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

Thiri Aung*, Fumito Koike

Graduate School of Environment and Information Sciences, Yokohama National University, 79-7 Tokiwadai, Hodogaya-ku, Yokohama 240-8501, Japan

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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.

1. 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

* Corresponding author.
E-mail addresses: thiriaungmyint@gmail.com (T. Aung), koikef@ynu.ac.jp (F. Koike).

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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 *P. 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 (Pasiecznik 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 (Pasiecznik 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 (Pasiecznik 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.

2. Materials and methods

2.1. 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).

2.2. 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 and Supplementary KML file). We used Google Earth 2011 and Forest Department 1:50,000 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.

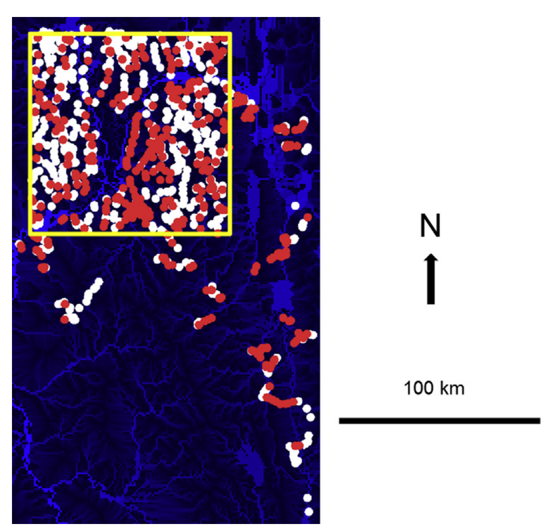

Fig. 1. *Prosopis* presence (red circles) and absence (open circles) in the vegetation survey plots in the central dry zone of Myanmar. The square marks the intensively surveyed 100 km × 100 km area. Background catchment area shows rivers and flood plains as brighter blue, and mountains and ridges as a dark color. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

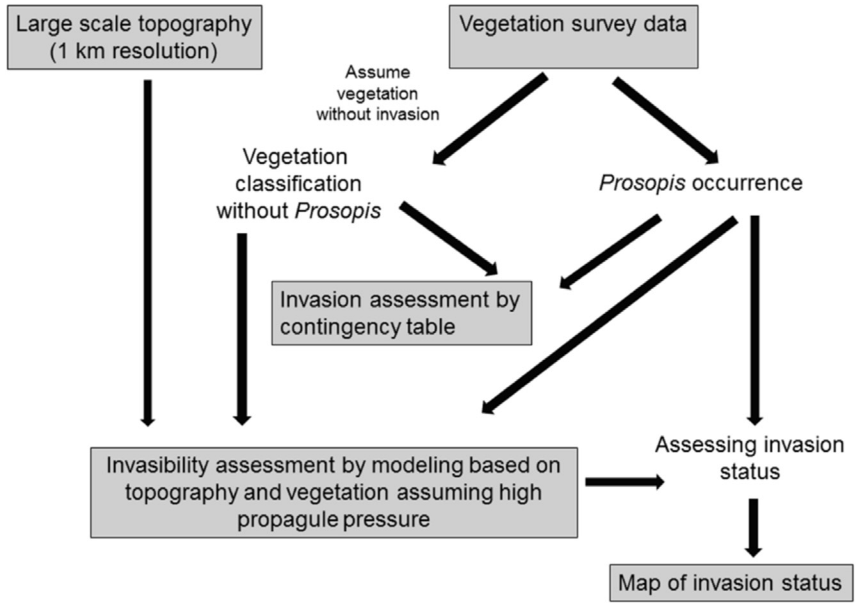

Fig. 2. Study approach for habitat invasibility assessment and invasion status identification.

2.3. 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. ΔAIC, 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:

$$Y = \frac{1}{1 + e^{-(\beta_0+\beta_1 X_1+\beta_2 X_2+\ldots+\beta_n X_n+\alpha_1+\alpha_2)}} \qquad (1)$$

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.

2.4. 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 × 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 jth circle, S_j, was evaluated as:

$$S_j = 1 - \prod_{i=1}^{k} (1 - Y_i) \tag{2}$$

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 ith 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).

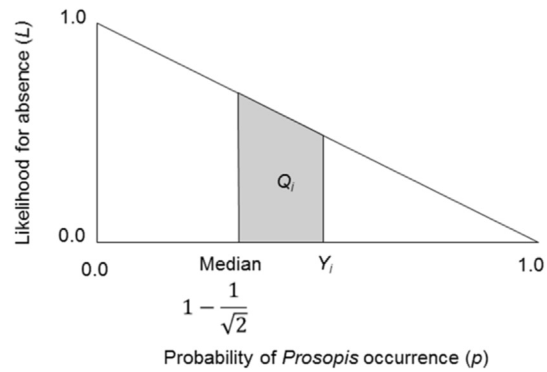

Fig. 3. The approach used to detect the propagule deficit. The likelihood distribution (triangular area below $L = 1 - p$ in this case) was of "absence" data in the vegetation survey. If the potential occurrence (Y_i) is larger than the median the plot is suitable for *Prosopis* and a propagule deficit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

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):

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

where Y_i is the estimated value for p according to the invasibility

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 *Prosopis* due to environment or biological community	Predicted invasibility < 0.1 as arithmetic mean of sites in the focal region
Suitable but *Prosopis* not yet arrived (Zone 1)	No *Prosopis* population is found in the suitable habitats	Not Zone 0 AND *Prosopis* is absent in all sites studied AND Predicted probability that *Prosopis* 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 *Prosopis* population is present	Not Zone 0 AND *Prosopis* occurs in at least one site studied AND At sites lacking *Prosopis*, (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)	*Prosopis* exists in more than 50% of potential habitats	Not Zone 0 AND Number of *Prosopis* present sites > expected number of present sites/2, at the significance level of 0.05

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.

3. Results

3.1. 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-Than 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-Than 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%).

3.2. 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-Than 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.

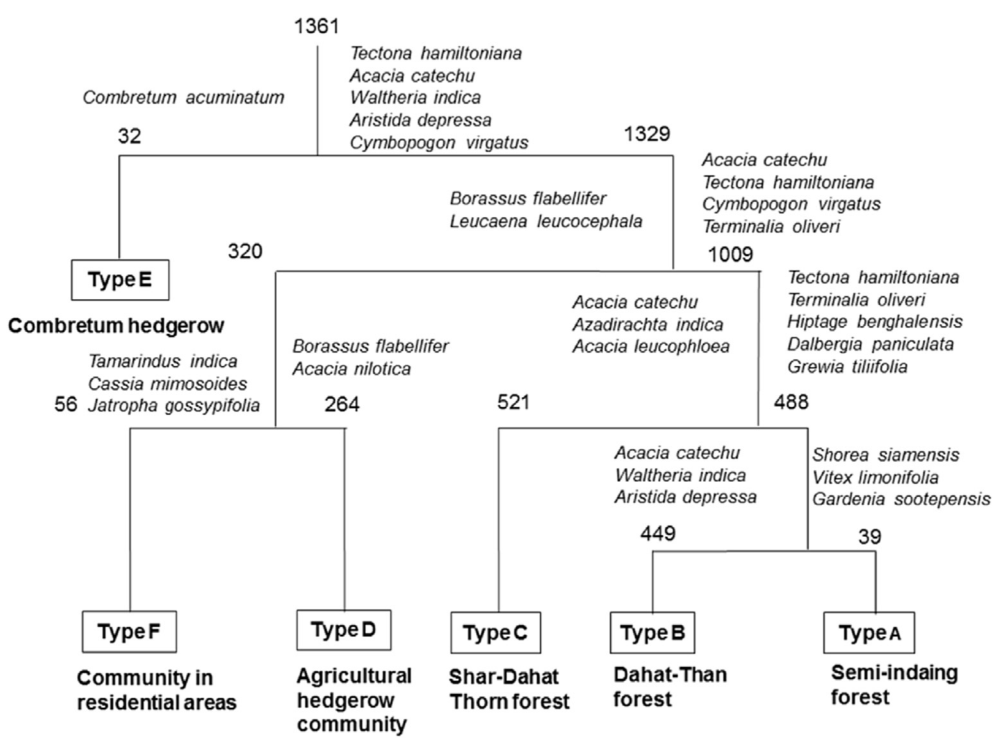

Fig. 4. Dendrogram showing the TWINSPAN classification of plant communities (without *Prosopis* data) with their indicator species. Significant differences between plant communities were verified by a chi-squared test at the 99% confidence level. The community division was stopped after the fifth level 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[a]	Total plots	Average number of species	Frequency of *Prosopis* (%)	Community description, management, and human use
Type A	Semi-Indaing forest	39	10.33	2.56	Remnant forest areas, conservation areas.
Type B	Dahat-Than forest (*Tectona hamiltoniana–Terminalia oliveri* forest)	449	10.19	6.46	Remnant forest areas, coppice tree patches.
Type C	Shar-Dahat Thorn forest (*Acacia catechu–Tectona hamiltoniana* 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	*Combretum* 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.

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

Table 3
The predictor variables and regression parameters of the best-fit logistic regression model (Eq. (1)). ΔAIC 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	ΔAIC
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	
Prosopis 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.

3.3. 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.

4. 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.

4.1. Habitat invasibility assessment model

Removing *Prosopis* data from the vegetation classification and

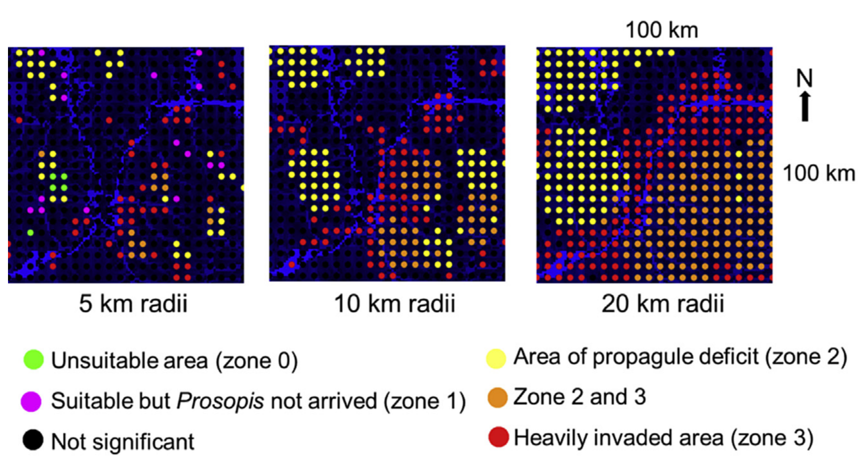

Fig. 5. Invasion status of *Prosopis* at our study area in the central dry zone of Myanmar. Unsuitable area for *Prosopis* (zone 0), areas lacking *Prosopis* in suitable habitats (zone 1), areas of *Prosopis* propagule deficit (zone 2), and heavily invaded areas (zone 3) were detected at spatial scales 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. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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 Chytry 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 (Pasiecznik 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).

4.2. 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.

4.3. Management recommendations

Spatial zoning of invasion status based on a habitat invasibility assessment model is useful for planning the management of invasive species (Bigsby 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 et al., 2012). 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*.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jaridenv.2015.04.016.

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