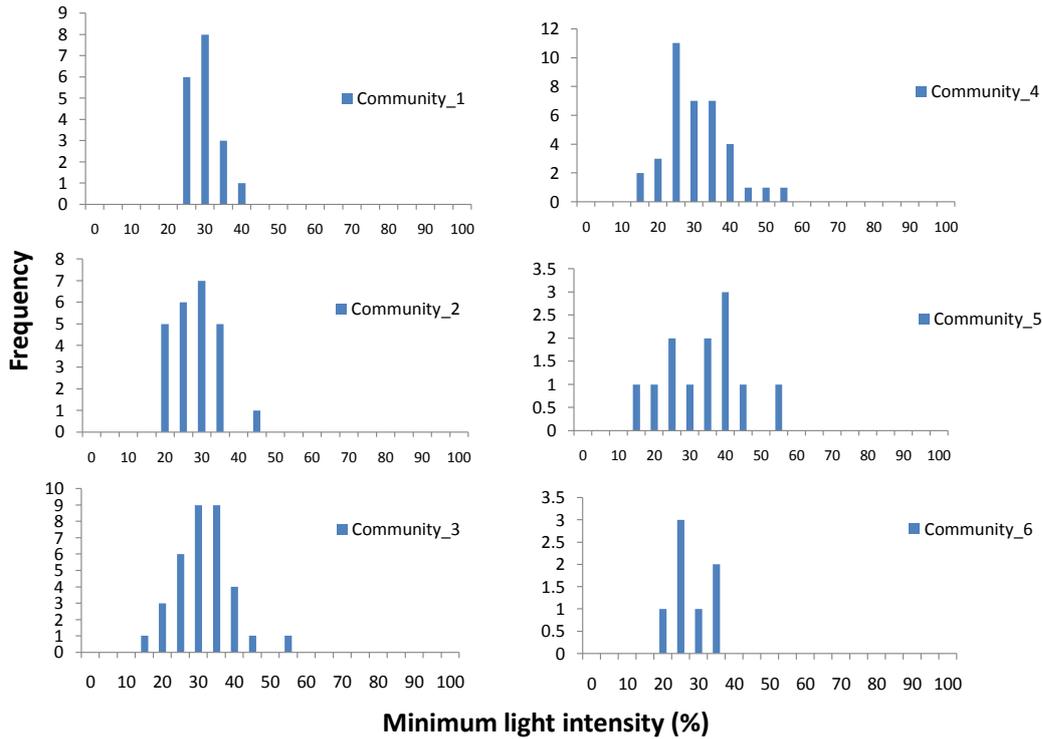


Fig.6 Frequency distribution of minimum light intensity for the most important characteristic species (20 % occurring species) in each community type

By likelihood gradient method, we obtained animal palatability values for 44 major species. Specific leaf area was recorded for 108 species. Mean SLA value of dry zone species was $10.89 \pm 4.93 \text{ mm}^2 \text{ mg}^{-1}$ (Mean \pm SD, $n= 108$) and ranged from 3.54 to $33.62 \text{ mm}^2 \text{ mg}^{-1}$. The mean value and range of SLA of dry zone species in Myanmar were observed corresponding with those in tropical deciduous forests (Chaturvedi et al. 2011).

Weighted-average community-trait values

Weighted-average values were calculated for community traits as in Eq 5.

$$Y_i = \frac{\sum_{n=1}^i x \times p}{\sum_{n=1}^i p} \quad \text{Eq.5}$$

Where y_i is weighted-average community-trait value, x is species trait value; and p is species occurrence probability (number of presence plots for a species in a community divided by total number of plots in that community)

Table 4 Weighted-average community trait values

Community Type	Maximum height (m)	Shade tolerance	Animal palatability	SLA (mm ² mg ⁻¹)
1	7.07	-1.44	0.34	8.52
2	6.90	-1.43	0.36	9.59
3	6.53	-1.46	0.28	8.62
4	6.50	-1.48	0.60	9.34
5	7.09	-1.50	0.07	8.29
6	8.57	-1.40	0.86	9.96

Prediction of species composition by plant trait analysis

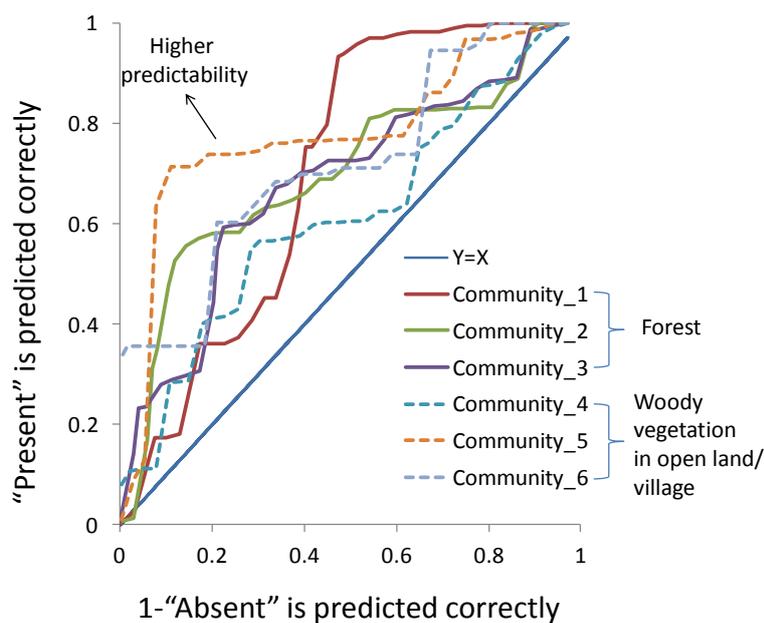
We had 36 species with complete plant traits and used them for logistic regression analysis (Appendix 1). The prediction models based on plant traits were significant for all community types (Table 5). Maximum height was an important trait and significantly showed positive correlation with species occurrence probability in all plant communities. Shade tolerance was the key in forest communities with higher plant diversity (Type 1 and 2) and in plant community in rural residential areas (Type 6). For three communities in open landscape; community 3, 4 and 5, shade tolerance showed negative correlation suggesting the relative light demanding nature of species in open landscape. In rural residential area, the domestic livestock are prevented from grazing in the human resettlement. Generally animal palatability showed negative correlation with the species occurrence probability in plant communities 1, 2, 3 and 5. We observed the vegetation inside and outside of agricultural hedgerow and that may explain the non –significant result of animal palatability in the agricultural community. SLA had negative correlation with the species occurrence in community 1, 2, 3 and 5 and positive correlation in agricultural hedgerow community 5. No significant correlation is shown for the rural residential area.

Tall, shade tolerance and animal unpalatable species have more abundance in the conserved remnant forest communities (Community 1 and 2). Shade tolerance was less important in open landscape and tall, light demanding and unpalatable species grew well in the community 3 and 5. In the arid environment of dry zone, the plant species with smaller SLA generally had higher abundance.

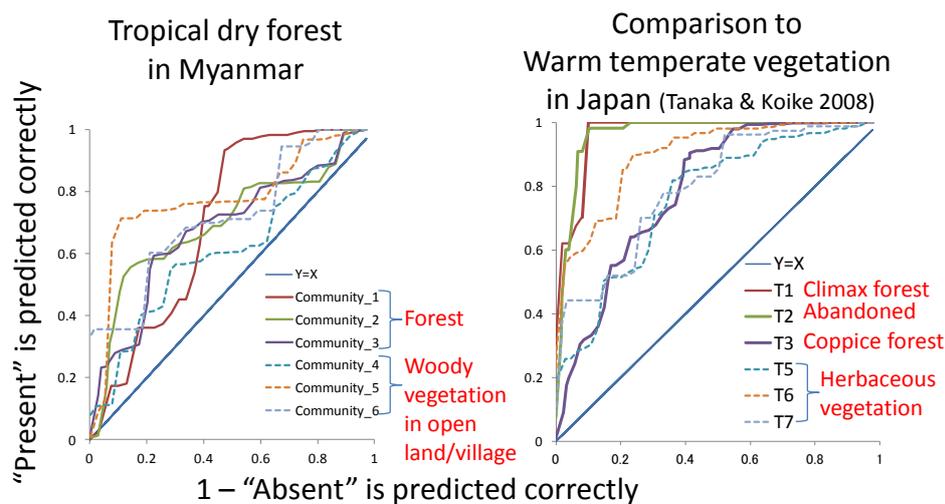
Table 5 the best fit model to predict the species abundance for each type of community

Model	Community type description	Significance of model parameters							
		Max. height	Δ AIC	Shade tolerance	Δ AIC	Animal palatability	Δ AIC	SLA ($\text{mm}^2 \text{mg}^{-1}$)	Δ AIC
1	Semi-indaing forest with <i>Shorea</i>	+0.08***	11.22	+1.65***	12.98	-0.24**	10.79	-0.08**	9.2
2	Than-Dahat forest	+0.04***	25	+0.1***	51	-0.35***	234.9	-0.07***	105.6
3	Shar-Dahat forest	+0.08***	94.3	-0.89***	36.1	-0.12***	25.2	-0.02*	2.5
4	Agricultural hedgerow community	+0.05***	32.7	-0.87***	35.9	NS	-	+0.02***	8.8
5	<i>Prosopis</i> species dominated community	+0.12***	79.79	-2.72***	122.12	-0.16***	16.15	-0.04***	14.34
6	Plant community in rural residential area	+0.20***	28.7	+3.09***	24.37	0.23**	4.24	Ns	

Evaluation of model predictability



27



30

Fig 7 Model predictability by ROC curves (a) to evaluate the predictability of the models and (b) to compare the predictability of the models for the tropical dry zone of Myanmar with those of warm temperate vegetation in Japan.

We can observe that there is no such difference between the models for the conserved remnant forests and those of other vegetation (Fig 7a). Predictability was the lowest for the agricultural hedgerow community (type 4) where human disturbance is relatively higher than

in other vegetation. When compared with vegetation of warm temperate region in Japan (Fig 7b), we could suggest the model predictability of tropical dry vegetation in Myanmar were relatively lower than those of warm temperate vegetation in Japan. Open forests (type 1, 2, 3 in Myanmar and T3 coppice stand in Japan) were observed to have similar predictability both in dry tropical and temperate regions. We suggested that higher predictability can be observed for the vegetation with less human activity.

Discussion

Evaluation of potential invasion risk of existing alien species

We can generally predict the probability that a locally new alien plant will invade into each type of community by the prediction model based on plant traits although the model predictability was relatively low. Shade tolerance followed by maximum height is the most important trait to predict the potential invasion risk of locally new alien species. Animal palatability and Specific Leaf Area also play role for the survival of plant species in the central dry zone. Tall species with high shade tolerance and animal unpalatability traits will be likely to impose high potential invasion risk on forest communities. Tall and light demanding species with animal unpalatability traits will be likely to become invasive in open forest and agricultural landscapes.

We can generally evaluate the future invasive potential of the existing alien species based on our model results. Animals do not prefer to eat *Prosopis* species (leaf and stem) (animal palatability value -0.7), and invasion risk is quite high in agricultural areas, whereas *Prosopis* species may have lower potential to invade forest communities due to its less shade tolerance. *Leucaena leucocephala* was preferred by animals (animal palatability value -1.1), and thus it may not be able to spread in woodlands of agricultural areas in tropical dry forest zone. *Eucalyptus* species was not included in our analysis, yet we have observed that *Eucalyptus* species was much eaten by domestic sheep and they may not become invasive in highly grazed agricultural area. *Eucalyptus* species was observed to have good natural regeneration around water reservoir area probably due to high soil moisture. *Acacia nilotica* was a good fodder species (animal palatability -2.7) and they may be easily controlled by animal farming in the agricultural landscape. One of the potential invasive species in agricultural areas is *Acacia senegal* (animal palatability -11.00) which are totally avoided by domestic animals due to its tannin content and crooked spine. *Lantana camara*, thicket-forming woody shrub of tropical American origin which is generally widespread invasive across the tropical and subtropical regions (Richardson, Rejmánek 2011)

are relatively less unpalatable (0.55) but have light demanding traits. They may remain as ruderal species spreading across open agricultural lands but may not become serious invaders in the forest communities.

Prediction models by plant traits were significant for all community types. Although maximum height and shade tolerance were the keys in conserved old-growth forests as in various forests of the world (Koike 2001), animal palatability was found to be a key trait in human-dominated landscape of tropical dry forest zone in Myanmar. In the tropical dry zone of Myanmar, plant species with its leaf favored by grazing are disadvantaged. The species composition of plant communities are mainly dominated by unpalatable species which may be the evolutionary traits of plant species in the human dominated environment (Diaz et al. 2007). Animal palatability was not significant in agricultural hedgerow vegetation where people prevent animal grazing inside the agricultural lands. Predictability was generally low in open forests of tropical dry zone. Agricultural hedgerow with high human disturbance had lowest predictability. The ecological risk by potential invasive species may become higher if we continue to introduce unpalatable species such as *Prosopis* species and *Acacia Senegal*. We may use tall and unpalatable tree species for restoration purpose, however, such species has a high risk of biological invasion in the dry zone.

Conclusion

Prediction of potential invasion risks of alien species was possible; however, predictability was lower than those in closed forests in temperate areas. Key traits in tropical dry zone in Myanmar were quite different from those of temperate moist regions. Animal palatability was an important trait in central dry zone of Myanmar. Risk assessment system as WRA (weed risk assessment) in Myanmar needs to consider such difference. We need to continue to identify key-traits (e.g. nutrient uptake: N/P ratio) for tropical dry zone to improve species risk assessment system.

Appendix 1 Complete trait measurement of 36 species collected in the study area

Scientific name	Local name (Myanmar name)	Maximum height (m)	Minimum light intensity (%)	Animal palatability	SLA (mm ² mg ⁻¹)
<i>Albizia lebbek</i>	Anya-kokko	15.03	23.41	-1.15	15.40
<i>Abutilon indicum</i>	Bauk-khway	1.25	40.22	-0.02	17.51
<i>Leucaena leucocephala</i>	Bawzagaing	11.17	18.79	1.18	10.41
<i>Hiptage benghalensis</i>	Bein-new	4.47	30.38	-0.75	5.18
<i>Tectona hamiltoniana</i>	Dahat	9.12	24.82	-0.44	11.03
<i>Cleome spp</i>	Gant-galar	0.33	44.99	-1.19	23.48
<i>Capparis sepiaria</i>	Hnget-kway-sa	3.33	38.66	0.77	5.06
<i>Shorea siamensis</i>	Ingyin	10.80	27.06	1.59	9.76
<i>Prosopis species</i>	Kandaya	5.98	33.81	-0.90	8.17
<i>Carissa spinarum</i>	Khanzat	2.74	31.19	1.59	3.54
<i>Grewia hirsuta</i>	Khwe-tayaw	1.99	24.13	-0.90	15.78
<i>Celosia allmanoides</i>	Kyet-mauk	0.50	27.68	0.56	15.00
<i>Vitex limonifolia</i>	Kyungauk-nwe	6.68	29.24	0.44	10.33
<i>Barleria cristata</i>	Leik-tha-ywe-pya	1.08	26.38	0.23	17.50
<i>Azima sarmentosa</i>	Moenan	2.55	26.28	0.92	6.82
<i>Combretum acuminatum</i>	Nabu	2.67	24.67	-0.25	12.68
Nwa-sa-nyoke	Nwa-sa-nyoke	0.40	26.33	7.59	5.00
<i>Ziziphus oenoplia</i>	Paungbet	4.68	19.72	0.54	10.03

<i>Senna auriculata</i>	Peik-thingat	3.71	33.06	-0.01	9.63
<i>Millettia multiflora</i>	Pingan	6.15	25.03	-0.02	5.55
<i>Rhus paniculata</i>	Pyizin	4.59	28.55	-0.92	9.22
<i>Lantana aculeate</i>	Seinnaban	2.39	42.57	0.01	11.21
(syn. <i>L. camara</i>)					
<i>Acacia catechu</i>	Sha	8.93	32.28	0.00	3.70
<i>Acacia nilotica</i>	Subyu	12.47	38.74	2.60	6.19
<i>Acacia pennata</i>	Suyit	5.77	19.40	1.47	7.11
<i>Azadirachta indica</i>	Tama	8.29	24.67	2.16	11.40
<i>Acacia leucocephloea</i>	Tanaung	12.00	36.27	0.45	4.94
<i>Dalbergia paniculata</i>	Tapauk	9.59	29.54	0.00	9.43
<i>Ehretia laevis</i>	Tawkunkauk	2.99	27.95	2.57	6.02
<i>Phyllanthus species</i>	Taw-zibyu	6.73	29.21	1.48	6.58
<i>Grewia tiliifolia</i>	Tayaw	4.73	27.19	0.77	7.30
<i>Terminalia oliveri</i>	Than	10.17	22.66	0.91	7.15
<i>Heterophragma sulfureum</i>	Thit-linda	6.08	35.07	-1.46	3.96
<i>Balanites aegyptiaca</i>	Thit-palwe	5.79	34.77	1.61	7.07
<i>Flueggea virosa</i>	Ye-chinya	2.78	24.19	-0.01	15.00
<i>Gardenia obtusifolia</i>	Yingat-gale	4.87	29.30	-0.32	9.10

References

- Akaike H (1974) A new look at the statistical model identification. *Automatic Control, IEEE Transactions on* 19:716-723
- Chaturvedi RK, Raghubanshi AS, Singh JS (2011) Plant functional traits with particular reference to tropical deciduous forests: A review. *Journal of Biosciences* 36:963-981
- Cornelissen JHC, Lavorel S, Garnier E, et al. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51:335-380
- Dansereau P (1951) Description and Recording of Vegetation Upon a Structural Basis. *Ecology* 32:172-229
- Davis JH (1964) *The Forests of Burma*. New York Botanical Garden
- Diaz S, Lavorel S, McIntyre S, et al. (2007) Plant trait responses to grazing – a global synthesis. *Global Change Biology* 13:313-341
- Khurana E, Singh JS (2001) Ecology of seed and seedling growth for conservation and restoration of tropical dry forest : a review. *Environmental Conservation* 28:39-52
- Koike F (2001) Plant traits as predictors of woody species dominance in climax forest communities. *Journal of Vegetation Science* 12:327-336
- Koike F (2013) Minna de GIS: Spatial data analysis system for education, research and environmental assessment by citizens., URL: <http://www13.ocn.ne.jp/~minnagis/>
- Koike F (2009) Sora to mori: URL: <http://vege1.kan.ynu.ac.jp/soratomori/index.html>
- Laughlin DC, Laughlin DE (2013) Advances in modeling trait-based plant community assembly. *Trends in Plant Science* 18:584-593
- Oo MZ, Shin T, Oosumi Y, et al. (2006) Biomass of planted forests and biotic climax of shrub and grass communities in the central dry zone of Myanmar. *Bulletin-forestry and forest*

products research institute ibaraki 5:271

R Development Core Team (2012) A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria., URL: [http:// http://www.r-project.org/](http://www.r-project.org/)

Richardson DM, Rejmánek M (2011) Trees and shrubs as invasive alien species – a global review. *Diversity and Distributions* 17:788-809

Stamp LD (1924) *The Vegetation of Burma: From an Ecological Standpoint*. University of Rangoon

Valladares F, Niinemets U (2008) Shade Tolerance, a Key Plant Feature of Complex Nature and Consequences. *Annual Review of Ecology Evolution and Systematics*. Annual Reviews, Palo Alto, pp. 237-257

Westoby M, Wright IJ (2006) Land-plant ecology on the basis of functional traits. *Trends in Ecology & Evolution* 21:261-268

Chapter 4: General discussion

Both abiotic (climatic and topographic factors) and biotic environments (native plant community) worked together to prevent the invasion of alien species into a particular area. We observed the distribution range of relatively unpalatable *Prosopis* species (of which only fruit pods are eaten by animals) have been expanding across the dry zone area. Although large-scale geographic range expansion (≥ 10 km) by *Prosopis* species has already been completed in the study area of the dry zone in Myanmar, local invasion at small scale is ongoing. The ecological degradation as a consequence of *Prosopis* invasion will be likely to increase if we cannot control the expansion of *Prosopis* species across the dry zone. Propagule pressure is one of the important effects on community invasibility and effective invasive control efforts will likely to benefit from measures to minimize the spread of propagules. We recommend that land managers avoid new plantings. As *Prosopis* seeds spread in the dung of livestock that consume *Prosopis* pods, feeding *Prosopis*-free fodder before moving livestock from highly infested areas to other areas may reduce new infestations. As animal farming is a common livelihood in human-dominated landscape of tropical dry forest zone in Myanmar, we need to develop a systematic pasture use to maintain sustainable dry forest ecosystem while ensuring the livelihood security for the local community.

The biological traits of native plant communities formed biotic resistance interacting together with local disturbance. Tall, shade tolerance and animal unpalatable species were found to have more abundance in the conserved remnant forest communities. Shade tolerance was less important in open agricultural landscape and tall, light demanding and unpalatable species grew better in open landscape. In the arid environment of dry zone, the plant species with smaller SLA had higher abundance to adapt with the stressful environment. Only the new alien species which can outperform the native species in terms of these biological traits in a given environment will have an opportunity to establish, naturalized and likely to become invasive.

Prosopis species may not easily invade to the natural forest communities due to its less shade tolerance however the likely degradation of forests in future may cause the expansion of *Prosopis* species into the forest landscape due to the increased light availability to the forest floor. Although *Prosopis* species are assumed to be useful for the substantial living of local people, we should not ignore their potential invasion risk which can have irreversible impact on sustainability of ecosystem services and local biodiversity.

The ecological risk by potential invasive species will become higher if we continue

to introduce unpalatable species such as *Prosopis* species and *Acacia Senegal*. We may use tall and unpalatable tree species for restoration purpose, however, such species has high risk of biological invasion in the dry zone.

This study was done as the fundamental step of invasive alien species research in Myanmar and we should do more research in other ecosystems within the country. We need to formulate a risk assessment system and the invasive potential of new alien species should be assessed before introducing to Myanmar. By considering environmental tolerances as pre-filtering in the native region, a risk assessment system based on plant traits will become available with our model.