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Determinants of Chinese and European Privet (*Ligustrum sinense* and *Ligustrum vulgare*) Invasion and Likelihood of Further Invasion in Southern U.S. Forestlands

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Chinese and European privets are among the most aggressive invasive shrubs in forestlands of the southern United States. We analyzed extensive field data collected by the U.S. Forest Service covering 12 states to identify potential determinants of invasion and to predict likelihood of further invasion under a variety of possible management strategies. Results of multiple logistic regression, which classified 75% of the field plots correctly with regard to species presence and absence, indicated probability of invasion is correlated positively with elevation, adjacency (within 300 m) to waterbodies, mean extreme maximum temperature, site productivity, species diversity, natural regeneration, wind disturbance, animal disturbance, and private land ownership and is correlated negatively with slope, stand age, site preparation, artificial regeneration, distance to the nearest road, fire disturbance, and public land ownership. Habitats most at risk to further invasion (likelihood of invasion > 10%) under current conditions occur throughout Mississippi, with a band stretching eastward across south-central Alabama, and in eastern Texas and western Louisiana. Invasion likelihoods could be reduced most by conversion to public land ownership, followed by site preparation, fire disturbance, artificial regeneration, and elimination of animal disturbance. While conversion of land ownership may be neither feasible nor desirable, this result emphasizes the opportunity for reducing the likelihood of invasions on private lands via increased use of selected management practices.

Nomenclature: Chinese privet, *Ligustrum sinense* Lour.; European privet, *Ligustrum vulgare* L.

Key words: Biodiversity, biological invasions, habitat quality, invasive species, multiple logistic regression model.

Invasive species have had enormous, sometimes irreversible, effects on biodiversity, human property, and economic activities throughout the world. In the forestlands of the southern United States, which account for 62% of U.S. timber production and provide a variety of ecological services (USDA Economic Research Service 2009), invasive plant species have eroded forest productivity, replaced native forest species, hindered forest use and management activities, increased the risk of wildfire, and degraded wildlife habitat and faunal diversity (Miller 2003; USDA Economic Research Service 2009). Chinese and European privets (*Ligustrum sinense* Lour. and *Ligustrum vulgare* L.) are among the most aggressive invasive shrubs threatening the ecological integrity and unique biodiversity of southern forestlands, having invaded almost 10% of the region (USDA Forest Service 2009b) (Figure 1).

Chinese privet was introduced into the United States in 1852 and European privet in the early to mid-1800s (Haragan 1996). Both species grow as perennial shrubs or small trees to a height of 9 m (29.5 ft), have multiple stems, and were planted throughout much of the southern region as an ornamental hedge (Miller 2003). Their foliage is evergreen to semi-evergreen, becoming deciduous in cold climates (Dirr 1998). A mature plant can produce hundreds of fruits containing millions of seeds (≈ 2.7 million) annually (Haragan 1996), and seeds germinate promptly without a period of moist cold (Young and Young 1992). Seeds are dispersed widely by birds and other wildlife (Dirr 1998). Both species can grow in low-nutrient soils and tolerate low light levels (Miller 2003) and, hence, can invade under dense forest canopies (Harrington and Miller 2005; Merriam and Feil 2002), dominating the understory of mesic forests throughout the southern United States (Haragan 1996).

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Management Implications

Biotic invasions have affected ecosystems worldwide. One of the greatest current challenges facing forest ecosystem management in the southern United States is the control of range expansions by invasive plant species. To move beyond reactive control efforts toward more proactive management requires prediction of potential ranges of invasive species on spatial scales relevant to forest managers. We drew upon extensive geo-referenced datasets on nonnative invasive plants maintained by the U.S. Forest Service to develop an invasion distribution model predicting possible range expansion of Chinese and European privets in forestlands of the southern United States. By identifying determinants of invasion and potential habitat, our analyses should assist land managers and restoration practitioners in planning proactive management strategies and control treatments.

Chinese and European privets continue to expand their ranges in the southern United States (Wilcox and Beck 2007), and reliable predictions of habitats at risk are needed urgently (Williams and Minogue 2008). In this paper, we analyze an extensive dataset collected as part of the Forest Inventory and Analysis (FIA) program of the U.S. Forest Service to identify potential determinants of invasion and to predict likelihood of further invasion under a variety of possible management strategies.

Materials and Methods

Study Area and Data Sources. We obtained data for the present study from FIA surveys conducted between 2000 and 2006 on 42,637 permanent, $\approx$ 4,000 m^2 (0.99 ac), forested plots in 12 of 13 states in the U.S. Forest Service's Southern Region (Alabama, Arkansas, Florida, Georgia, Kentucky, Louisiana, Mississippi, North Carolina, South Carolina, Tennessee, Texas, and Virginia; surveys had not yet begun in Oklahoma) (Figure 1). Plots were located within permanent, $\approx$ 2,428 ha (6,000 ac), invasive plant survey grids established by federal and state forest resource survey crews on both public and private forestlands (Rudis et al. 2006; USDA Forest Service 2011). The FIA sampling scheme, which is conducted as part of a national forest resource inventory begun by the U.S. Forest Service's Southern Research Station in 2000 (USDA Forest Service 2009a), involves surveying approximately one-fifth of the plots in each state each year on a continuing basis. Thus, the first full sampling cycle for the 12 states listed above was completed in 2006, and these 12 states define our study area.

From two U.S. Forest Service Southern Region FIA datasets, we drew on (1) the Nonnative Invasive Plants dataset to obtain the presence and absence of Chinese and European privets in all plots and (2) the traditional FIA dataset to obtain data on stand characteristics, site conditions, and management activities and disturbances

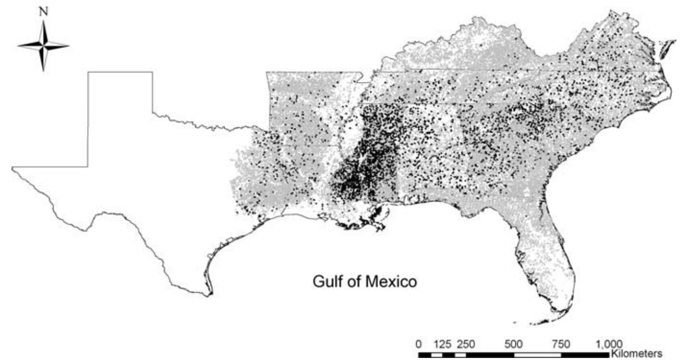

Figure 1. Current occupation of forestlands in the southern United States by Chinese and European privets (USDA Forest Service 2009a, 2009b). Gray and black dots represent absence and presence on U.S. Forest Service plots of Chinese and European privets, respectively.

(USDA Forest Service 2009a, 2009b). We should note that in the Nonnative Invasive Plants dataset no distintion is made between *L. sinense* (Chinese privet) and *L. vulgare* (European privet), and that *Ligustrum obtusifolium* Siebold & Zucc. actually may be more common in some of the areas sampled than either *L. sinense* or *L. vulgare*. Hence, potentially several *Ligustrum* species may be grouped together in the FIA data. We also obtained climatic data, including mean extreme maximum and minimum temperatures, from the National Oceanic and Atmospheric Administration Satellite and Information Service (NOAA 2008). We linked data from these three sets using the FIA plot identification numbers and locations and the latitude and longitude coordinates from the satellite data.

Potential Determinants of Invasion. Widely recognized determinants of invasion include the following: (1) Landscape features such as elevation and slope (Spittlehouse and Stathers 1990) and adjacency to waterbodies (Burns and Miller 2004); (2) climatic conditions such as mean extreme minimum and maximum temperatures (Bradley 2010; Simberloff 2000); (3) forest conditions such as stand age (Filipescu and Comeau 2007), site productivity (Lombardo et al. 2007), and tree species diversity (Wills et al. 1997); and (4) forest management activities and disturbances such as timber harvest (Miller 2003), site preparation (Miller 2003), artificial regeneration (Benson and Hartnett 2006), natural regeneration (Cain 1992; Merriam and Feil 2002), distance to the nearest road (Delgado et al. 2001; Flory and Clay 2009), fire disturbance (Galíndez et al. 2009; Grace et al. 2001), animal disturbance (Russo et al. 2006), and wind disturbance (including hurricanes and tornados) (Greene et al. 2004). We obtained data on these variables for plots within our study area directly from the traditional FIA dataset. Detailed definitions for these variables are presented in Table 1 and the Forest Inventory and Analysis

Table 1. Descriptions, values or units of measure, and means or frequencies of landscape features, forest conditions, and management activities and disturbances evaluated as potential determinants of site invasion by Chinese and European privets on forested plots in the southern United States.

Variable	Value or unit of measure	Mean (range of values) or frequency
Landscape features		
Elevation	m	139 (−36∼1,524)
Slope	Degree	5.39 (0∼77.5)
Adjacency to waterbodies within 300 m	0: no	0: 27,940
	1: yes	1: 6,731
Climatic conditions		
Mean extreme minimum temperature	C	−19.86 (−34.44∼4.44)
Mean extreme maximum temperature	C	42.17 (35.06∼43.33)
Forest conditions		
Stand age	yr	44.27 (1∼184)
Site productivity (height–age curve categories)	1: 0–1.39	1: 0.13819
	2: 1.40–3.49	2: 5,912
	3: 3.50–5.94	3: 17,270
	4: 5.95–8.39	4: 12,112
	5: 8.40–11.54	5: 5,609
	6: 11.55–15.74	6: 1,483
	7: >15.74 m^3 ha^{-1} yr^{-1}	7: 0.36944
Tree species diversity	Shannon's species diversity	1.48 (0∼3.02)
Management activities and disturbances		
Timber harvest[a,b]	0: No	0: 36,216
	1: Yes	1: 6,421
Site preparation[a,c]	0: No	0: 41,181
	1: Yes	1: 1,456
Artificial regeneration[a,d]	0: No	0: 31,545
	1: Yes	1: 11,092
Natural regeneration[a,e]	0: No	0: 41,663
	1: Yes	0.71806
Distance to the nearest road[a]	1: <30	1: 2,846
	2: 30–91	2: 4,732
	3: 91–152	3: 4,218
	4: 152–305	4: 7,409
	5: 305–805	5: 10,424
	6: 805–1,609	6: 4,339
	7: 1,609–4,828	7: 1,349
	8: 4,828–8,047	0.41597
	9: >8,047 m	0.43333
Fire disturbance[a,f,g]	0: No	0: 41,551
	1: Yes	1: 1,086
Animal disturbance[a,f,h]	0: No	0: 42,069
	1: Yes	0.43611
Wind disturbance[a,f,i]	0: No	0: 41,269
	1: Yes	1: 1,368

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Table 1. Continued.

Variable	Value or unit of measure	Mean (range of values) or frequency
Ownership		
Forestland ownership	0: Public	0: 5,349
	1: Private	1: 37,288

[a] Nominally within the past 5 yr.

[b] Harvest one or more trees from a stand.

[c] Clearing, slash burning, chopping, disking, bedding, or other practices clearly intended to prepare a site for regeneration.

[d] Planting or direct seeding resulting in at least 50% stocked with live trees of any size.

[e] Growth of existing trees, natural seeding, or both resulting in a stand at least 50% stocked with live trees of any size.

[f] A disturbance code of 1 indicates at least 25% of the trees in a stand are damaged.

[g] Disturbance from crown or ground fire, either prescribed or natural.

[h] Damages from beaver, porcupine, deer/ungulate, rabbit, or a combination of animals.

[i] Including, but not limited to, damages from hurricanes and tornados (USDA Forest Service 2009a, 2011).

Database: Database Description and User's Manual, version 5.1 (USDA Forest Service 2011). We also used the same dataset to compute tree species diversity, H_s (Shannon's index), for each plot (Filipescu and Comeau 2007; Wills et al. 1997),

$$H_s = -\sum_{i=1}^{n_s} (B_i/B)\ln(B_i/B) \qquad [1]$$

where B and B_i are the total stand basal area and the basal area of trees of species i, respectively, and n_s is the number of tree species.

We evaluated all potential determinants of invasion via stepwise multiple logistic regression, using a backwards elimination procedure (Gan et al. 2009):

$$\mathrm{logit}(p) = \log[p/(1-p)] = \alpha + \mathbf{X}'\beta \qquad [2]$$

where p is the probability of presence of invasion by Chinese and European privets, $p/(1-p)$ is the odds of the presence of Chinese and European privets, $\mathbf{X}$ is the vector of independent variables which are shown in Table 1, and α and β (a vector) are the regression coefficients. After we derived the regression coefficients, we calculated the odds ratio for each significant variable as e^{β}. Before running the multiple logistic regression, we ran a zero-inflated binomial regression and calculated Moran's I index to test for possible zero inflation and spatial autocorrelation (Martin et al. 2005; Overmars et al. 2003). When we ran the multiple logistic regression, we removed nonsignificant terms and re-estimated the model (Agresti 2007; Liang et al. 2007) until the Akaike information criterion (AIC; Akaike 1973) could not be lowered further. We then used Hosmer–Lemeshow's test to check for goodness of fit (Hosmer and Lemeshow 2000). Finally, we used the area under the receiver operating curve (AUC) to assess the reliability and validity of our model as fair ($0.50 < \mathrm{AUC} \le 0.75$), good ($0.75 < \mathrm{AUC} \le 0.92$), very good ($0.92 < \mathrm{AUC} \le 0.97$), or excellent ($0.97 < \mathrm{AUC} \le 1.00$) (Hosmer and Lemeshow 2000). We defined the cut-off criterion to convert continuous model predictions to binary classifications, which are required for calculation of the AUC (Agresti 2007), as the threshold value that maximized the sum of sensitivity (the proportion of actual positives correctly identified) and specificity (the proportion of negatives correctly identified). We tested potential threshold values at 0.001 intervals. For purposes of model assessment, we split the presence and absence data into test (7,966 data points, $\approx$ 20%) and training (34,671 data points, $\approx$ 80%) datasets. We conducted all statistical analyses using SAS 9.2 (SAS Institute Inc., Cary, NC).

Likelihood of Further Invasion. On the basis of regression results, we estimated the probability of presence of invasion of each forested plot as:

$$p(Y=1|\mathbf{X}) = \exp(\alpha + \mathbf{X}'\beta)/[1 + \exp(\alpha + \mathbf{X}'\beta)] \qquad [3]$$

where Y is a binary variable taking the value of 1 if privets are present on the site or 0 otherwise, and $p(Y=1)$ is the probability for $Y=1$ (i.e., the probability that the site is invaded by privets). We then superimposed these probabilities of occupancy on a map of the study area using ArcMap™ 9.1 (ESRI, Redlands, CA). To provide a more useful management perspective for each county, we also generated a map indicating the average probability for each county, which we calculated as the mean of the estimated probabilities of presence of invasions of all of the plots within the county, p'. We explored possible effects of five different management strategies on the likelihood of

Table 2. Potential determinants of Chinese and European privets invasion of forested plots in the southern United States as indicated by results of stepwise multiple logistic regression.[a]

Variable	Estimated coefficient	Estimated standard error	Estimated odds ratio[b]	95% Confidence intervals for the odds ratio: Lower	Upper
Landscape features					
Elevation	0.0006	< 0.0001	1.001	1.000	1.001
Slope	−0.0359	0.0039	0.965	0.957	0.972
Adjacency to waterbodies within 300 m	0.3433	0.0431	1.410	1.295	1.534
Climatic conditions					
Mean extreme maximum temperature	0.3230	0.0238	1.381	1.318	1.447
Forest conditions					
Stand age	−0.0107	0.0009	0.989	0.988	0.991
Site productivity	0.3520	0.0169	1.422	1.376	1.470
Species diversity	0.3242	0.0311	1.383	1.301	1.470
Management activities and disturbances					
Site preparation	−0.3789	0.1060	0.685	0.556	0.843
Artificial regeneration	−0.1359	0.0396	0.873	0.808	0.943
Natural regeneration	0.4433	0.0873	1.558	1.313	1.849
Distance to the nearest road	−0.1119	0.0111	0.894	0.875	0.914
Fire disturbance	−0.2739	0.1220	0.760	0.599	0.966
Animal disturbance	0.4238	0.1325	1.528	1.178	1.981
Wind disturbance	0.5351	0.0807	1.708	1.458	2.000
Ownership					
Forestland ownership	0.8710	0.0766	2.389	2.056	2.776
Constant	−8.9183	0.3973	—	—	—

[a] Table presents results from a backward selection model. Results from a forward selection model contained almost identical variables, except "fire disturbance" was excluded; however, the AIC and G^2 of the forward selection model was significantly larger than those of the backward selection model (AIC = 22,770, G^2 = 11,385, and df = 15 vs. AIC = 22,762, G^2 = 11,381, and df = 16).

[b] The estimated odds ratio indicates the change in the probability of invasion by Chinese and European privets that would result from a one-unit change in the value of the indicated variable. For example, a one-unit increase in site productivity signifies that invasion is 1.422 times more likely than before, after controlling for the other variables.

further invasion by assuming the occurrence in each county within the study area of: (1) site preparation (clearing, slash burning, chopping, disking, bedding, or other practices clearly intended to prepare a site for regeneration), (2) artificial regeneration (planting or direct seeding that has resulted in a stand at least 50% stocked with live trees of any size), (3) fire disturbance (including crown, ground fire, or both), (4) elimination of animal disturbance (including beaver, porcupine, and deer/ungulate), and (5) complete conversion to public land ownership. We represented each of the five strategies by changing the value of the corresponding element of the vector, **X**, of independent variables in Equation 3 from 0 to 1 (to represent site preparation, artificial regeneration, fire disturbance, and complete conversion to public land ownership) or from 1 to 0 (to represent elimination of animal disturbance).

Results

Potential Determinants of Invasion. Results of the analyses indicated probability of invasion is correlated positively with elevation, adjacency (within 300 m) to waterbodies, mean extreme maximum temperature, site productivity, species diversity, natural regeneration, wind disturbance, animal disturbance, and private land ownership and is correlated negatively with slope, stand age, site preparation, artificial regeneration, distance to the nearest

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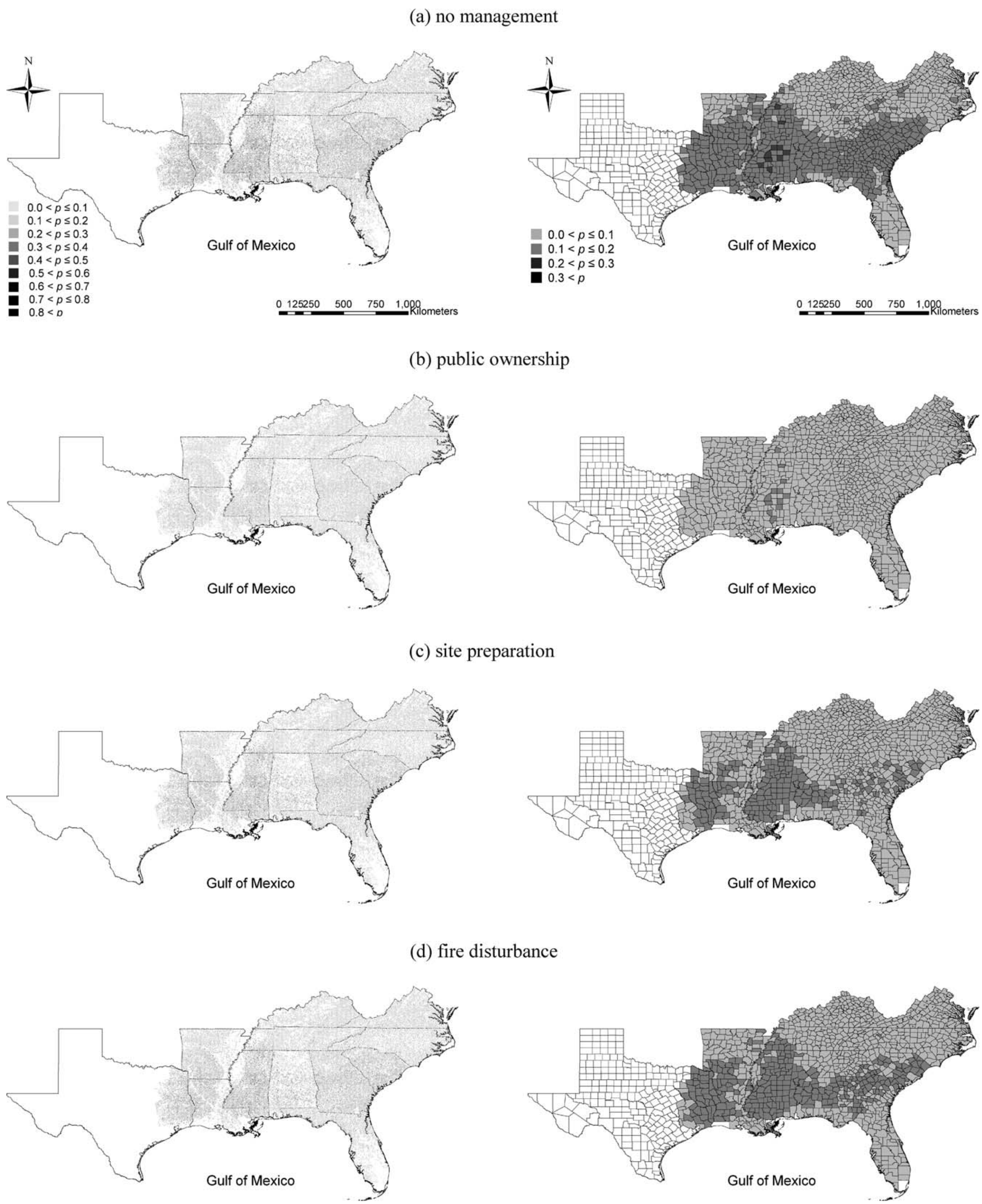

Figure 2. Estimated probability of occupancy of forestlands in each U.S. Forest Service plot (left) and average estimated probability in each county (right) in the southern United States by Chinese and European privets with (a) no management, (b) public ownership, (c) site preparation, (d) artificial regeneration, (e) fire disturbance, and (f) animal disturbance.

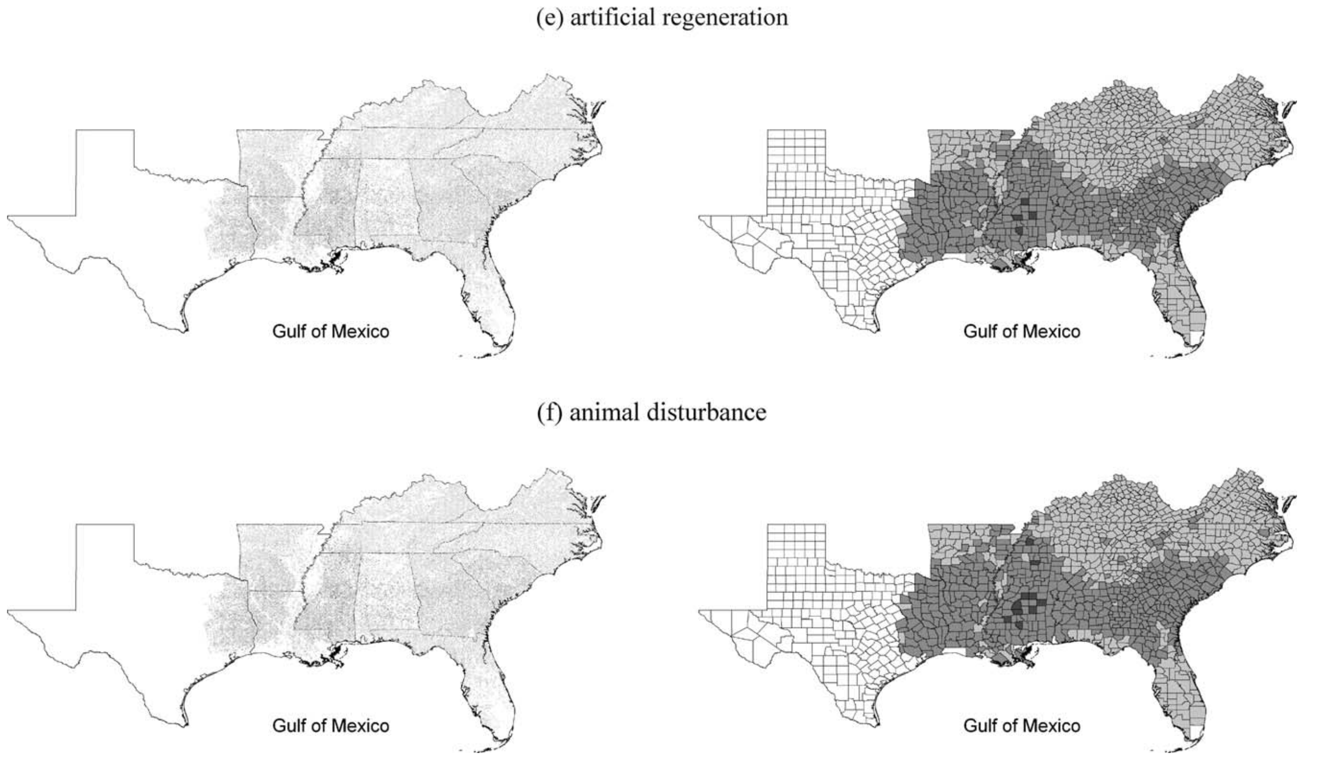

Figure 2. Continued.

road, fire disturbance, and public land ownership (Table 2). The model classified 74.7% of the plots correctly with regard to species presence and absence, and Hosmer and Lemeshow's goodness-of-fit test (P = 0.53) indicated no significant difference at the 5% significance level between observed and model-predicted occupancy values. The coefficient of zero inflation for the final multiple logistic regression model was not significant (P = 0.30) at the 5% significance level, indicating no statistical evidence of zero inflation. The AUCs for training (0.74) and test (0.77) data indicated model reliability and validity was fair/good. (We used a cut-off criterion of 0.12 to convert continuous model predictions to binary classifications.) The AIC and G^2 of the zero-inflated binomial model was significantly larger than the AIC and G^2 of the multiple logistic regression model (AIC = 23,743, G^2 = 11,856, and df = 16 vs. AIC = 22,702, G^2 = 11,334, and df = 17), indicating the multiple logistic regression model was preferred over the zero-inflated binomial model. Moran's I index (I = 0.04) indicated no statistically significant (P = 0.21) spatial autocorrelation at the 5% significance level.

Likelihood of Further Invasion. *Under Current Conditions.* Estimated probabilities of further invasion (p) were relatively low, with approximately 88.7% (≈ 70 million ha) of the plots falling within the $0 < p \leq 0.20$ category and another 11.2% (≈ 9 million ha) within the $0.20 < p \leq 0.50$ category. Only about 0.1% (≈ 80,000 ha) of the plots fell within the $p > 0.50$ category, the majority (46%) of which were located in Mississippi (Figure 2a). On a county-by-county basis, higher average estimated probabilities ($0.10 < p' \leq 0.20$) appeared throughout Mississippi, with a band stretching eastward across south-central Alabama, in eastern Texas and western Louisiana, and in several counties scattered within Georgia and South Carolina; 9 of the 10 counties with highest average probabilities ($0.20 < p' \leq 0.30$) were located in Mississippi and only one in Tennessee (Figure 2a). The higher estimated invasion probabilities in Mississippi resulted from a more favorable (for privets) combination of most of the model variables. Mississippi forestlands have flatter slopes, lower elevations, younger aged forests, more waterbodies and wind disturbances, higher site productivities, higher proportion of naturally regenerated forests, and higher mean extreme maximum temperatures than occur in the other states. (Note that the model successfully predicted 80.1% of current invasions in Mississippi.)

Under Alternative Management Strategies. Average estimated probabilities of further invasion (p') were reduced the most by conversion to public land ownership, followed by site preparation, fire disturbance, artificial regeneration, and elimination of animal disturbance (Figure 3). Conversion to public land ownership decreased overall p' from 0.10 to 0.04 and decreased the number of counties with $p' > 0.10$ from 480 to 13, with p' decreasing from 0.16 to 0.08 in

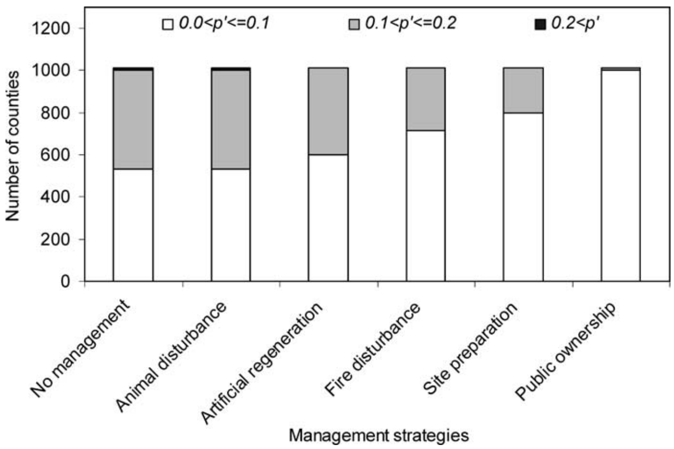

Figure 3. Number of counties within the indicated average estimated probability (p') range for invasion with no management, suppression of animal disturbance, artificial regeneration, fire disturbance, site preparation, and conversion to public ownership.

Mississippi where invasion probabilities were highest (Figures 2b and 3). Site preparation decreased overall p' from 0.10 to 0.06 and decreased the number of counties with $p' > 0.10$ from 480 to 218, with reductions most noticeable in Alabama, Arkansas, Louisiana, and Texas (Figures 2c and 3). Fire disturbance decreased overall p' from 0.10 to 0.06 and decreased the number of counties with $p' > 0.10$ from 480 to 299, with counties having $p' > 0.20$ disappearing from Arkansas, Louisiana, Georgia, North Carolina, and South Carolina (Figures 2d and 3). Artificial regeneration decreased overall p' from 0.10 to 0.07 and decreased the number of counties with $p' > 0.10$ from 480 to 416 (Figures 2e and 3). Animal disturbance decreased overall p' from 0.10 to 0.08 but did not change the number of counties with $p' > 0.10$ (Figures 2f and 3).

Discussion

Invasions by Chinese and European privets appear to be facilitated by certain landscape characteristics. About 80% of existing invasions into southern U.S. forestlands have occurred at elevations < 177 m and on slopes < 5°, which create favorable conditions for seedling survival and adult growth, with invasion probabilities diminishing markedly at higher elevations and steeper slopes. Adjacency to waterbodies also appears to favor invasion, with moist riparian soils providing conditions favorable for germination, establishment, and growth (Gan et al. 2009; Merriam 2003), as well as favorable habitat for songbirds, rodents, and other wildlife that are important vectors of privet seed dispersal (Christopher and Barrett 2006; Dirr 1998; Wilcox and Beck 2007). Although not documented for Chinese and European privets, seed dispersal by channel catfish (*Ictalurus punctatus*) has been documented for swamp privet [*Forestiera acuminata* (Michx.) Poir.] (Chick et al. 2003).

The effect of climate manifested itself via a positive correlation of invasions with mean extreme maximum temperatures. In fact, no invasion was detected in survey sites where the mean extreme maximum temperature was below 35 C (95 F). Miller (2003) has suggested that temperature restrictions on blooming time may serve as an important barrier to privet invasions.

Invasions also appear to be facilitated by certain characteristics of forest stands. About 50% of the existing invasions into southern U.S. forests have occurred in stands < 30 yr old. High site productivity also appears to favor invasions. Logically, relatively young, productive sites provide favorable conditions for native and invasive species alike (Davies et al. 2007). The main factor limiting invasion of mature forest stands by Chinese and European privets is low light availability, even though both species can tolerate a relatively low light environment (Miller, 2003). Likelihood of invasion in mature stands also is reduced because of fewer canopy gaps that provide opportunities for seed recruitment and sapling growth and lower levels of disturbance in general.

Intriguingly, forest stands characterized by high species diversity seem more vulnerable to invasion. Theoretically, plant communities with high species diversity should be most resistant to invasion (Elton 1958). Although many empirical studies support this hypothesis (e.g., Hector et al. 2001; Levine 2000; Lyons and Schwartz 2001; Naeem et al. 2000), numerous other empirical studies suggest that communities with higher biodiversity tend to be invaded more easily (e.g., Levine 2000; Lonsdale 1999; Stohlgren et al. 2003). Wiser et al. (1998) hypothesized that opportunities for plant invasion might be increased within species-rich plots by the increased temporal variability and spatial heterogeneity of resource availability, with invasive species finding a window of opportunity when the native community is not fully utilizing available resources. Viewing our results in light of this hypothesis, we noted that the majority of our study plots fell within either pine or oak/hickory forests. The pine forest plots were characterized by relatively fewer species (average H_s = 1.16) whose evergreen canopy presumably allowed little light to reach the forest floor year round. The oak/hickory plots were characterized by relatively more species (average H_s = 1.80) whose deciduous canopy might have provided a window of opportunity for the establishment of evergreen shrubs during the fall, winter, and early spring.

Of the management strategies we explored, the conversion to public land ownership was by far the most effective in reducing the likelihood of further invasions. Although conversion of land ownership may be neither feasible nor desirable, this result emphasizes the opportunity for reducing the likelihood of invasions on private lands via increased use of selected management practices (Smith and Darr 2004; USDA Forest Service 2009a). The potential negative effect of privet invasions is acknowledged widely among private organizations (Dibble et al. 2008; USDA Forest Service 2009b; Williams and Minogue 2008), and some have initiated control efforts (Wang 2009); however, the range of technical and financial assistance available to private landowners for the development of effective control methodologies remains limited (Williams and Minogue 2008).

Whether on private or public land, increased management efforts focused on site preparation via clearing, slash burning, chopping, disking, bedding, or a combination of these techniques followed by artificial regeneration via planting or direct seeding that results in a stand at least 50% stocked with live trees could reduce the temporal window of opportunity for site colonization by invasive species (USDA Forest Service 2011). Early control based on monitoring of animal disturbances that facilitate plant invasion also could reduce likelihood of subsequent establishment (Parendes and Jones 2000). However, privet seeds are spread widely throughout southern U.S. forestlands by a variety of songbirds and other animals such as white-tailed deer (*Odocoileus virginianus*), white-footed mice (*Peromyscus leucopus*), and golden mice (*Ochrotomys nuttalli*) (Christopher and Barrett 2006; Miller 2003; Rossell et al. 2007; Wilcox and Beck 2007), making complete prevention of colonization virtually impossible.

Postcolonization fire can be an effective means of reducing the likelihood of establishment of Chinese and European privets if invasions are detected early, but fire control of established invasions is difficult because, in older stands, privets usually shade out the understory vegetation that is required to carry a fire (Miller 2003). Furthermore, Chinese privets respond to fire by vigorously sprouting from the root crown (Faulkner et al. 1989). Williams and Minogue (2008) have suggested that repeated burning every 2 to 3 yr is necessary to control and eventually eliminate privets. Hence, although new, small invasions can be controlled by repeated burning, chemical and mechanical methods are preferred by invasion control companies (Hanula et al. 2009; Harrington and Miller 2005; Wang 2009).

In conclusion, our analyses suggest that continued range expansion by Chinese and European privets in forestlands of the southern United States is most likely throughout Mississippi, with a band stretching eastward across south-central Alabama, and in eastern Texas and western Louisiana, but that the opportunity exists for reducing the likelihood of invasions via increased use of selected management practices. Providing reliable predictions of habitats most at risk, distribution limits, and efficacy of management strategies for any invasive species remains a challenge. We have analyzed a large empirical dataset to identify landscape features, forest conditions, and management activities and disturbances that could be determinants of privet invasions and have used a statistical likelihood approach for projecting potential distributions under several management scenarios. We think that our analyses will be of use to forest managers in the early detection and eradication of newly established populations and allow them to manage high-risk areas proactively to increase invasion resistance.

Literature Cited

Agresti, A. 2007. An Introduction to Categorical Data Analysis. 2nd ed. Hoboken, NJ: John Wiley and Sons Inc.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 *in* S. Kotz and N. L. Johnson, eds. Second International Symposium on Information Theory. Budapest: Academia Kiado.

Benson, E. and D. Hartnett. 2006. The role of seed and vegetative reproduction in plant recruitment and demography in tallgrass prairie. Plant Ecol. 187:163–178.

Bradley, B. A. 2010. Assessing ecosystem threats from global and regional change: hierarchical modeling of risk to sagebrush ecosystems from climate change, land use and invasive species in Nevada, USA. Ecography 33:198–208.

Burns, J. H. and T. E. Miller. 2004. Invasion of Chinese tallow (*Sapium sebiferum*) in the Lake Jackson area, northern Florida. Am. Midl. Nat. 152:410–417.

Cain, M. D. 1992. Japanese honeysuckle in uneven-aged pine stands: problems with natural pine regeneration. Proc. South. Weed Sci. Soc. 45:264–269.

Chick, J. H., R. J. Cosgriff, and L. S. Gittinger. 2003. Fish as potential dispersal agents for floodplain plants: first evidence in North America. Can. J. Fish. Aquat. Sci. 60:1437–1439.

Christopher, C. C. and G. W. Barrett. 2006. Coexistence of white-footed mice (*Peromyscus leucopus*) and golden mice (*Ochrotomys nuttalli*) in a southeastern forest. J. Mammal. 87:102–107.

Davies, K. F., S. Harrison, H. D. Safford, and J. H. Viers. 2007. Productivity alters the scale dependence of the diversity–invasibility relationship. Ecology 88:1940–1947.

Delgado, J. D., J. R. Arévalo, and J. M. Fernández-Palacios. 2001. Road and topography effects on invasion: edge effects in rat foraging patterns in two oceanic island forests (Tenerife, Canary Islands). Ecography 24:539–546.

Dibble, A. C., K. Zouhar, and J. K. Smith. 2008. Wildland Fire in Ecosystems: Fire and Nonnative Invasive Plants. Ogden, UT: USDA Forest Service, Rocky Mountain Research Station General Technical Rep. RMRS-GTR-42-vol. 6. Pp. 61–90.

Dirr, M. A. 1998. Manual of Woody Landscape Plants: Their Identification, Ornamental Characteristics, Culture, Propagation and Uses. 5th ed. Champaign, IL: Stipes Publishing. 1250 p.

Elton, C. S. 1958. The ecology of invasions by animals and plants. London: Methuen & Co.

Faulkner, J. L., E.E.C. Clebsch, and W. L. Sanders. 1989. Use of prescribed burning for managing natural and historic resources in Chickamauga and Chattanooga National Military Park, USA. Environ. Manage. 13:603–612.

Filipescu, C. N. and P. G. Comeau. 2007. Competitive interactions between aspen and white spruce vary with stand age in boreal mixedwoods. For. Ecol. Manage. 247:175–184.

Flory, S. L. and K. Clay. 2009. Effects of roads and forest successional age on experimental plant invasions. Biol. Conserv. 142:2531–2537.

Galíndez, G., F. Biganzoli, P. Ortega-Baes, and A. Scopel. 2009. Fire responses of three co-occurring Asteraceae shrubs in a temperate savanna in South America. Plant Ecol. 202:149–158.

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. For. Res. 39:1346–1356.

Grace, J. B., M. Smith, S. L. Grace, S. Collins, and T. J. Stohlgren. 2001. Interactions between fire and invasive plants in temperate grasslands in North America. Pages 40–65 *in* K. Galley and T. Wilson, eds. Fire Conference 2000: The First National Congress on Fire, Ecology, Prevention and Management. Invasive Species Workshop: The Role of Fire in the Control and Spread of Invasive Species. Tallahassee, FL: Tall Timbers Research Station.

Greene, D. F., C. D. Canham, K. D. Coates, and P. T. Lepage. 2004. An evaluation of alternative dispersal functions for trees. J. Ecol. 92: 758–766.

Hanula, J. L., S. Horn, and J. W. Taylor. 2009. Chinese privet (*Ligustrum sinense*) removal and its effect on native plant communities of riparian forests. Invasive Plant Sci. Manage. 2:292–300.

Haragan, P. D. 1996. Privet (*Ligustrum vulgare, L. sinense, L. japonicum*). Pages 58–59 *in* J. M. Randall and J. Marinelli, eds. Invasive Plants: Weeds of the Global Garden. Brooklyn, NY: Brooklyn Botanic Garden.

Harrington, T. B. and J. H. Miller. 2005. Effects of application rate, timing, and formulation of glyphosate and triclopyr on control of Chinese Privet (*Ligustrum sinense*). Weed Technol. 19:47–54.

Hector, A., K. Dobson, A. Minns, E. Bazeley-White, and J. Hartley Lawton. 2001. Community diversity and invasion resistance: an experimental test in a grassland ecosystem and a review of comparable studies. Ecol. Res. 16:819–831.

Hosmer, D. W. and S. Lemeshow. 2000. Applied Logistic Regression. New York: John Wiley and Sons.

Levine, J. M. 2000. Species diversity and biological invasions: relating local process to community pattern. Science 288:852–854.

Liang, J., J. Buongiorno, R. A. Monserud, E. L. Kruger, and M. Zhou. 2007. Effects of diversity of tree species and size on forest basal area growth, recruitment, and mortality. For. Ecol. Manage. 243: 116–127.

Lombardo, K., J. S. Fehmi, K. J. Rice, and E. A. Laca. 2007. *Nassella pulchra* survival and water relations depend more on site productivity than on small-scale disturbance. Restor. Ecol. 15:177–178.

Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522–1536.

Lyons, K. G. and M. W. Schwartz. 2001. Rare species loss alters ecosystem function—invasion resistance. Ecol. Lett. 4:358–365.

Martin, T. G., B. A. Wintle, J. R. Rhodes, P. M. Kuhnert, S. A. Field, S. J. Low-Choy, A. J. Tyre, and H. P. Possingham. 2005. Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. Ecol. Lett. 8:1235–1246.

Merriam, R. W. 2003. The abundance, distribution and edge associations of six non-indigenous, harmful plants across North Carolina. J. Torrey Bot. Soc. 130:283–291.

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.

Miller, J. H. 2003. Nonnative invasive plants of southern forests: a field guide for identification and control. Asheville, NC: USDA Forest Service, Southern Research Station.

Naeem, S., J.M.H. Knops, D. Tilman, K. M. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos 91:97–108.

[NOAA] National Oceanic and Atmospheric Administration. 2008. Climate Maps of the United States. Temperature Maps. http://cdo.ncdc.noaa.gov/cgi-bin/climaps/climaps.pl. Accessed: June 15, 2010.

Overmars, K. P., G.H.J. de Koning, and A. Veldkamp. 2003. Spatial autocorrelation in multi-scale land use models. Ecol. Model. 164: 257–270.

Parendes, L. A. and J. A. Jones. 2000. Role of light availability and dispersal in exotic plant invasion along roads and streams in the H. J. Andrews Experimental Forest, Oregon. Conserv. Biol. 14:64–75.

Rossell, C. R., S. Patch, and S. Salmons. 2007. Effects of deer browsing on native and non-native vegetation in a mixed oak-beech forest on the Atlantic coastal plain. Northeast. Nat. 14:61–72.

Rudis, V. A., A. Gray, W. McWilliams, R. O'Brien, C. Olson, S. Oswalt, and B. Schulz. 2006. Regional monitoring of nonnative plant invasions with the Forest Inventory and Analysis program. Pages 49–64 *in* Proceedings of the Sixth Annual FIA Symposium. Denver, CO: USDA Forest Service Gen. Tech. Rep. WO-70.

Russo, S. E., S. Portnoy, and C. K. Augspurger. 2006. Incorporating animal behavior into seed dispersal models: implications for seed shadows. Ecology 87:3160–3174.

Simberloff, D. 2000. Global climate change and introduced species in United States forests. Sci. Total Environ. 262:253–261.

Smith, W. B. and D. Darr. 2004. US Forest Resource Facts and Historical Trends. Washington, DC: U.S. Department of Agriculture Forest Service FS-801.

Spittlehouse, D. L. and R. J. Stathers. 1990. Seedling Microclimate. Victoria, BC: Ministry of Forests, British Columbia, Land Management Rep. 65. Pp. 28–36.

Stohlgren, T. J., D. T. Barnett, and J. T. Kartesz. 2003. The rich get richer: patterns of plant invasions in the United States. Front. Ecol. Environ. 1:11–14.

[USDA] U.S. Department of Agriculture Economic Research Service. 2009. Agricultural Productivity in the United States. http://www.ers.usda.gov/data-products/agricultural-productivity-in-the-us.aspx. Accessed January 13, 2011.

USDA Forest Service. 2009a. FIA Data and Tools. http://fia.fs.fed.us/tools-data. Accessed November 4, 2010

USDA Forest Service. 2009b. Nonnative Invasive Plant Data Tool. http://srsfia2.fs.fed.us/data_center/index.shtml. Accessed August 10, 2011.

USDA Forest Service. 2011. The Forest Inventory and Analysis Database: Database Description and Users Manual Version 5.1. Arlington, VA: U.S. Department of Agriculture Forest Service.

Wang, H.-H. 2009. Occupation, Dispersal, and Economic Impact of Major Invasive Plant Species in Southern U.S. Forests. Ph.D dissertation. College Station, TX: Texas A&M University. 191 p.

Wilcox, J. and C. W. Beck. 2007. Effects of *Ligustrum sinense* Lour. (Chinese privet) on abundance and diversity of songbirds and native plants in a southeastern nature preserve. Southeast. Nat. 6:535–550.

Williams, R. and P. Minogue. 2008. Biology and Management of Chinese Privet. Milton, FL: School of Forest Resources and Conservation Department, Florida Cooperative Extension Service, Institute of Food and Agricultural Sciences, University of Florida.

Wills, C., R. Condit, R. B. Foster, and S. P. Hubbell. 1997. Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest. Proc. Natl. Acad. Sci. U. S. A. 94:1252–1257.

Wiser, S. K., R. B. Allen, P. W. Clinton, and K. H. Platt. 1998. Community structure and forest invasion by an exotic herb over 23 years. Ecology 79:2071–2081.

Young, J. A. and C. G. Young. 1992. Seeds of Woody Plants in North America. Portland, OR: Dioscorides.

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