

Modeling Potential Range Expansion of the Invasive Shrub *Leucaena leucocephala* in the Hengchun Peninsula, Taiwan

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Prediction of invasive species distributions from survey data is widely recognized as a significant component of forest management and conservation planning. *Leucaena leucocephala* is the most aggressive invasive shrub and tree in the Hengchun peninsula in southern Taiwan. We analyzed geo-referenced data to identify potential variables of invasion and to predict likelihood of further invasion using boosted regression trees. Our results, which classified 92% of the cells correctly with regard to species presence and absence, indicated probability of invasion is correlated with climatic conditions (temperature and precipitation), landscape features (altitude; slope ratio and aspect; percentages of natural or secondary forest, agriculture land, developed area, and water bodies; and distances to the nearest forest edge and river), and anthropogenic factors (length of forest edge, and distances to the nearest road and agriculture land). The most influential variables are average annual temperature, altitude, precipitation, and slope. Continued range expansion by *L. leucocephala* is most likely to proceed (1) from the eastern and western portions toward the central portion of Hengchun township and (2) throughout the southern and toward the eastern portions of Manjhou township. Our model should provide useful information to aid forest managers in the development of long term monitoring and control strategies for *L. leucocephala*, in the early detection and eradication of newly established invasions, and also a framework for the integration and analysis of new presence and absence field data as they become available.

Nomenclature: White leadtree, white popinac, and jumbay, *Leucaena leucocephala* (Lam.) de Wit.

Key words: Biological invasion, boosted regression trees, forest management, invasive species, species distribution models.

Increased global connectivity of the human population has amplified the frequency and effect of biological invasions (Crowl et al. 2008). Land use and climate change interact with human transportation networks to expedite the spread of invasive species (Simberloff 2000; With 2002). In forest ecosystems, invasive plants can alter native species richness and abundance (Merriam and Feil 2002), nutrient cycling (Ashton et al. 2005), fire regimes (Brooks et al. 2004), geomorphology and physical structure (Brown et al. 2006), and drainage patterns and water flow

(Stromberg et al. 2007). Considerable economic costs often are associated with these ecological consequences (Pimentel 2005), and management approaches that focus on early detection and rapid eradication can provide substantial ecological and economic benefits (Gan et al. 2009). Indeed, the urgency of anticipating and mitigating the impacts of introduced plant species has re-emphasized the need for invasion ecology to progress from a reactive to a proactive science (Lodge et al. 2006), and the prediction of species distributions from survey data has been recognized as a significant component of conservation planning (Austin 2002). Studies involving both species distribution modeling and ecological niche modeling have increased exponentially in recent years (Lobo et al. 2010), and a variety of methodologies are being employed. These include statistical models such as generalized linear models (Wang and Grant 2012; Wang et al. 2012) and generalized additive models (Owens et al. 2013; Suárez-Seoane et al. 2002), machine learning models such as CLIMEX (Pattison and Mack 2008), GARP (Jones et al. 2010), and Maxent (Phillips and Dudík 2008), as well as a method, boosted regression tree, which draws on insights and techniques

DOI: 10.1614/IPSM-D-13-00010.1

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Management Implications

Leucaena leucocephala continues to expand its ranges in the southern Taiwan, and reliable prediction of habitats at risk is needed urgently. We drew upon extensive geo-referenced datasets to develop an invasion distribution model predicting possible range expansion of *L. leucocephala* in the Hengchun peninsula, Taiwan. Our analyses suggest that continued range expansion of *L. leucocephala*. However, the opportunity exists for reducing the likelihood of invasions via increased monitoring and early control efforts focused on low-elevation lands with low slope ratios that are close to roads, water, and/or forest edges. Areas surrounding agricultural and developed areas also should be targeted for prompt inspection and potential control measures. The complementarity between controlling and preventing plant invasions suggests that coordinated efforts to enhance ecosystem health would be more cost effective. More efforts should be directed toward educating residents in the Hengchun peninsula with the goal of engaging them in the prevention of *L. leucocephala* invasions and the restoration of infested areas. Our model should provide useful information to aid forest managers in the development of long term monitoring and control strategies for *L. leucocephala*, in the early detection and eradication of newly established invasions, and also in educational efforts directed toward residents in the Hengchun peninsula. Our model also provides a framework for the integration and analysis of new presence and absence field data as they become available.

from both statistical and machine learning traditions (Elith et al. 2008).

The Hengchun peninsula has one of the most diverse monsoon forests in southeast Asia. Topographical and geological features include sand, reef, and rock seashores, limestone tableland and cliffs, isolated mountains, rivers, and lakes, as well as intermontane basins (Hsu et al. 2006). The peninsula borders the subtropical zone, and supports a rich flora and a wide variety of wildlife including 15 species of mammals, 310 species of birds, 59 species of reptiles and amphibians, 21 species of freshwater fish, and 216 species of butterflies (Hsu and Agoramorthy 1999). However, like many of the monsoon forests in southeast Asia, the native deciduous hardwood forests have a long history of encroachment by agriculture, and, more recently, by urban sprawl (Chung et al. 2006). In addition, the forestlands of the Hengchun peninsula in southern Taiwan are threatened by the introduction and range expansion of invasive plant species (Lai 1995). *Leucaena leucocephala* Lam., in particular, has been an aggressive invader throughout the Hengchun peninsula in southern Taiwan (Lu et al. 2009). Because *L. leucocephala* could be utilized for forage, firewood, timber, green manure, and shade and erosion control, well into the 20th century it was promoted as a “miracle tree” in Taiwan and elsewhere in subtropics (Baumer 1992). However, with improving economic conditions in Taiwan since the 1980s, cultivation of *L. leucocephala* for fuel and fodder has decreased drastically and it has escaped from abandoned cultivation sites and

spread aggressively (Lu et al. 2009). By 2007, it had invaded almost 15% of the Hengchun peninsula (Lu et al. 2008), primarily in the western portion of the peninsula, which includes Kenting National Park, and the invasion into southern Taiwan continues (Figure 1) (Lu et al. 2013).

Leucaena leucocephala exhibits two growth forms: the shrub-like Hawaiian type was introduced in Taiwan by the Dutch in 1645 and the tree-like Salvador type was introduced in the 1970s. Both forms were quickly naturalized (Chen et al. 2011; Kuo 2007). The most common form is a free-seeding, long-lived, thornless shrub that tends to grow on steep hillsides, although in sufficient sunlight it may grow as a tree to heights of 7 to 18 m (23 to 59 ft) (Kuo 2007). Leaves of *L. leucocephala* are bipinnate with 6 to 8 pairs of pinnae bearing 11 to 23 pairs of leaflets 8 to 16 mm (0.31 to 0.63 in) long. The inflorescence is a cream-colored globular shape that produces a cluster of flat brown pods 13 to 18 mm long containing 15 to 30 seeds (Shelton and Brewbaker 1994). *Leucaena leucocephala* tolerates a wide range of precipitation regimes (from 500 to 3,500 mm annually) (Marod et al. 2012) and can withstand dry seasons of 6–8 mo (Cronk and Fuller 1998). It is a shade-intolerant species, frequently invading along riverbanks, roadsides, and forest margins, as well as in cultivated lands and waste lands (Marod et al. 2012). Following establishment, *L. leucocephala* releases an amino acid (mimosine) that is poisonous to other plants (Matthews and Brand 2004), inhibiting the growth and reproduction of native species (Wolfe and Van Bloem 2012) and decreasing species diversity (Yoshida and Oka 2000).

Development of effective measures to control the invasion of *L. leucocephala* requires reliable predictions of its potential distribution and identification of the habitats most at risk. In this paper, we analyzed several variables describing climatic conditions, landscape features, and anthropogenic factors to predict the likelihood of occurrence of *L. leucocephala* throughout the forestlands of the Hengchun peninsula in southern Taiwan. More specifically, we used boosted regression trees (Elith et al. 2008; Friedman 2002) to (1) identify potential factors influencing the likelihood of invasion, (2) quantify the relative importance of each, and (3) predict where new invasions are most likely to occur.

Materials and Methods

Study Area and Data Sources. The Hengchun peninsula covers an area of 580 km² (143,321 ac) at the southern tip of Taiwan, including the townships of Checheng, Fangshan, Hengchun, Manzhou, Mudan, and Shihzih, and is bounded on the east by the Pacific Ocean and on west by the Taiwan Strait (Figure 1). Annual precipitation is

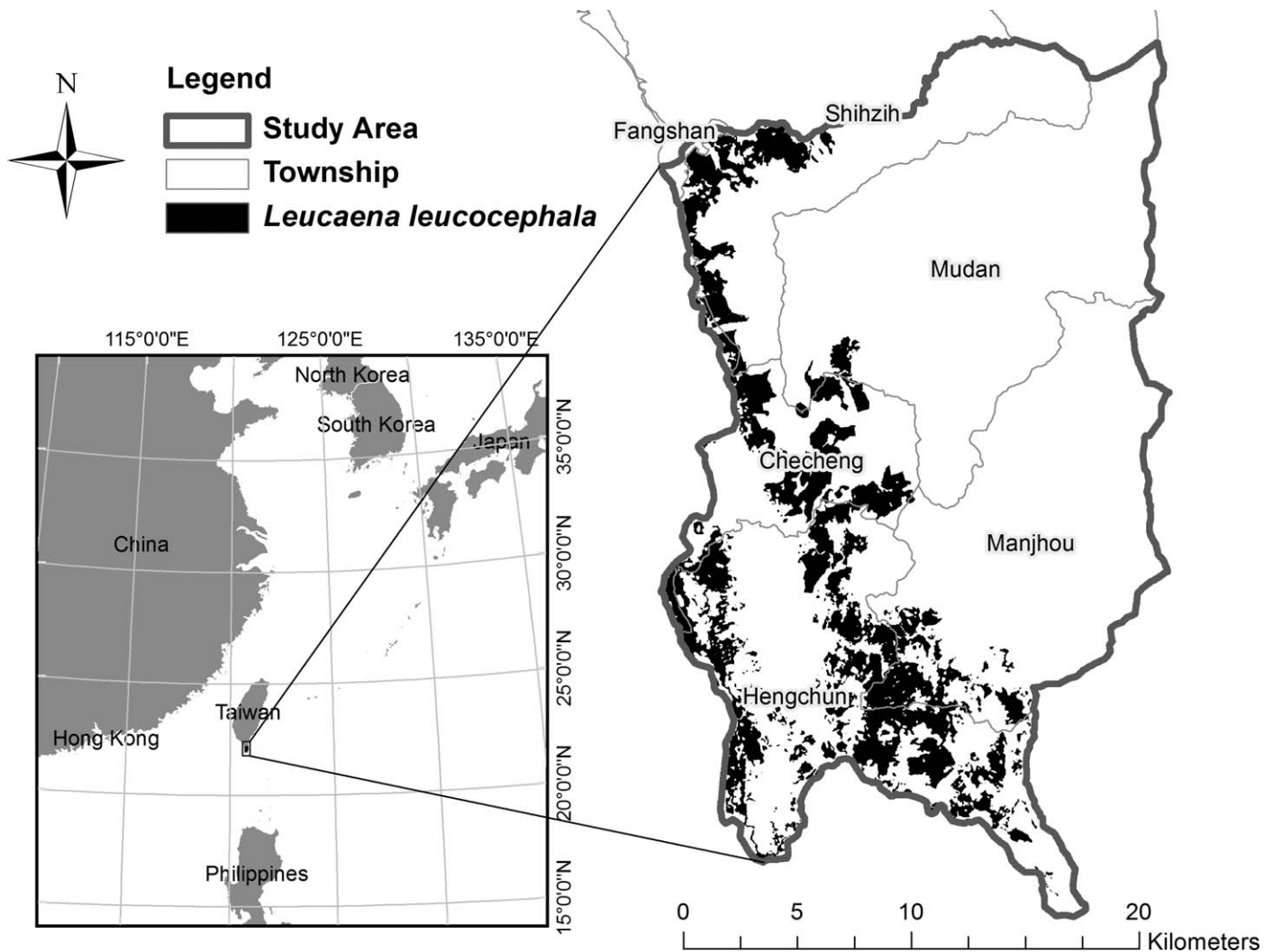


Figure 1. Study area and current distribution in 2007 of the invasive shrub *L. leucocephala* in the Hengchun peninsula, southern Taiwan.

between 2,018 and 3,437 mm with distinct wet and dry seasons. The wet season generally occurs from May to October (Lu et al. 2013), but can vary from 102 to 219 days depending on frequency of typhoons and thunderstorms during that period (Wang and Chiang 1994). During the dry season (November to April) monthly precipitation gradually decreases to < 100 mm because of the northeast monsoons. Mean annual temperature ranges from 25 to 25.5 C (77 to 78 F) on the west side of the peninsula and from 21.1 to 24.8 C on the east side (Lu et al. 2013).

We obtained geo-referenced data for the Hengchun peninsula on (1) the presence and absence of *L. leucocephala* (Lu et al. 2008), (2) climatic conditions (Liang 2004), (3) landscape features (ESRI 2009; METI and NASA 2009; NLSC 1993), and (4) anthropogenic factors (ESRI, 2009), and merged these data into a grid of 2,226 cells measuring 500 m by 500 m using ArcGIS (ESRI 2009).

Identification of Potential Factors Influencing Likelihood of Invasion. Widely recognized factors influencing the likelihood of invasion of *L. leucocephala* include: (1) climatic conditions such as average annual temperature (Banful et al. 2000; Ong et al. 1991) and annual precipitation (Ella et al. 1989; Shelton and Brewbaker 1994); (2) landscape features such as altitude (Aganga and Tshwenyane 2003; Jama et al. 1989), slope (Banda et al. 1994), aspect (Dhawan and Bhojwani 1985), and percentages of different land use and land cover (Erickson et al. 2002; Zimpfer et al. 1997); and (3) anthropogenic factors such as length of forest edge (Clinton and Pimm 2003; Meyer 2004), distance to the nearest road (Chandra Sekar et al. 2012), and distance to the nearest agriculture land (Meyer 2004) (Table 1).

Data Analysis. We analyzed relationships between the occurrence of *L. leucocephala* (in 575 cells out of a total of

Table 1. Descriptions, data sources, and descriptive statistics for the climatic conditions, landscape features, and anthropogenic factors evaluated as potential factors influencing the likelihood of invasion by *Leucaena leucocephala* into forestlands on the Hengchun peninsula, southern Taiwan.

Variable description	Mean (min, max) or frequency	Data source
Climatic conditions		
Average annual temperature (°C)	23.69 (20.04, 04.83)	Liang (2004)
Annual precipitation (mm)	2650.60 (2080.52, 3213.07)	Liang (2004)
Landscape features		
Altitude (m)	221.90 (2.35, 937.88)	METI and NASA (2009)
Slope ratio (%)	22.82 (1.44, 69.99)	ESRI (2009)
Slope aspect	E: 280 (12.58%) NE: 23 (1.03%) NW: 49 (2.20%) S: 574 (25.79%) SE: 573 (25.74%) SW: 456 (20.49%) W: 271 (12.17%)	ESRI (2009)
Percentage (%) of natural or secondary forest	56.32 (0.00, 100.00)	NLSC (1993)
Percentage (%) of forest plantation	18.84 (0.00, 100.00)	Guan and Chen (1995)
Percentage (%) of grassland	3.75 (0.00, 98.07)	NLSC (1993)
Percentage (%) of agriculture land	12.80 (0.00, 99.52)	NLSC (1993)
Percentage (%) of developed area	4.86 (0.00, 100.00)	NLSC (1993)
Percentage (%) of water body	1.55 (0.00, 99.80)	NLSC (1993)
Distance (m) to the nearest forest edge	145.25 (0.00, 2032.00)	ESRI (2009)
Distance (m) to the nearest river	166.83 (0.00, 3273.48)	ESRI (2009)
Anthropogenic factors		
Length (m) of forest edge within that cell	961.81 (0.00, 6407.50)	ESRI (2009)
Distance (m) to the nearest road	437.37 (0.00, 3273.48)	ESRI (2009)
Distance (m) to the nearest agriculture land	417.00 (0.00, 3860.40)	ESRI (2009)

996 cells) and the potential explanatory variables by aggregating the explanatory variable data associated with *L. leucocephala* presence into polygons representing a resolution of 500 m by 500 m cells in four townships (Checheng, Fangshan, Hengchun, and Shinzih). We excluded the other two townships (Manjhous and Mudan) because their datasets were dominated by absences caused by a lack of propagule pressure (Lu et al. 2013); this might have inflated our estimates of predictive performance (Olden and Jackson 2002). We conducted our analysis using boosted regression trees (also known as gradient boosting machine, gradient boosting, stochastic gradient boosting, and gradient tree boosting) which combines decision trees and a boosting algorithm with a form of logistic regression (Elith et al. 2008; Friedman 2002). For boosted regression trees, the probability (P) of species occurrence ($y = 1$) at a location with the potential explanatory variables (X) is given by $P(y = 1|X)$ and is modeled via the logit: $\text{logit } P(y = 1|X) = f(X)$. We fitted our model in R (R Development Core Team 2006 version 2.14.1) using the gbm package version 1.5–7 (Ridgeway 2006) and code provided by Elith et al. (2008). Our aim

here was to find the best combination of parameters (learning rate and tree complexity) that achieves minimum predictive error (minimum error for predictions of independent samples). The learning rate, also known as the shrinkage parameter, determines the contribution of each tree to the growing model, and the tree complexity controls whether interactions are fitted. We determined the optimal model following the recommendations of (Elith et al. 2008) by altering the learning rate and tree complexity (the number of split nodes in a tree) until the predictive deviance was minimized without over-fitting, and by limiting our choice of the final model to those that contained at least 1,000 trees. We included randomness into our model to reduce over-fitting and also to improve accuracy and speed of the model selection process (Friedman 2002). We represented randomness using a “bag fraction” that specifies the proportion of data to be selected at each step (Elith et al. 2008). We set the default bag fraction at 0.6, meaning that 60% of the data were drawn at random without replacement from the full training set at each iteration. When we obtained the optimal model, we evaluated model performance using a 10-fold cross-validation

(CV) procedure with resubstitution. For each CV trial, we randomly selected 60% of the dataset for model fitting and we used the excluded 40% for testing. We calculated the response variance explained, the area under the receiver operator characteristic curve (AUC), the overall accuracy, the omission error rate, and the commission error rate based on the aggregated CV results. We evaluated the reliability and validity of our models as fair ($0.50 < \text{AUC} \leq 0.75$), good ($0.75 < \text{AUC} \leq 0.92$), very good ($0.92 < \text{AUC} \leq 0.97$), or excellent ($0.97 < \text{AUC} \leq 1.00$) based on the value of AUC (Hosmer and Lemeshow 2000). We then used the gbm library to derive the relative influence of each potential explanatory variable in the model and constructed partial dependence plots for the most influential variables (Elith et al. 2008). Finally, we used this optimal model to calculate fitted values (probability of presence *L. leucocephala* at each sample location) in the whole Hengchun peninsula (including six townships: Checheng, Fangshan, Hengchun, Manjhou, Mudan, and Shinzih) and superimposed these probabilities of occupancy on a map of the study area using ArcMap 10 (ESRI, Redlands, CA, USA).

Results

We explored 250 combinations of tree complexity (ranging from 3 to 7) and learning rate (ranging from 0.001 to 0.05); these produced models with between 200 and 1,250 trees whose values of predictive deviance ranged from 0.597 to 670. The optimal model had a tree complexity of 5, a learning rate of 0.005, and a total of 1,250 trees. Model predictive deviance was 0.597 ± 0.031 with 89.4% of the total response variance explained. The AUC score was 0.947 ± 0.006 ("very good" ability to discriminate between species presence and absence) and the overall accuracy was 92.0%. The commission (false positive) error rate was 6.2% and the omission (false negative) error rate was 10.4%. Recursive feature elimination tests showed that 2 variables could be removed from the model before the resulting predictive deviance exceeded the initial predictive deviance of the model with all variables.

Examination of the relative contribution of the predictor variables indicated that the top six accounted for approximately 84% of the contribution in the overall model (Figure 2). Of the six most influential model variables, two were climatic conditions, three were landscape features, and one was an anthropogenic factor. Average annual temperature and annual precipitation were the first and third most influential variables, contributing 21.1% and 16.1%, respectively. Altitude, slope ratio, and percentage of natural or secondary forest were the second, fourth, and fifth most important variables, contributing 19.3%, 15.5%, and 7.11%, respectively. The most influential

anthropogenic factor, length of forest edge within the cell, had a relative contribution of only 5.0% in the overall model. Climatic conditions, landscape features, and anthropogenic factors had total contributions of 37.3%, 55.7%, and 7.0%, respectively (Figure 2).

Partial dependency plots indicated that *L. leucocephala* occurrences were associated with grid cells with an average annual temperature between 23 and 25 C (Figure 3b) and annual precipitation lower than 2,600 mm (Figure 3c). Landscape features usually included an altitude lower than 300 m (Figure 3a) and a slope ratio higher than 10% (Figure 3d), with slopes facing the northwest (Figure 3l). Occurrences were more likely in cells with greater than 20% natural or secondary forest (Figure 3e), less than 50% agricultural land (Figure 3g), less than 20% developed areas (Figure 3i), and less than 10% occupied by water bodies (Figure 3h). Distances to the nearest forest edge (Figure 3j) and to the nearest river (Figure 3k) usually were less than 300 m and greater than 1,000 m, respectively. Distances to the nearest road (Figure 3m) and to the nearest agricultural land (Figure 3n) usually were less than 800 m and less than 1,000 m, respectively, and the total length of forest edge within the cell usually was between 500 and 3,500 m (Figure 3f).

Our analyses suggest that continued range expansion by *L. leucocephala* in the Hengchun peninsula, considering its association with the landscape features mentioned in the previous paragraph, is most likely to proceed (1) from the eastern and western portions toward the central portion of Hengchun township and (2) throughout the southern and toward the eastern portions of Manjhou township (Figure 4). Estimated probabilities of potential invasion (p) were approximately 38% over the entire research area, with approximately 53% ($\approx 29,000$ ha) of the plots falling within the $0 < p \leq 0.25$ category, 15% ($\approx 8,000$ ha) the $0.25 < p \leq 0.50$ category, 6% ($\approx 3,000$ ha) within the $0.50 < p \leq 0.75$ category, and about 26% ($\approx 14,000$ ha) within the $p > 0.75$ category, the majority (56%, $\approx 31,000$ ha) of which were located in Hengchun township (Figure 4).

Discussion

The prediction of species distributions from survey data has been recognized as a significant component of conservation planning (Austin 2002). Although *L. leucocephala* is naturalized and is found in most land use types on the Hengchun peninsula (Lu et al. 2013), its distribution continues to expand into new areas with suitable habitats (Lu et al. 2013). Our predictions of the likelihood of further invasion should allow managers to focus attention on high risk and environmentally sensitive areas, and identification of the determinants of invasion should assist managers in selecting appropriate strategies for reducing or

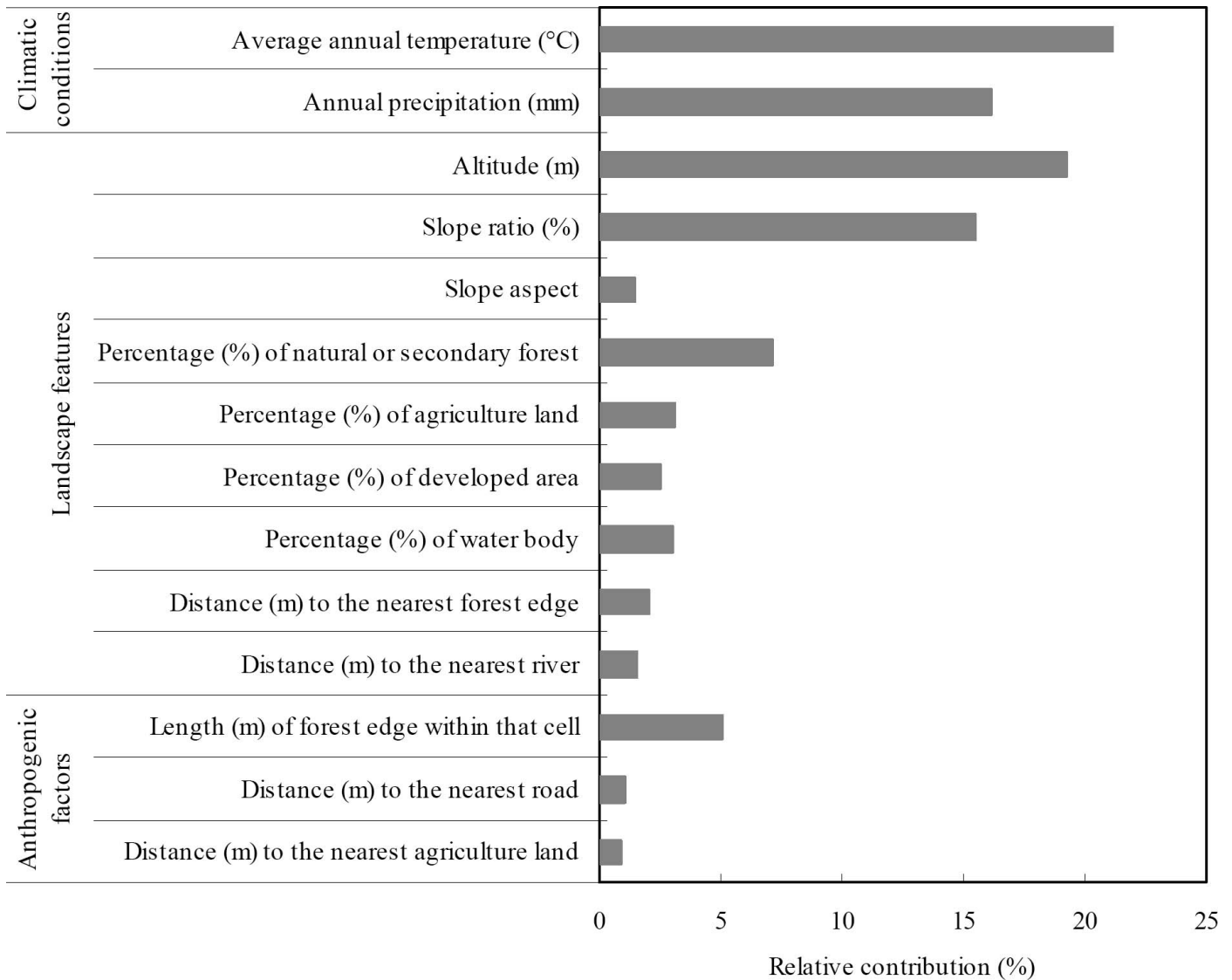


Figure 2. Relative percentage contributions of the most 14 influential variables in the model.

mitigating risk in areas where further invasions are likely (Wang et al. 2012).

Regarding determinants of invasion, not surprisingly, we found climatic conditions and landscape features to be the most influential factors. The intensity of invasion generally declined with decreasing average annual temperature and increasing annual precipitation. *Leucaena leucocephala* is a tropical species requiring warm temperatures (25 to 30 C) for optimal growth (Brewbaker et al. 1985). Although crowns may tolerate cool winter temperatures and regrow vigorously with multiple branches the following summer, heavy frosts will kill all aboveground plant parts (Isarasenee et al. 1984). We detected no invasion in our research area where the average annual temperature was below 22 C. *Leucaena leucocephala* generally thrives in well-drained areas over a broad range of precipitation regimes (from 650 to 3,000 mm yr⁻¹), but can be limited by high precipitation

in poorly-drained areas (Brewbaker et al. 1985). In Taiwan, typhoons and thunderstorms drastically increase annual precipitation in some areas (> 2,650 mm), creating poorly-drained conditions (Chang 1996). Hence, in our research area, we detected *L. leucocephala* primarily in areas with average annual precipitation between 2,000 and 2,650 mm and detected no *L. leucocephala* in areas with average annual precipitation > 2,650 mm.

Among landscape features, we found that about 96% of the land on the Hengchun peninsula currently occupied by *L. leucocephala* occurs at altitudes < 300m, about 86% occurs on south- or west-facing slopes, and about 72% occurs on lands with a slope ratio > 10%. Brewbaker et al. (1985) reported that growth of *L. leucocephala* is reduced at higher altitudes, and several studies have noted that *L. leucocephala* exhibits outstanding root mechanical properties for slope stabilization (Normaniza et al. 2008;

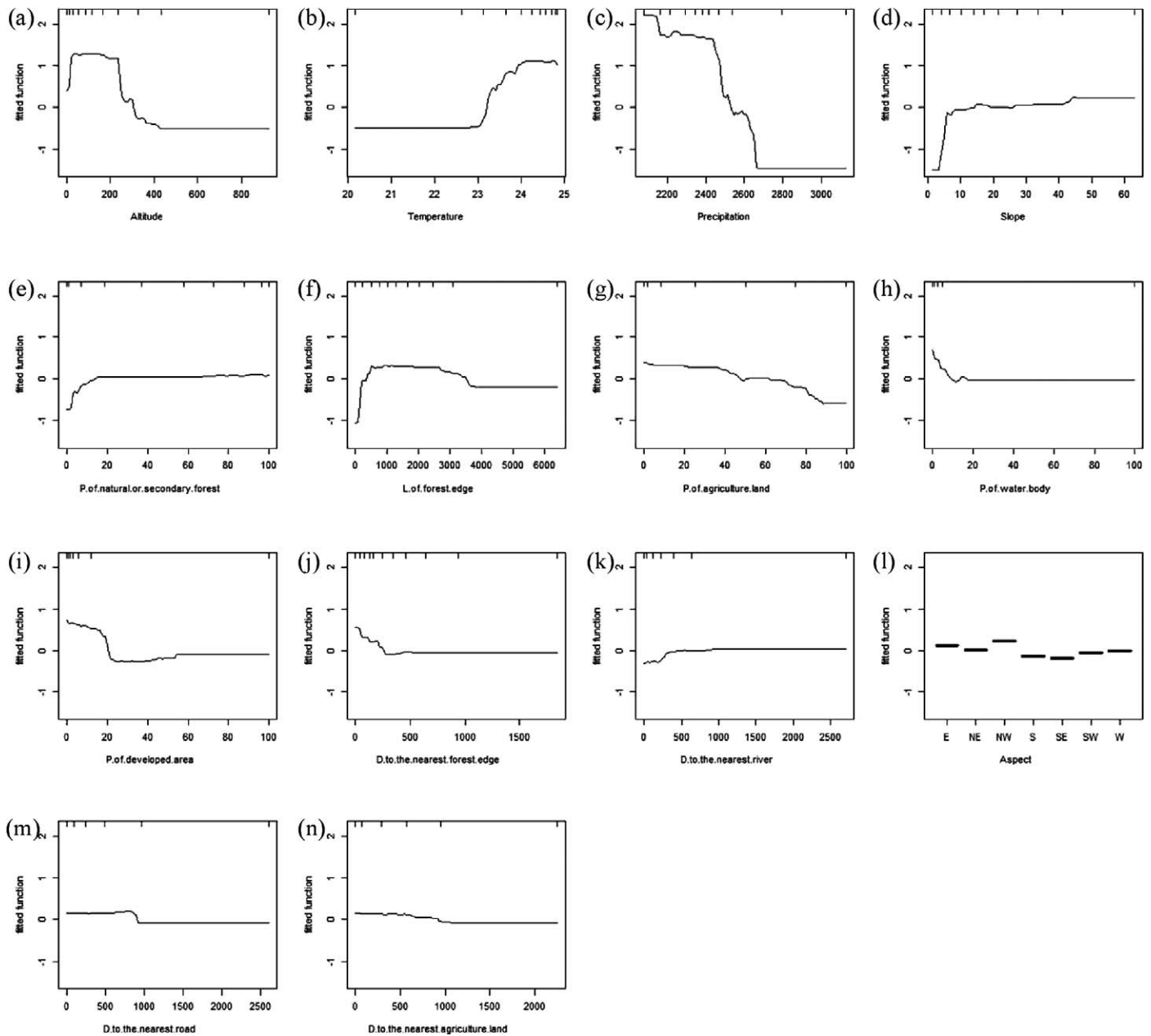


Figure 3. Partial dependence plots for the explanatory variables included in the optimal boosted regression tree models for *L. leucocephala* based on analyses of the 14 most influential variables. Hash marks at the top of each plot indicate the locations of sample sites along the range of the indicated variable. Y axis based on the logit scale is used for each plot.

Saifuddin and Osman 2012). Also, areas on the Hengchun peninsula with steep, south- and west-facing slopes are affected directly by typhoons, making them wetter, as well as warmer, than north- and east-facing slopes (Chien et al. 2008), while relatively low, flat areas are devoted primarily to agriculture or urban expansion, or are otherwise disturbed by human activities (Lu et al. 2009).

Previous studies indicate that land use and land-use history are among the most influential factors determining the distribution of invasive species (Hobbs 2000; Sax and

Brown 2000). Land use and land-use history directly affect likelihood of invasion via modification of disturbance regimes and environmental conditions (Pauchard and Alaback 2004) and by creating sources of plant propagules within the landscape (Hobbs 2000). Forest land use changes in the Philippines, similar to those occurring on the Hengchun peninsula, have created suitable habitat for *L. leucocephala*, favoring an increase in its relative abundance compared to native species (Lasco and Pulhin 2000).

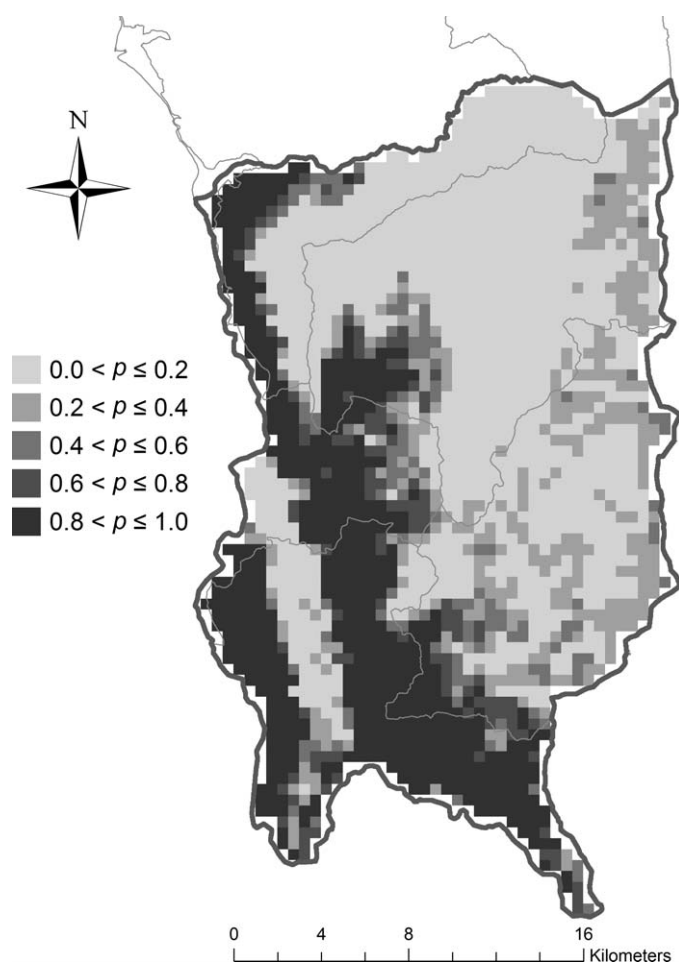


Figure 4. Estimated probability of occurrence of *L. leucocephala* in the Hengchun peninsula, southern Taiwan.

Previous studies also indicate that areas of high human activity, such as agricultural land and developed areas, serve as sources for invasions into more pristine environments (Pauchard and Alaback 2004). Propogule pressure from these sources appears to be the most influential mechanism by which land use affects the abundance and disturbance of invasive plants along roads (Pauchard and Alaback 2004). In the Hengchun peninsula, abandoned agricultural areas (included in our agricultural land category) where *L. leucocephala* was cultivated commercially are a major source of *L. leucocephala* invasions (Lu et al. 2009). As more of these abandoned agricultural lands are being transformed into developed lands, it is becoming increasingly common to see *L. leucocephala* along nearby roadsides that, in turn, are becoming new sources of invasions (Lu et al. 2009). Since *L. leucocephala* exhibits rapid vegetative growth in light gaps (Aganga and Tshwenyane 2003), it is likely that roads act as corridors for, rather than barriers to, spread (Paynter et al. 2003). Accordingly, our results indicate that *L. leucocephala* occurrence is negatively correlated with distance to the nearest road.

Our results also indicate that *L. leucocephala* is negatively correlated with distance to the nearest forest edge, and positively correlated with the length of forest edge (within a cell). Among the major concerns related to forest fragmentation is that micro-environmental changes at forest edges have led to shifts in species composition (Yates et al. 2004). These micro-environment differences between edges and interiors of forest fragments include amount of available light, wind speed, relative humidity, and temperature (Groom and Schumaker 1993). Although fragmentation and an increase in length of edge often lead to an increase in total species diversity, such increases may be caused by the increase of invasive species with low conservation value (Wang and Grant 2012; Yates et al. 2004). Indeed, growth of *L. leucocephala* along forest edges in the Hengchun peninsula likely is promoted by increased light availability, and seed dispersal likely is promoted by increased wind speeds, thus increasing habitat suitability (Green et al. 2004).

By associating areas at risk to invasion with climatic conditions, landscape features, and anthropogenic factors, our model should aid forest managers in identifying likely invasion corridors and in developing long term monitoring and control plans for slowing the range expansion of *L. leucocephala* in the Hengchun peninsula. One important caveat with respect to our projections of range expansion is that they do not explicitly include propagule pressure as a potential limiting factor. Thus, given the relatively small range of seed dispersal of *L. leucocephala*, and the fact that propagule pressure can limit the invasion process (Fukasawa et al. 2009), we may have overestimated invasion rates. Nonetheless, we feel our model offers important insights into the management of *L. leucocephala*, which threatens to continue its invasion throughout the Hengchun peninsula.

Literature Cited

- Aganga, A. A. and S. O. Tshwenyane. 2003. Lucerne, lablab, and *Leucaena leucocephala* forages: production and utilization for livestock production. *Pak. J. Nutr.* 2:46–53.
- Ashton, I. W., L. A. Hyatt, K. M. Howe, J. Gurevitch, and M. T. Lerdau. 2005. Invasive species accelerate decomposition and litter nitrogen loss in a mixed deciduous forest. *Ecol. Appl.* 15:1263–1272.
- Austin, M. P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecol. Model.* 157:101–118.
- Banda, A. Z., J. A. Maghembe, D. N. Ngugi, and V. A. Chome. 1994. Effect of intercropping maize and closely spaced *Leucaena* hedgerows on soil conservation and maize yield on a steep slope at Ntcheu, Malawi. *Agroforest. Sys.* 27:17–22.
- Banful, B., A. Dzieror, I. Ofori, and O. Hemeng. 2000. Yield of plantain alley cropped with *Leucaena leucocephala* and *Flemingia macrophylla* in Kumasi, Ghana. *Agroforest. Sys.* 49:189–199.
- Baumer, M. 1992. Trees as browse and to support animal production. Pages 1–10 in A. Speedy and P.-L. Pugliese, eds. *Expert Consultation on Legume Trees and other Fodder Trees as Protein Sources for Livestock*. Kuala Lumpur, Malaysia: FAO.

- Brewbaker, J. L., N. Hegde, E. M. Hutton, R. J. Jones, J. B. Lowry, F. Moog, and R. van den Beldt. 1985. *Leucaena* — Forage Production and Use. Hawaii: NFTA. 39 p.
- Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. *BioScience* 54:677–688.
- Brown, K. A., F. N. Scatena, and J. Gurevitch. 2006. Effects of an invasive tree on community structure and diversity in a tropical forest in Puerto Rico. *Forest Ecol. Manag.* 226:145–152.
- Chandra Sekar, K., R. Manikandan, and S. Srivastava. 2012. Invasive alien plants of Uttarakhand Himalaya. *Proc. Natl. Acad. Sci. India B* 82:375–383.
- Chang, J.-C. 1996. Natural hazards in Taiwan. *GeoJournal* 38: 251–257.
- Chen, H.-M., H.-C. Lo, C.-C. Cheng, and C.-D. Wu. 2011. Application of remote sensing on monitoring the dispersal of *Leucaena leucocephala* in Penghu area. *Q. J. Chinese Forest.* 44:133–144 [in Chinese]
- Chien, F.-C., Y.-C. Liu, and C.-S. Lee. 2008. Heavy rainfall and southwesterly flow after the leaving of typhoon Mindulle (2004) from Taiwan. *J. Meteorol. Soc. Japan Ser. II* 86:17–41.
- Chung, Y.-L., S.-T. Wu, and M.-L. Lu. 2006. Using SPOT satellite imagery to monitor the forest dynamic at landscape level on the Nanjen mountain ecological reserve in Taiwan 27th Asian conference on remote sensing. Ulaanbaatar, Mongolia: Curran.
- Clinton, N. J. and S. L. Pimm. 2003. How big is the global weed patch? *Ann. Mo. Bot. Gard.* 90:172–178.
- Cronk, Q.C.B. and J. L. Fuller. 1998. Plant invaders: the threat to natural ecosystems. *Biodivers. Conserv.* 7:267–269.
- Crowl, T. A., T. O. Crist, R. R. Parmenter, G. Belovsky, and A. E. Lugo. 2008. The spread of invasive species and infectious disease as drivers of ecosystem change. *Front. Ecol. Environ.* 6:238–246.
- Dhawan, V. and S. S. Bhojwani. 1985. In vitro vegetative propagation of *Leucaena leucocephala* (Lam.) de Wit. *Plant Cell Rep.* 4:315–318.
- Elith, J., J. R. Leathwick, and T. Hastie. 2008. A working guide to boosted regression trees. *J. Anim. Ecol.* 77:802–813.
- Ella, A., C. Jacobsen, W. W. Stür, and G. Blair. 1989. Effect of plant density and cutting frequency on the productivity of four tree legumes (*Calliandra calothyrsus*, *Sesbania grandiflora*, *Leucaena leucocephala*, *Gliricidia sepium*). *Trop. Grasslands* 23:28–34.
- Erickson, H., E. Davidson, and M. Keller. 2002. Former land-use and tree species affect nitrogen oxide emissions from a tropical dry forest. *Oecologia* 130:297–308.
- ESRI. 2009. ArcGIS. Redlands, CA, USA: Environmental Systems Research Institute.
- Friedman, J. H. 2002. Stochastic gradient boosting. *Comput. Stat. Data Anal.* 38:367–378.
- Fukasawa, K., F. Koike, N. Tanaka, and K. Otsu. 2009. Predicting future invasion of an invasive alien tree in a Japanese oceanic island by process-based statistical models using recent distribution maps. *Ecol. Res.* 24:965–975.
- Gan, J., J. H. Miller, H.-H. Wang, and J. W. Taylor. 2009. Invasion of tallow tree into southern US forests: influencing factors and implications for mitigation. *Can. J. Forest Res.* 39:1346–1356.
- Green, P., P. S. Lake, and D. O'Dowd. 2004. Resistance of island rainforest to invasion by alien plants: influence of microhabitat and herbivory on seedling performance. *Biol. Invasions* 6:1–9.
- Groom, M. J. and N. Schumaker. 1993. Evaluating landscape change: patterns of worldwide deforestation and local fragmentation. Pages 24–44 in P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, eds. *Biotic Interactions and Global Change*. Sunderland, MA: Sinauer Associates.
- Hobbs, R. J. 2000. Land use changes and invasions. Pages 385–421 in H. A. Mooney and R. J. Hobbs, eds. *Invasive Species in a Changing World*. Washington, DC: Island.
- Hosmer, D. W. and S. Lemeshow. 2000. *Applied Logistic Regression*. New York: Wiley.
- Hsu, M.-J. and G. Agoramoorthy. 1999. Conserving the biodiversity of Taiwan's Kenting National Park: present status and future challenges. Pages 62–72 in Y.-S. Lin, ed. *Biodiversity*. Taipei, Taiwan: National Taiwan University Press.
- Hsu, M. J., K. Selvaraj, and G. Agoramoorthy. 2006. Taiwan's industrial heavy metal pollution threatens terrestrial biota. *Environ. Pollut.* 143:327–334.
- Isarasenee, A., H. M. Shelton, and R. M. Jones. 1984. Accumulation of edible forage of *Leucaena leucocephala* cv. Peru over late summer and autumn for use as dry season feed. *Leucaena Res. Rep.* 5:3–4.
- Jama, B., P. Nair, and P. Kurira. 1989. Comparative growth performance of some multipurpose trees and shrubs grown at Machakos, Kenya. *Agroforest. Sys.* 9:17–27.
- Jones, C. C., S. A. Acker, and C. B. Halpern. 2010. Combining local- and large-scale models to predict the distributions of invasive plant species. *Ecol. Appl.* 20:311–326.
- Kuo, Y.-L. 2007. The ecological character and management plan of the invasion species: *Leucaena leucocephala*. *Q. J. Taiwan Mus.* 94:86–89. [in Chinese]
- Lai, M.-J. 1995. *Directories of Botanic Species in Taiwan*. Taipei, Taiwan: Di-Jing. [in Chinese]
- Lasco, R. and F. Pulhin. 2000. Forest land use change in the Philippines and climate change mitigation. *Mitig. Adapt. Strat. Glob. Ch.* 5: 81–97.
- Liang, Y.-C. 2004. *Studies on Zoning the Ecoregion at Domain and Division Levels in Taiwan*. Master's Thesis. Taipei, Taiwan: National Taiwan University. 122 p.
- Lobo, J. M., A. Jiménez-Valverde, and J. Hortal. 2010. The uncertain nature of absences and their importance in species distribution modelling. *Ecography* 33:103–114.
- Lodge, D. M., S. Williams, H. J. MacIsaac, K. R. Hayes, B. Leung, S. Reichard, R. N. Mack, P. B. Moyle, M. Smith, D. A. Andow, J. T. Carlton, and A. McMichael. 2006. Biological invasions: recommendations for U.S. policy and management. *Ecol. Appl.* 16:2035–2054.
- Lu, M.-L., J.-Y. Huang, and Y.-L. Chung. 2009. Spatial dynamics and regional analysis of *Leucaena leucocephala* in the Hungchun Peninsula, Taiwan. *J. Photogrammetry Remote Sens.* 14:1–9. [in Chinese]
- Lu, M.-L., J.-Y. Huang, Y.-L. Chung, and C.-Y. Hung. 2013. Modeling the invasion of a central American Mimosoid tree species (*Leucaena leucocephala*) in a tropical coastal region of Taiwan. *Remote Sens. Lett.* 4:485–493.
- Lu, M.-L., C.-L. Yeh, Y.-L. Chung, and Y.-T. Hsieh. 2008. The ground spectral analysis of four dominant vegetation in the Kenting National Park, Taiwan. *J. Photogrammetry Remote Sens.* 13:19–28. [in Chinese]
- Marod, D., P. Duengkae, U. Kutintara, S. Sungkaew, C. Wachrinrat, L. Asanok, and N. Klomwattanakul. 2012. The influences of an invasive plant species (*Leucaena leucocephala*) on tree regeneration in Khao Phluang Forest, northeastern Thailand. *Kasetsart J., Nat. Sci.* 46: 39–50.
- Matthews, S. and K. Brand. 2004. *Africa invaded: the growing danger of invasive alien species*. Cape Town, South Africa: Global Invasive Species Programme. 79 p.
- Merriam, R. W. and E. Feil. 2002. The potential impact of an introduced shrub on native plant diversity and forest regeneration. *Biol. Invasions* 4:369–373.
- METI and NASA. 2009. *ASTER Global Digital Elevation Map*. Japan and the United States.
- Meyer, J.-Y. 2004. Threat of invasive alien plants to native flora and forest vegetation of eastern Polynesia. *Pacific Sci.* 58:357–375.
- NLSC. 1993. *National Land Use Investigation Data*. Taipei, Taiwan.

- Normaniza, O., H. A. Faisal, and S. S. Barakbah. 2008. Engineering properties of *Leucaena leucocephala* for prevention of slope failure. *Ecol. Eng.* 32:215–221.
- Olden, J. D. and D. A. Jackson. 2002. A comparison of statistical approaches for modelling fish species distributions. *Freshwater Biol.* 47:1976–1995.
- Ong, C. K., J. E. Corlett, R. P. Singh, and C. R. Black. 1991. Above and below ground interactions in agroforestry systems. *Forest Ecol. Manag.* 45:45–57.
- Owens, H. L., L. P. Campbell, L. L. Dornak, E. E. Saupe, N. Barve, J. Soberón, K. Ingenloff, A. Lira-Noriega, C. M. Hensz, C. E. Myers, and A. T. Peterson. 2013. Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. *Ecol. Model.* 263:10–18.
- Pattison, R. R. and R. N. Mack. 2008. Potential distribution of the invasive tree *Triadica sebifera* (Euphorbiaceae) in the United States: evaluating climex predictions with field trials. *Global Change Biol.* 14:813–826.
- Pauchard, A. and P. B. Alaback. 2004. Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of south-central Chile. *Conserv. Biol.* 18: 238–248.
- Paynter, Q., S. M. Csurhes, T. A. Heard, J. Ireson, M. H. Julien, J. Lloyd, W. M. Lonsdale, W. A. Palmer, A. W. Sheppard, and R.D.v. Klinken. 2003. Worth the risk? Introduction of legumes can cause more harm than good: an Australian perspective. *Aust. Syst. Bot.* 16: 81–88.
- Phillips, S. J. and M. Dudík. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31:161–175.
- Pimentel, D. 2005. Environmental and economic costs of the application of pesticides primarily in the United States. *Environ. Develop. Sustain.* 2:229–252.
- Ridgeway, G. 2006. Generalized Boosted Regression models. Documentation on the R package ‘gbm’, version 1-5-7. <http://www.i-pensieri.com/gregr/gbm.shtml>. Accessed Oct. 2, 2012.
- Saifuddin, M. and N. Osman. 2012. Comparative studies of four legume tree species and screening the potential species using their physiological and root properties. *Life Sci. J.* 9:1509–1518.
- Sax, D. F. and J. H. Brown. 2000. The paradox of invasion. *Global Ecol. Biogeogr.* 9:363–371.
- Shelton, H. M. and J. L. Brewbaker. 1994. *Leucaena leucocephala* — the most widely used forage tree legume. Pages 15–29 in R. C. Gutteridge and H. M. Shelton, eds. *Forage Tree Legumes in Tropical Agriculture*. Oxon, UK: CAB International.
- Simberloff, D. 2000. Global climate change and introduced species in United States forests. *Sci. Total Environ.* 262:253–261.
- Stromberg, J. C., S. J. Lite, R. Marler, C. Paradzick, P. B. Shafroth, D. Shorrocks, J. M. White, and M. S. White. 2007. Altered stream-flow regimes and invasive plant species: the *Tamarix* case. *Global Ecol. Biogeogr.* 16:381–393.
- Suárez-Seoane, S., P. E. Osborne, and J. C. Alonso. 2002. Large-scale habitat selection by agricultural steppe birds in Spain: identifying species-habitat responses using generalized additive models. *J. Appl. Ecol.* 39:755–771.
- Wang, H.-H. and W. E. Grant. 2012. Determinants of Chinese and European privet invasion and likelihood of further invasion in southern US forestlands. *Invasive Plant Sci. Manage.* 5:454–463.
- Wang, H.-H., C. L. Wonkka, W. E. Grant, and W. E. Rogers. 2012. Potential range expansion of Japanese honeysuckle (*Lonicera japonica* Thunb.) in southern U.S. forestlands. *Forests* 3:573–590.
- Wang, W.-L. and Y.-M. Chiang. 1994. Potential economic seaweeds of Hengchun peninsula, Taiwan. *Econ. Bot.* 48:182–189.
- With, K. A. 2002. The landscape ecology of invasive spread. *The J. Soc. Conserv. Biol.* 16:1192–1203.
- Wolfe, B. T. and S. J. Van Bloem. 2012. Subtropical dry forest regeneration in grass-invaded areas of Puerto Rico: understanding why *Leucaena leucocephala* dominates and native species fail. *Forest Ecol. Manag.* 267:253–261.
- Yates, E. D., D. F. Levia Jr, and C. L. Williams. 2004. Recruitment of three non-native invasive plants into a fragmented forest in southern Illinois. *Forest Ecol. Manag.* 190:119–130.
- Yoshida, K. and S. Oka. 2000. Impact of biological invasion of *Leucaena leucocephala* on successional pathway and species diversity of secondary forest on Hahajima Island, Ogasawara (Bonin) Islands, northwestern Pacific. *Jap. J. Ecol.* 50:111–119.
- Zimpfer, J. F., C. A. Smyth, and J. O. Dawson. 1997. The capacity of Jamaican mine spoils, agricultural and forest soils to nodulate *Myrica cerifera*, *Leucaena leucocephala* and *Casuarina cunninghamiana*. *Physiol. Plant.* 99:664–672.

Received February 1, 2013, and approved June 7, 2013.