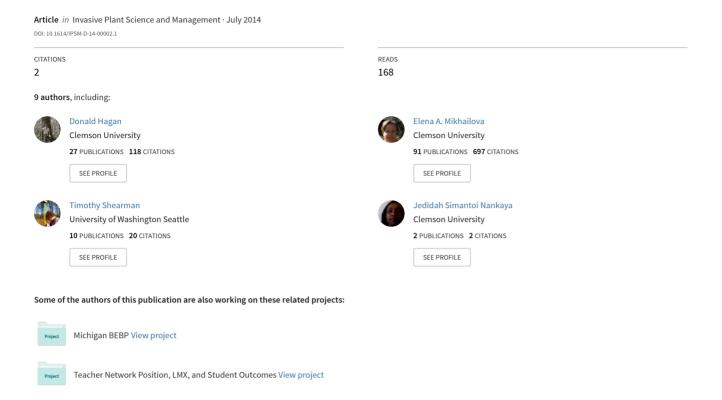
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Author(s): Donald L. Hagan, Elena A. Mikhailova, Timothy M. Shearman, Patrick T. Ma, Jedidah S.

Nankaya, Samantha K. Hart, Hillary E. Valdetero, William C. Bridges, and He Yun

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The Role of Soil and Landscape Factors in Chinese Privet (*Ligustrum sinense*) Invasion in the Appalachian Piedmont

Donald L. Hagan, Elena A. Mikhailova, Timothy M. Shearman, Patrick T. Ma, Jedidah S. Nankaya, Samantha K. Hart, Hillary E. Valdetero, William C. Bridges, and He Yun*

There is a limited understanding about the ecological mechanisms that enable certain plant species to become successful invaders of natural areas. This study was conducted to determine the soil and landscape characteristics that correlate with invasion of Chinese privet (CHP), and to develop a model to predict the probability of CHP invasion in Piedmont forests. A landscape ecosystem classification (LEC) system—based on the percentage of clay in the B horizon, depth to maximum clay (cm), exposure, terrain shape, and aspect (degrees)—was used to determine the soil moisture characteristics of invaded and uninvaded plots. Additional measurements included the cover classes of CHP and other species, litter depth (cm), slope (degrees), overstory basal area (m² ha⁻¹), and soil chemical properties. CHP invasion was negatively correlated with overstory basal area and slope and positively with litter depth and pH. A stepwise logistic regression model containing these four variables was highly sensitive, with an overall accuracy of 78%. Given the accuracy of this model, we propose that it can be used to calculate the probability of invasion in a given area, provided that some basic, readily obtainable site characteristics are known.

Nomenclature: Chinese privet, Ligustrum sinense Lour.

Key words: Alien species, disturbance, exotic, forests, management, nonnative.

The effects of invasive alien plant species on terrestrial ecosystems have been well documented in the ecological literature. These include reductions in species richness and diversity (Hejda et al. 2009), modified disturbance regimes (Mack and D'Antonio 1998), altered nutrient cycling processes (Ehrenfeld 2003), and dramatic changes to forest structure (Hughes and Denslow 2005). Plant invasions also have significant economic implications. Pimentel et al. (2005), for example, estimated the financial impacts of plant invasions (including control costs) to be in the tens of billions of dollars annually in the United States alone. Because of these factors, invasive alien plants and their impacts have been the subject of considerable research interest in recent years (Kolar and Lodge 2001; Richardson 2011). This research, however, has largely been limited to a select handful of species, with a paucity of information currently available about many of the most problematic

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* First, second, third, fourth, fifth, sixth, seventh, and ninth authors: Lecturer, Associate Professor, and graduate students, School of Agricultural, Forest, and Environmental Sciences, Clemson University, Clemson, SC 29634; eighth author: Alumni Distinguished Professor, Mathematical Sciences, Clemson University, Clemson, SC 29634. Corresponding author's E-mail: dhagan@clemson.edu

invasive alien plants (Hulme et al. 2013). Consequently, we still have a limited understanding about the ecological mechanisms that enable certain alien plant species to become such successful invaders, as well as the characteristics that influence a site's susceptibility to invasion (Richardson 2011).

Chinese privet (CHP) was introduced into the United States in 1852 as an ornamental plant around homes, latrines, and for landscaping, because of its fragrant flowers, evergreen or semievergreen foliage, and its ability to do well in many environments—from areas with abundant sunlight, to dense shade (Hanula et al. 2009). It has become widely naturalized in the southeastern United States and is reported to have invaded thousands of acres (Mitchell et al. 2011; Ward 2002). It generally has multiple stems and a shrub-like growth form, with heights ranging from 1.5 to 3.6 m (5 to 12 ft), although it occasionally becomes treesized (Greene and Blossey 2011). CHP has a shallow but extensive root system and it readily forms dense monotypic thickets in forest understories, in many cases converting open park-like forest floors into impenetrable walls of dense vegetation (Greene and Blossey 2011). The transformative success of CHP in forest ecosystems is thought to be largely due to its prolific production of viable seeds and the dispersal of these seeds by birds (Panetta 2000), flowing

Management Implications

Chinese privet (CHP) (*Ligustrum sinense* Lour) is one of the most common woody invasive alien plant species in the Appalachian Piedmont. An improved understanding of the factors that correlate with CHP invasion will benefit land managers in the region, as this species can reduce native diversity, alter forest structure, and be costly to control. We found CHP invasion to be negatively correlated with overstory basal area and slope and positively correlated with litter depth and pH. A model containing these four variables was highly sensitive, being able to predict CHP invasion 78% of the time. By identifying the areas that are most likely to be invaded, this model could facilitate early detection and control of CHP, thereby slowing its spread and helping to conserve native flora and fauna.

water (Ward 2002), and other agents. Because CHP thrives in shade, it spreads rapidly in forests with good canopy cover (Hart and Holmes 2013).

Much of the previous research on CHP has focused on growth characteristics, response to flooding, dispersal rates, impacts on native plants and forest regeneration, and influences on decomposition and nutrient availability (Hanula et al. 2009; Merriam and Feil 2002; Mitchell et al. 2011; Morris et al. 2002). Research in the Piedmont region of the United States has indicated that CHP invasion suppresses herbaceous understory, causing decreases in plant species richness and diversity (Greene and Blossey 2011; Merriam and Feil 2002; Wilcox and Beck 2007). CHP litter has a lower C: N ratio than most of the understory vegetation that it displaces, which results in accelerated nutrient mineralization, especially during summer months (Mitchell et al. 2011). The rapid rate at which CHP spreads impedes the ability of native pine (Pinus spp.), oak (Quercus spp.), and hickory (Carya spp.) to obtain space on the forest floor and adequate light to thrive. As such, CHP can negatively affect a forest's resilience to recover from years of poorly managed agricultural use.

Despite its superior competitive ability, it has been observed that CHP often has a patchy distribution in Piedmont forests (Merriam and Feil 2002). That is, areas that have been densely infested for years are often immediately adjacent to areas where no CHP is present. It is not known if this is due to dispersal limitation or recruitment limitation, but the former seems unlikely considering CHP's prolific rates of fruit production (Urbatsch 2000) and that seeds are readily dispersed by birds, water, and other vectors (Maddox et al. 2010). The possibility that abiotic factors influence a site's susceptibility to CHP invasion (i.e., recruitment limitation) has only recently been suggested. Wang and Grant (2012), created a model based on regional-scale Forest Inventory and Analysis (FIA) data and determined that elevation, proximity to water and a mean extreme maximum temperature of 35 C, along with numerous land use and tenure/ownership variables, correlated strongly with Chinese and European privet (L. *vulgare*) invasion in forests in the southeastern United States. Private lands, particularly those lacking active silvicutural management programs (e.g., fire, site preparation), were particularly susceptible to invasion. Their analyses, however, did not include soils, nor did their study design incorporate within-stand variables such as microsite differences in slope, litter depth, etc. However, studies conducted with other species have indicated that factors such as soil texture, nutrient concentrations, landscape, slope, and terrain shape correlate strongly with invasion (Mitchell et al. 2011). Determining how site characteristics such as these are related with CHP invasion could be an important management tool in deterring its spread, prioritizing resources for early detection and control, and maintaining understory and overstory diversity in southeastern forests (Wang and Grant 2012).

This study was conducted to determine if soil and landform characteristics influence the distribution and abundance of CHP in Piedmont forests in the southeastern United States. We used the Piedmont Landscape Ecosystem Classification (LEC) model along with additional soil measurements and plant surveys to develop a model capable of predicting the probability of invasion by this problematic invasive plant.

Materials and Methods

Study Location. The 7,082 ha (17,500 ac) Clemson Experimental Forest (CEF, Web site: http://www.clemson. edu/cafls/cef/) is primarily an oak/hickory complex located within the Piedmont region of the United States (Figure 1). The forest was planted in the 1930s in order to reclaim eroded agricultural lands, with terracing still visible in some areas today (Hartman and Rentz 1938). The soil orders of this region include Ultisols, Entisols, and Inceptisols. More specifically, the main soil series is Pacolet (fine, kaolinitic, thermic Typic Kanhapludults), although there are two other significant soil series, Cataula (fine, kaolinitic, thermic Oxyaquic Kanhapludults), and Cecil (fine, kaolinitic, thermic Typic Kanhapludults) (U. S. Department of Agriculture–Natural Resources Conservation Society [USDA/NRCS] 2008). The CEF is in the udic moisture regime and thermic temperature regime with a mean annual precipitation of 117.22 cm (46.15 in.) and a mean annual temperature of 17.57 C (63.63 F) (U.S. Historical Climatology Network 2013). Primary overstory species in late-successional sites in the CEF include white oak (Quercus alba L.), water oak (Quercus nigra L.), northern red oak (Quercus rubra L.), yellow-poplar (Liriodendron tulipifera L.), pignut hickory (Carya glabra [Mill.] Sweet) and American beech (Fagus grandifolia Ehrh.). Primary understory species include Japanese honeysuckle (Lonicera

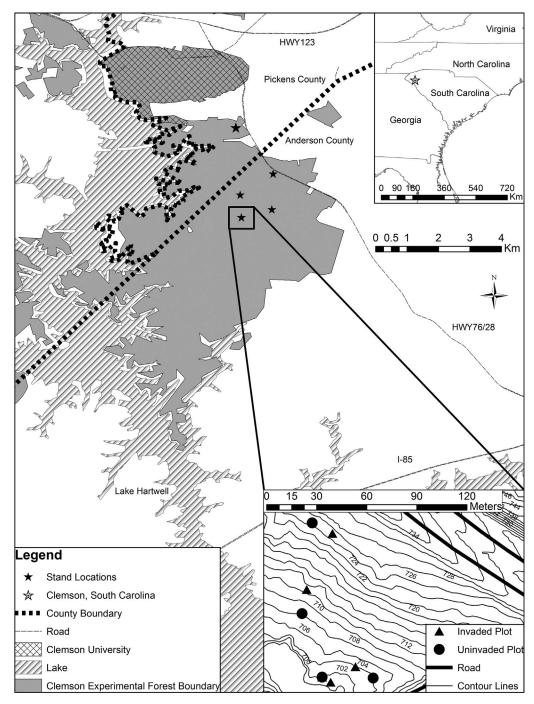


Figure 1. Map of the five study sites (stands) in the southern Clemson Experimental Forest (CEF), in Pickens and Anderson Counties, South Carolina. Inset map (lower right) illustrates the arrangement of invaded and uninvaded plot pairs.

japonica Thunb.), Christmas fern (*Polystichum acrostichoides* [Michx.] Schott), and seedlings and saplings of white oak, northern red oak, water oak, and multiple species of maples (*Acer* spp.).

Soil and Vegetative Sampling. In each of five invaded stands in the CEF (Figure 1), the landscape was divided

into four sections: the topslope; one-third of the way down slope, two-thirds of the way downslope, and the toeslope. At each point on the slope, the plot most severely invaded by CHP was selected (based on a visual estimation of density and cover). Each of these plots was paired with an adjacent uninvaded plot. Uninvaded plots were randomly selected by blindly throwing a ball approximately 15 m in a

random direction. Exceptions were made in sites where the majority of the surrounding area was dominated by CHP. In these cases the nearest uninvaded site was selected.

The location of the plots was recorded using a handheld global positioning system (GPS) device. In the field, a landscape ecosystem classification (LEC) system, adopted from Shelburne et al. (2002), was used. This system uses depth to maximum clay (cm), percent clay at maximum, aspect (degrees), landform index (exposure), and terrain shape index (concavity vs. convexity) to assign an "ecological site unit" score—a measure of where a site falls on a xeric to mesic continuum of site productivity. Additionally, slope (degrees) was measured with the use of a 4-m line level and a carpenter's square. In order to obtain litter depth, we randomly selected four spots in a 4-m² quadrat and measured the litter depth to the nearest cm. Cover for CHP and other species were estimated visually in the same quadrat with the use of the 10 cover classes from Peet et al. (1998). A 10-factor prism was used to estimate overstory basal area (m² ha⁻¹) at each plot center. Dominant overstory and understory composition were also noted. A composite soil sample from the surface horizon was collected from four randomly selected sites in each quadrat. Soils were analyzed for organic matter (loss on ignition), water extractable pH, and Mehlich-1 extractable nutrients (Clemson Agricultural Service Laboratory; Website: http://www. clemson.edu/public/regulatory/ag_svc_lab/index.html).

Statistical Analysis. A stepwise logistic regression was used to identify a set of significant variables that could be used to predict whether or not a site would be invaded by CHP. We checked for multicollinearity by examining the variance of inflation (VIF) for each predictor variable. A receiver operating characteristic (ROC) curve was constructed to determine the adequacy of the model. The ROC curve is a diagnostic measure of a model's usefulness (Hosmer and Lemeshow 2000). The curve measures sensitivity, the probability of making true positive predictions, versus 1specificity, the proportion of making false-positive predictions for different decision thresholds. The decision threshold is the point where we decide between which probabilities we consider to be positive (the plot is invaded) and which probabilities are said to be negative (the plot is not invaded). Adjusting the threshold has consequences. At lower thresholds (moving to the right on the curve), more true positives are predicted, which consequently also leads to more false positive predictions. Likewise, higher thresholds lead to fewer false-positive predictions, but also less true-positive predictions. The higher the area under the curve (AUC), the more accurate the model, with an AUC of 1 being a perfect model (always making a correct prediction).

Jackknife validation was used to evaluate the accuracy of the model further by removing one observation, running the model on the remaining 39 observations, and predicting the outcome of the removed observation (Hosmer and Lemeshow 2000). A decision threshold of 0.6 was used in making predictions (i.e., if the probability was greater than or equal to 0.6, the site was classified as invaded, otherwise the site was considered not invaded). The results of the jackknife validation were then put into a confusion matrix, which showed the ratio of correct predicted and actual observations.

The predictors of invasion from the stepwise logistic regression were also used as response variables in a series of paired-sample t tests. This series of tests enabled us to examine mean differences in the predictors between invaded and uninvaded sites. Paired t tests eliminate the interference of multiple confounding factors beyond our control that could mask the mean differences in the predictors. Differences were considered statistically significant at alpha = 0.05. The Sharipo-Wilk test was used to verify the assumption of normality for the t tests. Moran's I test was used to confirm that the data were not spatially autocorrelated. All analyses were conducted in R Version 3.0.1 (R Core Team 2013).

Results and Discussion

Cover for CHP-invaded plots ranged from 1.5 to 85%, with a mean of 30.4%. Cover was highest in toeslope plots (43.0%), which were generally classified (based on the Piedmont LEC model) as mesic, and in topslope plots (34.8%), which were generally classified as intermediate. CHP coverage values in plots 1/3 and 2/3 of the way down the slope, which ranged from submesic to mesic, were 17.4% and 30.5%, respectively. However, these differences in cover were not statistically significant. Mean non-CHP cover was significantly higher in uninvaded plots (29.1%) than in invaded plots (15.4%) ($t_{19} = 4.96$, P < 0.01). This likely reflects the superior competitive ability of CHP and it underscores the importance of early detection and rapid response, as suggested by Wang and Grant (2012).

CHP is often described as an invader of riparian areas (Merriam and Feil 2002) and disturbed sites (e.g., forest edges and along roadsides) (Kuhman et al. 2010). Our findings somewhat contradict these assertions, as we observed dense infestations irrespective of landscape position. That is, CHP was found not only in wetter toeslope sites (usually near a creek or drainage) and drier topslope sites (usually near a road), but also in interior sites. Although it is likely that the initial CHP invasion occurred in wet or roadside areas, it is clear that the species is not restricted to these sites. These results suggest that microsite differences may be a more important determinant of where CHP can be found—especially in stands with a long history of invasion, such as those where we conducted this study. It is important, therefore, that land managers do not

Table 1. Results of a logistic regression model indicating the soil and landscape variables most significant as predictors of Chinese privet invasion in plots in the Piedmont of South Carolina (n = 40). See Equation 1 for full model formula.

| Predictor | Standard error | P value |
|--------------|----------------|---------|
| Basal area | 0.108 | 0.019 |
| Litter depth | 0.18 | 0.007 |
| Slope | 0.254 | 0.006 |
| Soil pH | 0.18 | 0.047 |

limit their detection, monitoring and control efforts to edge and/or riparian zones, as this would likely cause them to overlook infestations in the forest interior.

The stepwise logistic regression model showed that lower basal area, higher leaf litter depths, flatter slopes, and higher soil pH values were significant for predicting

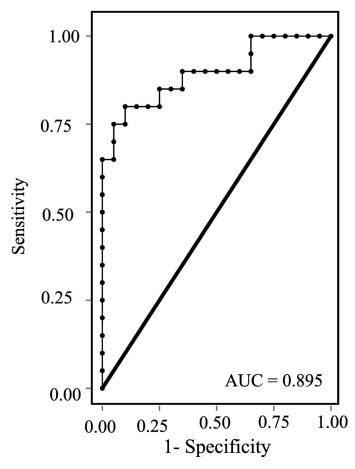


Figure 2. Receiver operating characteristic (ROC) curve for the fitted logistic regression of Chinese privet invasion in Piedmont forests in South Carolina. The curve measures the proportion of true positive predictions (sensitivity) against the proportion of false positive predictions (1-specificity) at different decision thresholds. The diagonal isocline represents the ratio of true positive to false positive expected by chance.

Table 2. Confusion matrix of predicted and observed outcomes of the jackknife validation for the logistic regression model. The model gives probabilities of invasion of Chinese privet in plots in the South Carolina Piedmont. Decision threshold was set to 0.6; predicted probabilities higher than 0.6 were considered invaded.

| | Observed | |
|----------------------|-----------|---------|
| Predicted | Uninvaded | Invaded |
| Uninvaded Invaded | 16 4 | 5 15 |

invaded plots, with P values of 0.019, 0.007, 0.006, 0.047, respectively (Equation 1; Table 1).

$$P(invaded) = \exp[-5.856 - 0.253(BA) + 0.486(litter) -0.694(Slope) + 2.379(soil pH)] -1 + \exp[-5.856 - 0.253(BA) + 0.486(litter) -0.694(Slope) + 2.379(soil pH)]$$
[1]

The ROC curve for the fitted logistic regression is seen in Figure 2. The high AUC (0.895) suggests that this model is a good predictor of the likelihood of invasion. Results of the jackknife model validation further illustrate the accuracy of the model. Table 2 shows the confusion matrix of predicted and observed outcomes with a threshold of 0.6. The model predicted 16 uninvaded plots correctly, with 4 incorrectly identified invaded. The model also predicted 15 invaded plots correctly, with 5 incorrectly predicted as uninvaded. Overall accuracy of the model was 78%, with 80% accuracy in predicting uninvaded sites, and 75% accuracy in predicting invaded sites.

The paired t tests of uninvaded vs. invaded plots yielded several significant relationships. Although invaded and uninvaded plots had identical minimum and maximum basal areas (11.48 m² ha⁻¹ to 32.14 m² ha⁻¹, respectively), the mean basal area of the former was 4.59 m² ha⁻¹ lower than that of the latter (25.94 vs. 21.35 m² ha⁻¹). This difference was statistically significant ($t_{19} = -4.204$, P = 0.0002) (Figure 3).

The basal area in the uninvaded plots was similar to basal areas found in closed-canopy, mature, and old growth deciduous stands (Parker et al. 1985, Means et al. 2000, Jenkins et al. 2001). As basal area is a known function of woody biomass production (Cannell 1984), the uninvaded areas in our study sites are likely to have approached maximum biomass, similar to that of a steady-state forest. In addition to the established canopy trees, the middle, and understory shrubs and seedlings have likely monopolized available space, light, and soil resources. Thus, one possibility explaining the invasion of CHP in areas of

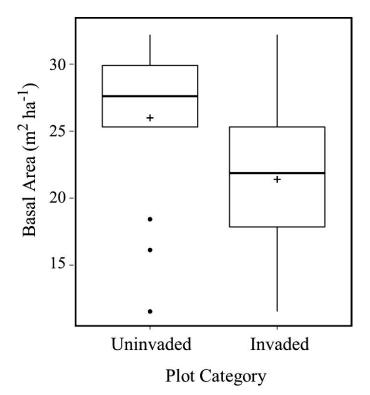


Figure 3. Box plots of basal area (m^2 ha⁻¹) of uninvaded plots (n = 20) compared to invaded plots (n = 20) of Chinese privet in Piedmont forests in South Carolina. Plus signs indicate overall mean of the 20 plots. Boxes represent the interquartile range (IQR). The horizontal line in each box represents the median of the 20 plots. Whiskers extend to plots within 1.5 * IQR. Points outside the whiskers are more than 1.5 * IQR.

lower basal area, and not in sites with higher basal area, is that CHP may have a more difficult time becoming established because of tighter resource competition in high basal area sites. Because many invasive species have been noted to inhabit disturbed sites (Wiser et al. 2002), it may also be possible that CHP invaded low basal area sites after a localized disturbance (e.g., windthrow) resulted in the loss of several large-stemmed trees and scarified the soil, thereby resulting in a pulse of available light and soil resources. If CHP establishment is indeed facilitated by small-scale disturbance such as this, as has been suggested by Wang and Grant (2012), it is imperative that land managers monitor disturbed sites regularly to ensure that invasion does not occur — especially if CHP is already present in the surrounding forest matrix.

In uninvaded plots, the slope ranged from 3 to 17° , with a mean of 7.45° . By comparison, the slope in invaded plots ranged from 1 to 11° , with a mean of 5.65° . Differences between means were statistically significant ($t_{19} = 2.75$, P = 0.01239) (Figure 4).

Physically, flatter sites are more likely to retain more nutrients and soil moisture than steeper ones because of a

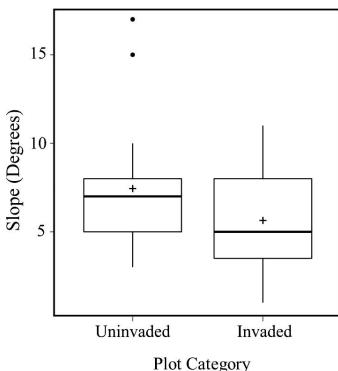


Figure 4. Box plots of slope (degrees) of uninvaded plots (n = 20) compared to invaded plots (n = 20) of Chinese privet in Piedmont forests in South Carolina. Plus signs indicate overall mean of the 20 plots. Boxes represent the interquartile range (IQR). The horizontal line in each box represents the median of the 20 plots. Whiskers extend to plots within 1.5 * IQR. Points outside the whiskers are more than 1.5 * IQR.

lower probability of soil losses during erosion events (Chukwu 2000), and the increased likelihood that rainwater infiltrates rather than runs off (Brady and Weil 2002). Along with providing valuable soil resources, as well as a more optimal seedbed for germination, recruitment may also be enhanced in flatter microsites by the increased likelihood that CHP fruits and seeds accumulate in these

Soil pH in uninvaded plots ranged from 4.3 to 6.0, with a mean of 5.08. Invaded plots had a pH that ranged from 4.2 to 6.0, with a mean of 5.29. When compared to uninvaded plots, invaded plots had a significantly higher mean pH ($t_{19} = 2.78$, P = 0.01724) (Figure 5).

Although we concluded that CHP is more likely to be found in soils with higher soil pH, we cannot determine whether CHP has an increased likelihood of establishment in microsites with higher pH, or if CHP caused this change. The latter, however, may be plausible, as studies have shown that invasive plants frequently alter soil chemical and microbiological properties (Ehrenfeld 2003). Additionally, although there was a trend of higher litter depth in invaded plots (9.05 vs. 7.72 cm), and litter depth was a

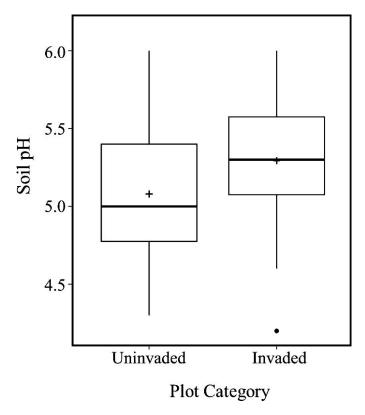


Figure 5. Box plots of soil pH of uninvaded plots (n=20) compared to invaded plots (n=20) of Chinese privet in Piedmont forests in South Carolina. Plus signs indicate overall mean of the 20 plots. Boxes represent the interquartile range (IQR). The horizontal line in each box represents the median of the 20 plots. Whiskers extend to plots within 1.5 * IQR. Points outside the whiskers are more than 1.5 * IQR.

significant predictor of our model, the results of the paired t test were not conclusive ($t_{19} = -1.4076$, P = 0.18; Figure 6). Thicker litter depths may be the result of increased litter accumulation in flatter microsites. Additionally, the accumulation, and subsequent decomposition, of overstory litter may have contributed to the altered soil chemical properties described above. Fire, which has long been suppressed from most Piedmont forests, plays an important role in reducing litter depths and modifying the seedbed to facilitate native plant establishment (Brose et al. 2001).

This study represents one of the first attempts to document the relationship between soil and landscape factors with CHP and develop a model to predict the susceptibility of forest stands to CHP invasion. Overall, our findings suggest that sites with low basal areas and flatter slopes are susceptible to invasion by CHP. Conversely, steep slopes and high overstory basal areas appear to constitute a substantial recruitment limitation. Therefore, land managers may be able to prevent the spread of CHP more efficiently by focusing their early detection

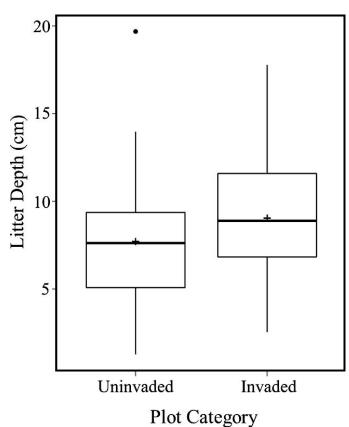


Figure 6. Box plots of litter depth (cm) of uninvaded plots (n = 20) compared to invaded plots (n = 20) of Chinese privet in Piedmont forests in South Carolina. Plus signs indicate overall mean of the 20 plots. Boxes represent the interquartile range (IQR). The horizontal line in each box represents the median of the 20 plots. Whiskers extend to plots within 1.5 * IQR. Points outside the whiskers are more than 1.5 * IQR.

and monitoring efforts on these most susceptible areas. Although some unique soil characteristics were associated with invaded sites, specifically pH and litter depth, we cannot—due to the observational nature of this study—conclude that this was a result or a cause of invasion. A pertinent future study would involve evaluating the performance of artificial plantings of CHP seeds in sites with the four attributes identified in our model. This would help confirm whether or not these site characteristics indeed limit CHP recruitment. Additionally, it would be useful to scale up and assess the factors that influence the dispersal and recruitment of CHP at the landscape scale.

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