THE INFLUENCE OF PAST AND PRESENT LAND USE ON NON-NATIVE PLANT INVASION IN THE SOUTHERN APPALACHIANS

by

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DEDICATION

This thesis is dedicated to my father, Gary L. Kuhman (1946-2004), who encouraged me to follow my dreams to the ends of the earth and taught me that there was no limit to what I could achieve given determination and hard work. His appreciation for the natural world, his passion for life, and his devotion to family have been inspirational. Though his life ended far too early, his legacy will live on.

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ABSTRACT

THE INFLUENCE OF PAST AND PRESENT LAND USE ON NON-NATIVE PLANT INVASION IN THE SOUTHERN APPALACHIANS

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Some non-native invasive plants are well adapted for spread in forested landscapes. Such species pose a threat to forest communities in the southern Appalachians. Both contemporary and historic land use can affect invasion by non-native plants. Factors related to land use, the biotic community, and the abiotic template were investigated at local to regional scales in western North Carolina to determine their roles in shaping the distributions of forest invaders. The influence of agricultural land-use history and roads was evaluated in a forested watershed where cultivated areas had been abandoned a century earlier. A field seeding experiment with non-native Oriental bittersweet (*Celastrus orbiculatus*) was implemented to elucidate the specific factors related to land-use history that might be facilitating invasion. Finally, roadside surveys were conducted throughout a four-county region to determine the distribution of a suite of non-native forest invaders, and the factors explaining their distributions were examined at local and regional scales using linear and generalized linear models. Land-use history was an important determinant of invasion, particular at local scales. Areas with agricultural land-use histories often had overstory communities with high tulip poplar (*Liriodendron tulipifera*) dominance. Such areas had more invasive plants than comparable sites that were never cultivated and

typically dominated by oaks (*Quercus* spp). Field experiment results indicated that higher invasibility in tulip poplar stands could be attributed to thinner leaf litter layers and moister soil conditions. Results from the broader-scale survey showed that the factors explaining distributions of forest invaders throughout the region varied among species and between scales of analysis. At the regional scale, many species were more common closer to the city center (Asheville, NC), at lower elevations, and in watersheds with less forest cover. At the local scale, species responded more strongly to land use and land cover; many were more common in areas with greater forest regrowth and less total forest cover. Overall, results emphasize the important role of land-use history and provide insights regarding the interactions between historic land use and the contemporary landscape that influence non-native plant invasion in the forest-dominated southern Appalachians.

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Dr. Monica G. Turner, Professor of Zoology

INTRODUCTION

Human land use plays a prominent role in shaping landscapes and ecosystems around the world. Between one third and one half of earth's terrestrial surface has been directly transformed by human activities in one way or another (Vitousek et al. 1997). The consequences of such pervasive land-use change are numerous (Foley et al. 2005) and warrant considerable concern regarding their impacts on both local and global ecosystems (Millenium Ecosystem Assessment 2005). By gaining a better understanding of how historic land use and contemporary land-use change affect ecosystems, we can provide a basis for making informed land-use decisions aimed at minimizing detrimental effects and maintaining ecosystem integrity.

Non-native invasive plants pose a serious threat to natural ecosystems throughout the U.S. and worldwide (Vitousek et al. 1996, Mack et al. 2000, Millenium Ecosystem Assessment 2005). Many are capable of displacing native species, disrupting natural succession, and altering ecosystem structure and function (Vitousek et al. 1996, Mack and D'Antonio 1998). Invasive species often present a serious economic concern for landowners and land managers by degrading or displacing valuable crops and natural resources (Pimentel et al. 2000). Understanding and predicting the spread of invasives poses a fundamental challenge to ecology and conservation.

Studies of non-native plant distribution and spread have provided a number of important insights into the factors associated with invasions. Some have taken a trait-based approach to determine what life history attributes of the invasive species themselves make them effective invaders and to predict where they might be most likely to invade (Newsome and Noble 1986, Richardson et al. 1994, Rejmanek and Richardson 1996, Rejmanek 2000), while others have

focused on their current distributions to determine what factors related to landscape or site characteristics tend to influence the observed patterns of invasion (Stohlgren et al. 2002, Bashkin et al. 2003). At broad scales species invasion is often positively correlated with native species richness (Levine and D'Antonio 1999, Stohlgren et al. 2003), suggesting that intact ecosystems with high diversity may be less resistant to invasion than previously thought. Others have underscored the importance of human land use and land-use change in determining patterns of invasion (D'Antonio and Vitousek 1992, Arroyo et al. 2000, Hobbs 2000).

The concept of *invasibility*, as described by Lonsdale (1999) is important for understanding patterns of plant invasion related to land use. Invasibility is determined by the intrinsic qualities of the system itself that make it more or less susceptible to invasion – propagule pressure and the inherent characteristics of a species also influence invasion success. It has long been recognized that disturbance plays a major role in determining invasibility of an ecosystem (Elton 1958, Crawley 1987, Hobbs and Huenneke 1992). One possible explanation for this trend was offered by Davis et al. (2000) who suggested that fluctuations in the levels of resources might contribute to the invasibility of a system. If, for example, a disturbance event such as that caused by human land use increases resource availability, species that were previously limited by one or more of those resources could become established. Changes in light conditions, soil chemistry, or soil/litter structure that are associated with land use may thus provide an opportunity for invasion.

Intact forests have often been described as resistant to invasion by non-native plants (Crawley 1987, Rejmánek 1989, Brothers and Spingarn 1992, Von Holle 2005), perhaps owing to the slower invasion rates and smaller pool of invaders capable of spread in forested landscapes as compared to more open, disturbed habitats (Martin et al. 2009). Nonetheless, certain non-

native plants are well suited to establishment and spread in areas of intact forest, and such species can pose a considerable threat to forest ecosystems (Wyckoff and Webb 1996, Meekins and McCarthy 1999, Ehrenfeld et al. 2001). Contemporary land use patterns (e.g., those related to roads, residential development, and agriculture/forestry) might influence forest invasion by providing conduits for rapid spread and the propagule pressure necessary for invasion of adjacent forest by non-native plants. Land-use history can also affect plant invasion (Lundgren et al. 2004, DeGasperis and Motzkin 2007, Von Holle and Motzkin 2007), though the specific reasons for its influence are poorly understood.

The research described herein aims to address the following overarching question: **How do land-use history and contemporary patterns of land use in the southern Appalachians affect invasion by non-native plants?** In Chapter 1, I begin by asking whether forested areas that were cultivated and subsequently abandoned roughly a century ago had more non-native invasive plants than nearby reference areas without agricultural land-use histories. The study was conducted in a 2500-ha watershed in western North Carolina, and employed a field survey methodology for determining presence/absence and abundance of invasive plants in the respective areas. Effects of road proximity and local topography on invasive distribution were also considered.

Chapter 2 details a set of field experiments designed to follow up on findings described in Chapter 1, which revealed that historic agricultural areas that were dominated by tulip poplar (*Liriodendron tulipifera* L.) were more likely to contain non-native invasive plants and in higher abundance than the reference areas, which were typically dominated by oaks. The purpose of the field experiments was to determine the specific factors that might be facilitating invasion of Oriental bittersweet (*Celastrus orbiculatus* Thunb.), a common forest invader in the study area.

Leaf litter manipulations and potted soil translocations were used to address the respective roles of litter, soils, and site conditions that might explain differences in germination and first-year survival of *C. orbiculatus*.

In Chapter 3, I take a broader-scale look at the distribution of a suite of fifteen non-native invasive plants capable of spread in southern Appalachian forests. Field surveys were conducted along roads in twenty-five watersheds throughout a four-county region of western North Carolina that represented a range of forest cover and development intensity. Linear and generalized linear models were subsequently used to determine which factors related to contemporary land use, landscape context, land-use history, and topography explained invasive presence/absence and abundance at both the local and watershed scales. This multi-species, multi-scale approach allows for generalizations to be made regarding the ways in which forest invaders respond to the various factors being considered and to determine how the scale of analysis can affect conclusions.

Overall, the work described herein provides valuable insights regarding the roles of contemporary and historic land use in shaping patterns of invasion by non-native plants in the southern Appalachians. In particular, the results underscore the important influence of land-use history on the invasion process, and they impart a general reminder of the enduring legacies that human land use can bestow on ecosystems. Although land-use history in forests is frequently overlooked by all but the most discerning eyes, it can profoundly affect forest communities and interact with the contemporary landscape to create complex patterns to which species respond. Given the rich land-use history of forests in eastern North America and many other regions around the world, greater efforts should be made to document local and regional land-use histories and to closely examine their role in shaping contemporary ecosystems.

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CHAPTER 1

Agricultural land-use legacies and non-native plant invasion in a southern Appalachian forest 100 years after abandonment[1]

Abstract

Land-use history can play a considerable role in shaping contemporary landscapes and ecological communities. In this study we considered how agricultural land-use history affects the distribution of non-native invasive plants in a forested southern Appalachian watershed approximately a century after abandonment. We addressed two overarching questions: (1) Does agricultural land-use history affect the presence and abundance of invasive plants in the forest understory? (2) What specific abiotic and biotic factors are associated with their presence and abundance? The study was conducted at the Bent Creek Experimental Forest in western North Carolina, USA. Areas that were previously in cultivation and abandoned around 1905 were compared with nearby reference sites that were never cultivated. The most common invasive plant species encountered were Oriental bittersweet (*Celastrus orbiculatus* Thunb.), Japanese stiltgrass (*Microstegium vimineum* Trin.) and Japanese honeysuckle (*Lonicera japonica* Thunb.). Invasive plants occurred more frequently and in higher abundance in the formerly cultivated sites. Non-native invasive plants were more abundant in plots adjacent to roads than in plots 50 m away, but presence/absence of invasives was not significantly affected by road adjacency. Plots positioned downslope from roads had greater likelihood of presence and higher abundance of invasives. Soil exchangeable cation concentration and pH were positively correlated with presence and abundance of invasive plants. Areas in which tulip poplar (*Liriodendron tulipifera*

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L.) was the dominant overstory species had higher concentrations of soil cations, higher pH and greater abundance of invasive plants. These tulip poplar-dominated stands typically occurred in historic agricultural areas. Results suggest that agricultural land-use history at Bent Creek may be acting indirectly to facilitate plant invasion by causing a shift in overstory community composition via succession that in turn creates more suitable edaphic and understory conditions for the invaders. Disentangling the cause/effect relationships between historic land use, the biotic community and the abiotic template presents a challenge, but understanding the role of land-use legacies may provide important insights regarding the mechanisms underlying the establishment and spread of invasive plant species in forest ecosystems.

Introduction

Non-native invasive plants represent a significant driver of change in natural ecosystems. Many invasive species are capable of displacing native species, disrupting natural succession and altering ecosystem structure and function (Vitousek et al. 1996, Mack et al. 2000). They often present a serious economic concern for landowners and land managers by degrading or displacing valuable crops and natural resources (Pimentel et al. 2000). In the forests of the southeastern U.S., an increasing number of invasive plant species are proliferating and threatening forest biodiversity and economically important timber regeneration (SAMAB 1996). Understanding and predicting the spread of non-native species poses a fundamental challenge to ecology and conservation. In this study we seek to gain a better understanding of the factors influencing the establishment and spread of non-native invasive plants in the southern Appalachians. Of particular interest is the role that historic land use plays in determining patterns of invasion in the forest understory a century after agricultural abandonment.

A number of studies have addressed the impacts of land-use legacies and demonstrated their long-lasting effects on biotic and abiotic characteristics of ecosystems (Koerner et al. 1997, Compton and Boone 2000, Dupouey et al. 2002, Foster et al. 2003, Flinn and Vellend 2005). A handful of studies from the northeastern United States have implicated land-use history in the establishment and spread of non-native invasive plants. For example, past land use was the most important predictor of invasive cover and richness in a forested New England landscape, with more invasives occurring in formerly residential or agricultural areas (Lundgren et al. 2004). In another study, the shade-tolerant invasive, *Berberis thunbergii* was more common in post-agricultural forests than in areas that were continuously forested in Massachusetts (DeGasperis and Motzkin 2007). VonHolle and Motzkin (2007) similarly found that areas in coastal New England that were previously cultivated had more invasive plants than areas without a soil disturbance history. Meiners et al. (2002) noted that although invasive plant abundance declined after 20 years of forest regrowth in ten New Jersey old fields, a new suite of shade-tolerant invasive species were increasing in abundance, possibly representing the next wave of invasion. These studies provide important insights regarding the influence of land-use history on contemporary patterns of plant invasion. However, little is known about the relationship between historic land use and plant invasion outside the northeastern United States, and to our knowledge no studies have employed a paired sampling design to control for differences in topography and edaphic conditions that might be correlated with the land-use history.

Contemporary land use and landscape context is also likely to influence patterns of invasion. Roads, for example, provide a conduit for the spread of many invasive plants; the perpetual disturbance and high light conditions along roads provide suitable conditions for the establishment, growth, and propagation that can facilitate spread into adjacent forest (Luken and

Goessling 1995, Parendes and Jones 2000, Watkins et al. 2003, Flory and Clay 2006). Historic land-use patterns are overlain by the contemporary landscape to create a complex mosaic to which invasive plants respond. If we are to understand patterns of plant invasion, we likely need to consider both the contemporary landscape context and the less obvious patterns of historic land use.

Little is known about the specific factors related to land-use history that might facilitate invasion. While there is evidence that land-use history can be the *ultimate* driver of invasion in certain areas, the *proximate* causes are often poorly understood. In some cases, land use may create a disturbance that provides an immediate opportunity for invasion by increasing light availability or creating a seedbed through removal of litter and/or disturbance of the surface soil (Hobbs and Huenneke 1992). Once the species becomes thus established, it may be possible for it to persist throughout successional stages at that site. In other cases, land-use change may facilitate invasion by causing fluctuations in levels of resources such as soil nutrients that persist for some period of time (Davis et al. 2000), e.g., soil amendments added to agricultural fields. Still another possibility is that land-use history may facilitate invasion only *indirectly* through its influence on succession, resulting in a community assemblage that differs from that which was present prior to the land use and in turn alters site conditions in a manner that facilitates invasion.

Disentangling the factors related to land-use history that influence invasion presents a considerable challenge given the dearth of information regarding pre-agricultural conditions in most areas and the inevitable correlations among factors that might be contributing to invasibility. However, by employing a paired sampling design to control for differences in topography and geology between historic agricultural and reference sites in this study, we are well suited to identify potential mechanisms underlying the invasion process. We address two

overarching questions: (1) Does agricultural land-use history affect the presence and abundance of non-native invasive plants in the forest understory? (2) What abiotic and biotic factors are associated with the presence and abundance of invasive plants in the forest understory? We subsequently discuss how these factors relate to and/or interact with land-use history to influence invasion by non-native plants. In doing so, we explore the underlying mechanisms driving invasion in historically altered forests.

Methods

Study Area

The study was conducted at the Bent Creek Experimental Forest (BCEF), 15 km southwest of Asheville, North Carolina, USA (Fig. 1). The 2500-ha BCEF is situated within the French Broad River Basin in the Southern Blue Ridge Province. The elevation range at BCEF is 700-1100 meters. It receives on average 120 cm of precipitation per year. Mean winter temperature is 4℃ and mean summer temperature is 22℃ (Southeast Regional Climate Center 2006). Granites, gneisses and schists dominate the bedrock geology of the Bent Creek basin, and soils are predominantly Ultisols and Inceptisols. The basin is covered primarily by mixed mesophytic and mixed oak forest. Common overstory species include *Quercus coccinea, Q. velutina, Q. prinus, Q. alba, Oxydendrum arboreum, Pinus rigida* and *P. echinata* on xeric sites. On the more mesic lower slopes and coves, dominant species include *Liriodendron tulipifera* and *Q. rubra,* with *Tsuga canadensis, Fagus grandifolia* and *Cornus florida* also relatively common. Other common species found throughout the basin include *Acer rubrum, Carya* spp. and *P. strobus*.

The first Europeans settled the basin beginning in the 1790s, eventually displacing the Native American inhabitants who preceded them. Between 1795 and 1900, a road network and over 100 homes were constructed in the basin, and approximately 600 ha (23% of the basin) were cleared for cultivation (Nesbitt and Netboy 1946). Timber extraction occurred largely for construction and fuel wood purposes and, beginning in the late 1800s, for commercial purposes as well. George W. Vanderbilt purchased most of the basin between 1900 and 1910 to expand the vast Biltmore estate, at which time nearly all cultivated land was abandoned. Subsequent forest regrowth ensued, with periodic timber harvesting throughout the basin. The U.S. Department of Agriculture Forest Service has managed the basin since the establishment of BCEF in 1925.

Data Collection

Data were collected between June and August 2006. Twenty study sites were chosen *a priori* based on a land-use history report and corresponding map produced for BCEF (Nesbitt 1941). Four 20 x 20 m plots were established at each site, for a total of 80 plots distributed throughout the watershed. At each site, two plots (one adjacent to the road and one 50 m from the road edge) were established in an area that was previously cultivated (hereafter *historic agricultural* or *HA* plots), and two plots (one adjacent to the road and one 50 m away) were established in a nearby reference area that was never in cultivation. HA plots were located in areas that had been in cultivation for between 30 and 100 years prior to abandonment. Reference plot locations were selected based on physiographic similarities and proximity to their paired HA plots to control for differences in topography and bedrock geology. All plots were in relatively

mature forest stands (with basal area >20 m^2ha^{-1}); locations with obvious silvicultural treatments (e.g., recent timber harvest or plantation stands) were avoided.

Slope was determined for each plot using a clinometer. Aspect was converted from degrees azimuth (θ) to an environmental index of moisture availability (A') adapted from Beers et al. (1966): $A' = \cos(22.5^\circ-\theta)+1$. North-northeast (22.5º) is considered here to represent the aspect with the highest moisture availability (Day and Monk 1974) and takes on a value of 2. Correspondingly, the aspect with the lowest moisture availability (SSW) takes on a value of 0, and the index increases symmetrically from 0 to 2 as the compass direction changes in either direction from SSW to NNE. A terrain shape index (TSI) was used to estimate the concavity or convexity of the local landform by averaging slope gradients recorded from the center of the plot to its edge in the eight sub-cardinal directions (McNab 1993). A positive TSI indicates a concave landform, whereas a negative TSI indicates a convex landform.

Soils were sampled to a depth of 15 cm after removal of the organic layer. In each plot five soil samples were collected using a 5-cm diameter soil corer and combined as a composite sample. Soils were dried, sieved and later analyzed by the University of Wisconsin-Madison Soil and Plant Analysis Lab to determine total N (organic-N, NH_4^+, NO_3^- and NO_2), organic matter, P, K^+, Ca^{++}, Mg^{++} and pH. We also performed soil particle-size analysis using the hydrometer method (Gee and Bauder 1986) to determine percent clay, silt and sand for each of the soil samples.

Overstory canopy cover was estimated using a spherical densiometer. Measurements were taken at the plot center and at each of the vertices; the five measurements were then averaged to estimate the canopy cover for the plot. The overstory community was surveyed by identifying and measuring the diameter of all trees >10 cm DBH within the 20 x 20 m plots.

Understory vegetation sampling was conducted in 25 1-m^2 quadrats arranged in a 5 x 5 grid, spaced every five meters within the 20 x 20 m plot. In each quadrat non-native plant species were identified, and their cover was estimated using eight modified Braun-Blanquet cover classes (Braun-Blanquet 1932). Total native ground layer vegetation cover (within 0.5 m the ground) and total native shrub layer cover (0.5 to 2.5 m above the ground) were estimated similarly. Quadrat-level native species richness was determined by tallying all vascular plant species within each quadrat that occurred within 0.5 m of the ground. Litter depth was estimated for each quadrat using a wire probe inserted through the leaf litter to the surface of the soil. Quadrat-level measurements were averaged across all quadrats in a plot to calculate mean plot-level values. In the case of vegetation measurements, the cover classes were converted to percent cover using the midpoint of each class before averaging across the quadrats to estimate percent cover for the plot.

Data Analysis

A two-way Chi-square analysis was used to test for differences in the frequency of invasive presence in plots that differed in land-use history (HA vs. reference) and proximity to roads (adjacent vs. 50 m away). Tests of partial independence (Zar 1996) were performed to determine the respective roles of land-use history and proximity to roads.

We used generalized linear mixed models (GLMMs) to determine which variables best explained the presence/absence of non-native invasive plants observed in the plots (n = 80). These logistic GLMMs were fitted using the *lmer* function in R (R Development Core Team 2006) with a logit link. The function employs the Laplace approximation for parameter estimation (Bates and Sarkar 2006). Linear mixed-effects (LME) models were similarly used to

explain the abundance (cover) of invasive species for those plots in which they were present (*n* = 38). The *lme* function (Pinheiro and Bates 2000) was used in R to fit the linear mixed models using the restricted maximum likelihood (REML) method of parameter estimation. In both cases, *site* was treated as a random effect. In the case of the LME models, invasive cover was log transformed to achieve normality prior to model fitting. Backward stepwise model selection was used to determine which explanatory variables to include in the models. Variables with estimated *z*-values (for logistic GLMMs) or *t*-values (for linear mixed models) >2 were selected for inclusion in the models. Explanatory variables used in model selection included land-use, biotic, topographic, and edaphic variables (see Table 1). In addition to road adjacency, we included a variable describing whether plots were located upslope or downslope from the road. Due to correlations among soil chemistry and texture variables, principal components analysis (PCA) was used to reduce the number of variables by using the axis scores from the resulting ordination (McCune and Mefford 1999). Elevation was excluded from model selection because of the narrow altitudinal range represented by the Bent Creek watershed. Quadrat-level native species richness was excluded due to high (positive) correlation with the soils PCA axis 1 scores (exchangeable cations and pH).

We considered the relationship between overstory community composition and land-use history using non-metric multidimensional scaling (NMDS). Similarly, NMDS was used to explore how overstory composition was related to the presence/absence and abundance of non-native invasive plants. Total basal area (of trees >10-cm DBH) for each species was square root transformed prior to ordination of sampling units (plots). NMDS was performed in R (R Development Core Team 2006) using the *metaMDS* function in the vegan package (Oksanen et al. 2005). The function employs multiple starting configurations to ensure that a stable solution

is reached. Sørenson (Bray-Curtis) distance was used to generate the dissimilarity matrix. The relationship between the overstory species and the NMDS solution was explored by plotting their centroids in the ordination space. We explored the relationship between overstory community composition and environmental variables through a vector fitting procedure using the *envfit* function in the vegan package (Oksanen et al. 2005). Correlations were calculated between the respective environmental variables and the NMDS solution. Significance of fitted vectors was assessed using permutation tests with 1000 permutations.

Results

The three most common invasive plant species in the understory at BCEF were *Celastrus orbiculatus* Thunb. (in 44% of plots), *Microstegium vimineum* Trin. (in 18% of plots) and *Lonicera japonica* Thunb. (in 13% of plots). Less common invasive species included *Rosa multiflora* Thunb., *Elaeagnus umbellata* Thunb., and *Albizia julibrissin* Durazz. These invasive plant species frequently co-occurred in the forest understory. Initial analyses were performed separately for the species and indicated very similar results. Subsequent analyses therefore grouped all non-native invasive plant species together.

Based on the two-way contingency table (Table 2), a Chi-square analysis of partial independence showed that presence/absence of invasives was dependent on land-use history (χ^2 = 16.9, $P < 0.001$), with invasives more likely to occur in the historic agricultural (HA) plots than in the reference plots. However, presence/absence of invasives was independent of proximity to roads (χ^2 = 2.6, P = 0.456). Abundance (percent cover) of invasives also varied with land-use history. For those plots in which invasive species were present, cover was higher in the HA plots (paired *t*-test: t = 2.61, P = 0.013); the mean cover in the HA plots was 4.0% (*SE*

= 1.3, *N* = 28) and the mean cover in the reference plots was 0.6% (*SE* = 0.2, *N* = 10).

PCA results for the soils data revealed two axes to be used in the regression models (Table 3). Axis 1 represents a gradient of exchangeable cations (Ca^{++}, K^{+} and Mg^{++}) and pH (all positively correlated with axis 1), explaining 35.2% of the variation. Axis 2 explained 25.2% of the variation and represented a gradient in soil texture and organic matter. Higher axis 2 values are associated with sandier soils and lower organic matter. Phosphorus and total N were included independently in the regression analyses since they were not strongly correlated with PCA axis 1 or 2.

Results from the logistic GLMMs revealed several important variables for explaining the presence/absence of non-native invasive plants (Table 4). The best model included land-use history (invasives more likely present in HA sites), topographic position with respect to roads (more likely downslope from roads) and soils PCA axis 1 (more likely in plots with higher exchangeable cation concentrations and pH).

Results from the linear mixed model selection, in which invasive cover was the response variable, were similar to those for the presence/absence model selection (Table 5). The best model for explaining the abundance of invasive plants again included land-use history (higher abundance in HA sites), topographic position with respect to roads (higher abundance downslope from roads), and soils PCA axis 1 (higher abundance in plots with higher exchangeable cation concentrations and pH). Proximity to roads was also included in the best model for invasive abundance, with greater cover in plots adjacent to the road than those 50 m away.

A two-dimensional NMDS solution was chosen for the overstory community ordination, with a final stress of 0.23 (Fig. 2). Successional species such as *Liriodendron tulipifera*, *Betula lenta* and *Prunus serotina* were positively correlated with the first NMDS axis, and the oak

species, *Quercus coccinea*, *Q. alba*, *Q. velutina* and *Q. prinus* were negatively correlated (Fig. 3), suggesting a land-use history gradient (see Appendix 2 for average basal areas of overstory species in historic agriculture and reference plots). *Q. prinus* was positively correlated with the second NMDS axis and the three pine species, *Pinus strobus*, *P. rigida* and *P. virginiana* were negatively correlated, perhaps revealing a gradient in topographic position. Both historic land use and presence of invasive species were positively correlated with the first axis (Fig. 2). The abundance (percent cover) of invasive species was also much higher in plots represented along the upper end of the first NMDS axis (Appendix 1).

Correlations between environmental vectors and the NMDS solution (Fig. 4 and Table 6) revealed several notable relationships. The concentrations of exchangeable cations (Ca^{++}, Mg^{++} and K^{+}), pH and total N were all positively correlated with axis 1 (dominance by *L. tulipifera* and other successional species vs. *Quercus* spp.). Average quadrat-level native species richness was also positively correlated with the first axis, and litter depth was negatively correlated. The most notable correlations with the second axis (dominance by *Q. prinus* vs. dominance by *Pinus* spp.) were the positive correlations with slope and soil organic matter.

Discussion

Non-native plant invasion at BCEF was associated with several abiotic and biotic factors including land-use history, contemporary landscape context, soil chemistry and overstory composition. Understanding how these factors interact and how they might be influencing invasion presents a challenge but may offer important insights into mechanisms underlying the invasion process. Although the shade-tolerant invasive species observed in our study vary in

their life history traits, physiology, growth form and dispersal mechanisms, it is noteworthy that they seem to be responding to similar factors and invading similar areas at BCEF.

There was a marked influence of land-use history on non-native invasive plants at BCEF. The likelihood of invasive presence and the abundance of invasive plants were both considerably higher in areas that were previously cultivated. Among plots in which invasives were present, they were on average seven times more abundant in the historic agricultural (HA) sites.

With respect to the contemporary landscape, abundance of invasive plants varied depending on position relative to roads, but presence did not. The importance of roads as conduits for invasive plants is well known, particularly for shade-intolerant, "weedy" species (D'Antonio et al. 1999, Forman et al. 2003, Gelbard and Belnap 2003, Christen and Matlack 2006). Less is known about the role of roads in facilitating invasion of intact forest, but several studies have highlighted their importance for invasion of the understory by shade-tolerant species (Luken and Goessling 1995, Parendes and Jones 2000, Watkins et al. 2003, Flory and Clay 2006). Our results indicate that where invasive plants were present along roads, they commonly occurred beyond 50 m from the road corridor, albeit at lower abundance, suggesting that populations of invasives close to roads may be facilitating spread into intact forest. The shade-tolerant invasive plant species encountered in our study exhibit considerable plasticity in their response to light conditions, with photosynthetic and/or growth rates increasing with light availability [e.g., *Celastrus orbiculatus* (Ellsworth et al. 2004, Leicht and Silander 2006), *Microstegium vimineum* (Horton and Neufeld 1998) and *Lonicera japonica* (Baars and Kelly 1996)]. This response may enhance growth in populations adjacent to roads, and the more robust populations may then exert sufficient propagule pressure to facilitate invasion of the adjacent forest understory. Though population densities may be low away from road edges, the presence

of invasive plants in the forest understory has implications for forest management; subsequent disturbance events such as windthrow or timber harvest could result in a rapid increase in the local abundance of these sparsely established invasive plants.

Topographic position with respect to roads was important in explaining both the presence and abundance of invasive plants at BCEF. Invasives were more likely to be present and in higher abundance in plots located downslope from roads. This pattern underscores the importance of road corridors as propagule sources for invasion of the adjacent forest, and it suggests that short-distance dispersal agents such as gravity and surface water likely exert a disproportionate propagule pressure downslope from roads. A similar pattern of invasion was observed for *Phytophthora lateralis*, a root pathogen of Port Orford cedar in the US Pacific Northwest where infection was considerably more common in host trees positioned downslope from roads (Jules et al. 2002). The role of topographic position with respect to roads also has implications for forest management. It suggests, for example, that a disturbance downslope from a road along which invasive plants are established would likely result in a disproportionate increase in invasive abundance compared to a disturbance upslope from the road.

Areas at BCEF where invasive plants were present and in higher abundance were associated with high soil cation concentrations and pH. Such areas were commonly found in formerly cultivated sites. Land-use history can have long-lasting effects on soil chemistry (Koerner et al. 1997, Compton and Boone 2000, Dupouey et al. 2002), but it remains unclear whether differences in soil chemistry are the direct results of the land use itself or whether they are indirectly related. There are several possible explanations for the relationship between soil chemistry and agricultural land-use history at BCEF. (1) European settlers could have preferentially chosen more fertile sites as those most suitable for cultivation. Although soil

fertility undoubtedly played a role in selection of suitable agricultural sites, the reference sites in our study were chosen to represent the same topographic and edaphic conditions as the respective HA sites; it is therefore unlikely that the observed differences in soil chemistry between these paired sites are strictly due to variation in pre-agricultural site conditions. (2) The differences in soil chemistry observed today could be a direct result of the agricultural activities (e.g., soil amendments and/or management) that have persisted for a century after agricultural abandonment. However, the agriculture practiced at BCEF was low-input subsistence agriculture, and cultivation lasted only a few decades to a century in any given site. Although crop rotations of corn, wheat and rye were common (Nesbitt and Netboy 1946), it is unlikely that any soil amendments were applied. (3) Ecosystem-level processes that were set in motion at the time of agricultural abandonment could have produced and perpetuated the differences in soil chemistry that are apparent in the HA areas today. Forest succession likely resulted in a community composition following abandonment that differed considerably from that prior to cultivation and from adjacent uncultivated areas. The observed differences in soil chemistry may be a product of these differences in community composition.

Many of the historic agricultural sites at BCEF were associated with dominance by early successional tree species, particularly tulip poplar (*Liriodendron tulipifera* L.). Tulip poplar is a long-lived tree species capable of persisting in the canopy for over 200 years (Beck 1990). In the southern Appalachians, tulip poplar is well suited to both cove hardwood and mid-slope mixed hardwood forests and achieves its highest dominance in even-aged stands following larger-scale disturbances. In an experimental forest-to-grassland-to-forest conversion experiment in western North Carolina, there was a shift from oak dominance before forest clearance to tulip poplar dominance after 30 years of forest regrowth (Elliott et al. 1998). A clear-cut experiment

conducted in the same region showed a similar shift to tulip poplar dominance after 20 years of forest regrowth (Elliott et al. 2002).

Our results indicate that tulip poplar dominance was positively correlated with soil exchangeable cation concentration and pH and negatively correlated with litter depth (see Figs. 3 and 4). Certain tree species are known to regulate the cycling of calcium and other base cations in forest ecosystems (Blair 1988, Dijkstra and Smits 2002, Fujinuma et al. 2005, Tripler et al. 2006, Dauer et al. 2007). The leaves of such trees have high concentrations of base cations and decompose rapidly after abscission, thus redistributing the cations from deeper horizons to the soil surface via litter fall (Thomas 1969, Dijkstra and Smits 2002). The leaves of *L. tulipifera* decompose rapidly due to their relatively low lignin and C:N ratio (Mudrick et al. 1994, Adams and Angradi 1996, Kominoski et al. 2007), and they contain high cation concentrations (Coile 1937, Shugart Jr et al. 1976, Boettcher and Kalisz 1990, Adams and Angradi 1996). Others have noted that areas with high tulip poplar dominance in the southern Appalachians tend to have soils with high concentrations (Kalisz 1986) and less spatial heterogeneity (Fraterrigo et al. 2005) of exchangeable cations, particularly calcium.

While studies have demonstrated the importance of cations in forest ecosystems (Wilmot et al. 1996, Van Breemen et al. 1997, Finzi et al. 1998), little is known about their role in the spread of invasive exotic plants. One study in southeastern New York forests determined that plant invasion was positively correlated with soil Ca^{++} and Mg^{++} concentrations (Howard et al. 2004). Soil pH was also found to be positively correlated with invasion by *M. vimineum* (Cole and Weltzin 2004) and *C. orbiculatus* (Silveri et al. 2001, Pande et al. 2007). Further study is required to determine whether soil cation concentrations and pH influence invasibility in the

southern Appalachians and whether the overstory community is indeed responsible for these differences in soil chemistry.

Although tulip poplar dominance has not explicitly been implicated in plant invasions, certain invaders seem to have an affinity for successional forests. For example, *C. orbiculatus* was more common in successional forest stands with reduced oak dominance at BCEF (McNab and Loftis 2002) and in southern Illinois (Pande et al. 2007). Aside from soil chemistry, there are other factors that differ between the oak-dominated stands that are common in areas without a large-scale disturbance history and the tulip poplar-dominated successional stands. Some of these factors could also influence their invasibility. For example, the layer of course organic material tends to be thicker in the oak-dominated stands and may provide a physical barrier to establishment by invasive plants. Other factors related to difference in the native understory, light conditions, or soil microbial communities could also explain differences in invasibility between the stand types.

It is noteworthy that in our study the areas with higher concentrations of soil cations and pH (i.e., those dominated by tulip poplar) also had higher native species richness. This suggests that conditions in the tulip poplar-dominated stands may be more favorable for plant growth in general, enhancing overall species richness in their understories. The similar response by many native and non-native species alike to favorable conditions may in part explain the oft-observed phenomenon whereby areas with higher native species richness also contain more non-native species (Levine and D'Antonio 1999, Stohlgren et al. 1999).

The success of an invasion depends on numerous factors related to the invader itself and the environment to which it is responding, and disentangling these factors to determine the specific drivers of invasion presents a challenge. Land-use history plays an important role in

shaping the ecosystems that we see today, and there is mounting evidence that historic agricultural land use contributes to invasibility of forested landscapes (Meiners et al. 2002, DeGasperis and Motzkin 2007, Von Holle and Motzkin 2007). However, our limited understanding of the specific mechanisms whereby land-use history facilitates invasion merits further investigation. More field studies are needed in regions that have undergone agricultural land abandonment to determine which factors are most frequently associated with plant invasions. There are inherent difficulties in determining which factors related to land-use history actually drive invasion, but field and greenhouse experiments may provide a means for such factors to be addressed in isolation and in controlled combinations. Our study suggests that historic land use may affect invasion indirectly through changes in understory and edaphic conditions associated with forest succession following agricultural abandonment. In particular, the results demonstrate the need to further explore the relationship between land-use history, overstory community, soil chemistry and invasion by non-native plants. The mosaic of historic land use may also interact in important ways with the contemporary landscape to influence patterns of invasion. This study imparts a general reminder of the important role that land-use history can play in shaping contemporary ecosystems.

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Table 1. Explanatory variables used in model selection. The same explanatory variables were used in both the generalized linear mixed-effects logistic models (GLMM) with invasive presence/absence as the response variable and the linear mixed-effects (LME) models with invasive abundance (cover) as the response variable.

Explanatory variable	Description of explanatory variable
Land use	
HA	Historic agricultural site (1) vs. reference site (0)
Road	Adjacent to road (1) vs. 50 m from the road (0)
Downslope	Positioned downslope (1) vs. upslope from the road (0)
Topography	
Slope	Slope gradient (%)
Aspect	Moisture availability index [$A' = \cos(22.5^{o} - \theta) + 1$]
TSI	Local terrain shape index (convex < 0 < concave)
Biotic community	
BA	Total basal area of trees >10 cm DBH
Canopy	Overstory canopy cover (average % cover)
Shrub	Average shrub cover (0.5–3 m above ground)
Native cover	Ave. native ground layer cover (<0.5 m above ground)
Soils and litter	
Soils A1	Soils PCA 1 scores (exchangeable cations and pH)
Soils A2	Soils PCA 2 scores (soil texture and organic matter)
Total N	Total nitrogen (not explained by PCA 1 or 2)
P	Phosphorus (not explained by PCA 1 or 2)
Litter	Average litter depth

Table 2. Two-way contingency table for the presence/absence of non-native invasive plants in 20x20-m plots (N = 80) located in historic agricultural (HA) or reference plots, and either adjacent to the road or 50 m away. Presence/absence of invasives was dependent on land-use history (χ^2 = 16.9, P < 0.001), with invasives more likely to occur in the historic agricultural (HA) plots than in the reference plots. However, presence/absence of invasives was independent of proximity to roads (χ^2 = 2.6, P = 0.456).

	Adjacent to road (N = 40)		50 m from road (N = 40)	
	Invasives present	Invasives absent	Invasives present	Invasives absent
HA plots (N= 40)	**15**	**5**	**13**	**7**
Reference plots (N= 40)	**7**	**13**	**3**	**17**

Table 3. Axis loadings for soil variables used in the principal components analysis (PCA). Pearson correlation coefficients (*r*) are reported, and values of $|r| > 0.6$ are shown in bold. Mean and standard error (*SE*) values are across all plots ($N = 80$).

Soil Variables	Mean (*SE*)	PCA axis 1 (*r*)	PCA axis 2 (*r*)
total nitrogen (mgL^{-1})	0.12 (0.005)	0.554	-0.598
organic matter (%)	6.1 (0.2)	0.244	**-0.764**
phosphorus (ppm)	3.2 (0.1)	-0.183	-0.120
pH	4.6 (0.04)	**0.703**	0.054
potassium (ppm)	59.9 (2.8)	**0.859**	-0.080
calcium (ppm)	118.3 (23.5)	**0.836**	0.353
magnesium (ppm)	37.5 (4.7)	**0.901**	0.237
clay (%)	19.8 (0.5)	-0.134	**-0.690**
sand (%)	52.1 (0.7)	-0.093	**0.801**

Table 4. Summary of the best logistic regression model for presence/absence of non-native invasive plants. The generalized linear mixed effects model (GLMM) used the Laplace approximation to estimate model parameters. *Site* was treated as a random effect. Backward stepwise selection was used to determine the best model using $z \geq 2$ as the criterion for inclusion in the model.

Predictor Variable	Estimate	SE	*z*	*P*
Intercept	-1.683	0.606	-2.78	0.0054
Historic agriculture (binary)	2.222	0.684	3.25	0.0012
Downslope from road (binary)	2.073	0.780	2.66	0.0079
Soils PCA-1 (cations & pH)	1.185	0.332	3.57	0.0004

Table 5. Summary of the best linear mixed effects (LME) regression model for abundance (log-transformed cover) of non-native invasive plants for plots in which they were present (N = 38). Model parameters were estimated using restricted maximum likelihood (REML). *Site* was treated as a random effect. Backward stepwise selection was used to determine the best model using $t \geq 2$ as the criterion for inclusion in the model.

Predictor Variable	Estimate	SE	*df*	*t*	*P*
Intercept	-3.873	0.600	17	-6.46	<0.0001
Historic agriculture (binary)	1.165	0.535	16	2.18	0.0448
Road adjacency (binary)	1.543	0.459	16	3.36	0.0040
Downslope from road (binary)	2.035	0.460	16	4.43	0.0004
Soils PCA-1 (cations & pH)	0.562	0.117	16	4.82	0.0002

Table 6. Correlations (*r*) for environmental vectors fitted on the overstory community non-metric multidimensional scaling (NMDS) ordination. *P*-values are based on permutation tests. Variables with $P < 0.05$ are shown in bold and are included as significant environmental vectors in Fig. 4.

Environmental Variable	*r*	*P*
Total N (soil)	**0.55**	**<0.001**
Organic matter (soil)	**0.39**	**0.001**
P (soil)	**0.31**	**0.014**
pH (soil)	**0.51**	**<0.001**
K^+ (soil)	**0.58**	**<0.001**
Mg^{++} (soil)	**0.56**	**<0.001**
Ca^{++} (soil)	**0.54**	**<0.001**
Clay content	0.14	0.442
Sand content	0.07	0.827
Litter depth	**0.57**	**<0.001**
Slope	**0.53**	**<0.001**
Local terrain shape (TSI)	0.26	0.072
Quadrat-level native species richness	**0.59**	**<0.001**

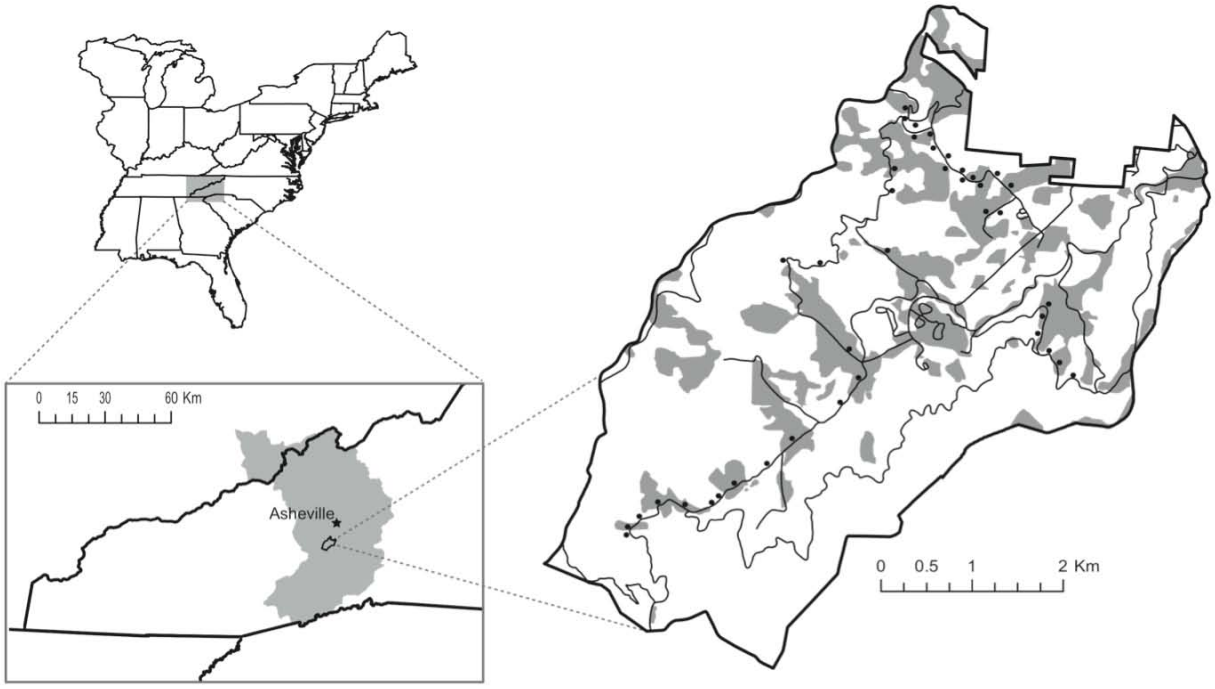


Figure 1. Map of the study area. The inset map of western North Carolina on the left shows the location of the Bent Creek Experimental Forest (BCEF) in relation to Asheville, North Carolina, USA. The area in gray indicates the French Broad River Basin. BCEF is shown in the enlarged map on the right. Black circles along the roads indicate sampling locations. Areas that were previously in cultivation (historic agricultural areas) are shown in gray.

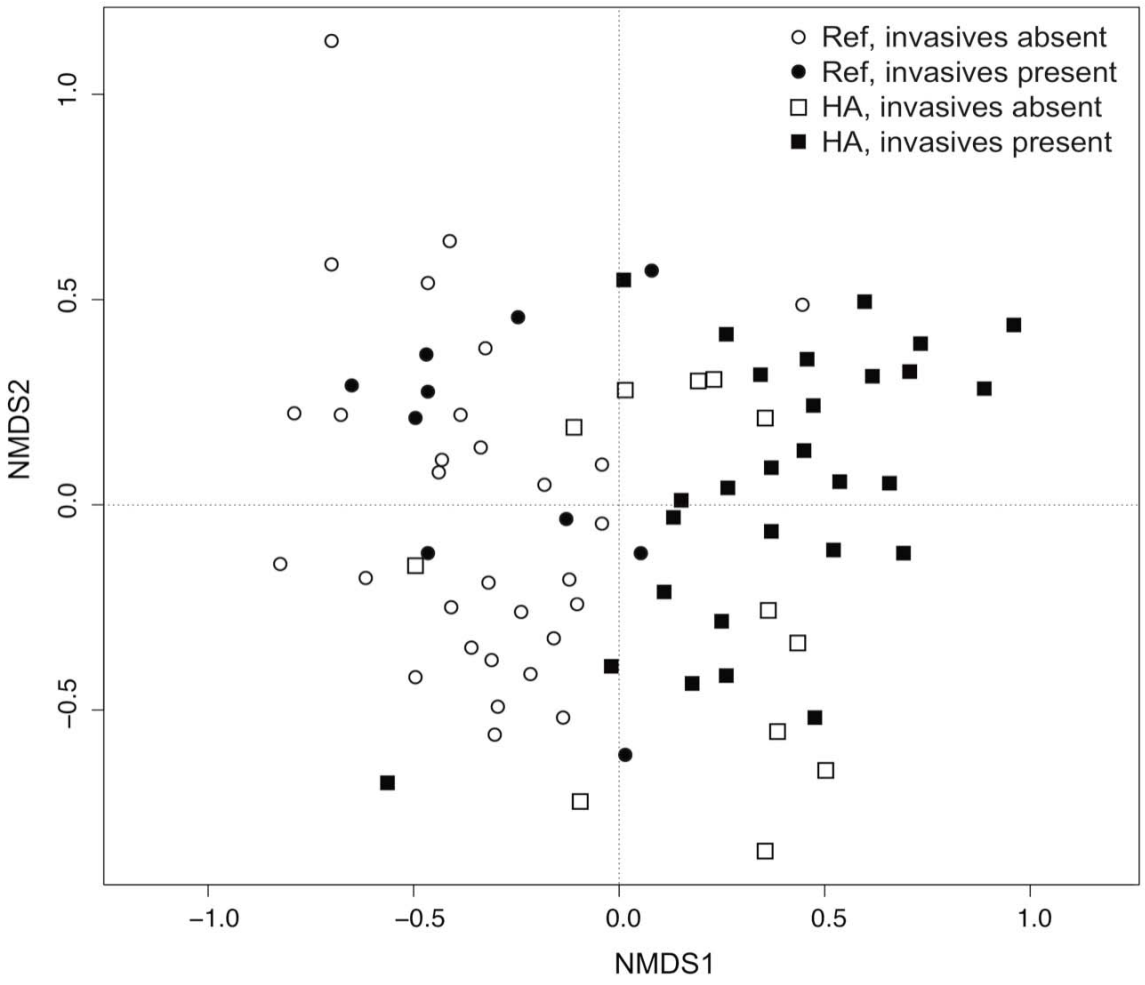


Figure 2. Non-metric multidimensional scaling (NMDS) based on overstory species composition (basal area of trees >10 cm DBH). Sampling units (plots) are coded based on their land-use history (circles = reference, squares = historic agriculture) and presence/absence of non-native invasive plants.

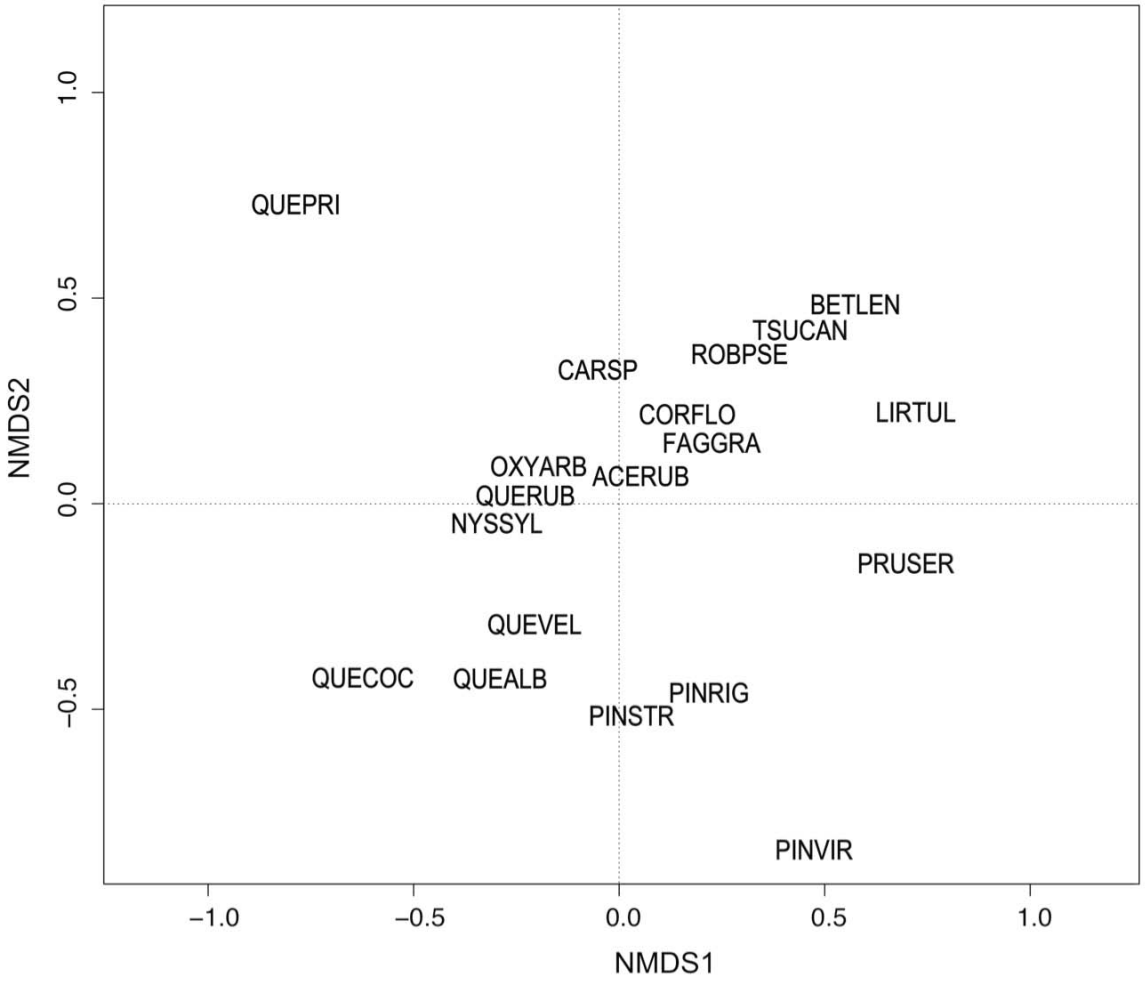


Figure 3. Overstory species centroids from the NMDS ordination. Species abbreviations: ACERUB = *Acer rubrum*, BETLEN = *Betula lenta*, CARSP = *Carya* spp., CORFLO = *Cornus florida*, FAGGRA = *Fagus grandifolia*, LIRTUL = *Liriodendron tulipifera*, NYSSYL = *Nyssa sylvatica*, OXYARB = *Oxydendrum arboreum*, PINRIG = *Pinus rigida*, PINSTR = *Pinus strobus*, PINVIR = *Pinus virginiana*, PRUSER = *Prunus serotina*, QUEALB = *Quercus alba*, QUECOC = *Quercus coccinea*, QUEPRI = *Quercus prinus*, QUERUB = *Quercus rubra*, QUEVEL = *Quercus velutina*, ROBPSE = *Robinia pseudoacacia*, TSUCAN = *Tsuga canadensis*. (See Appendix 2 for average basal areas of overstory species in historic agriculture and reference plots.)

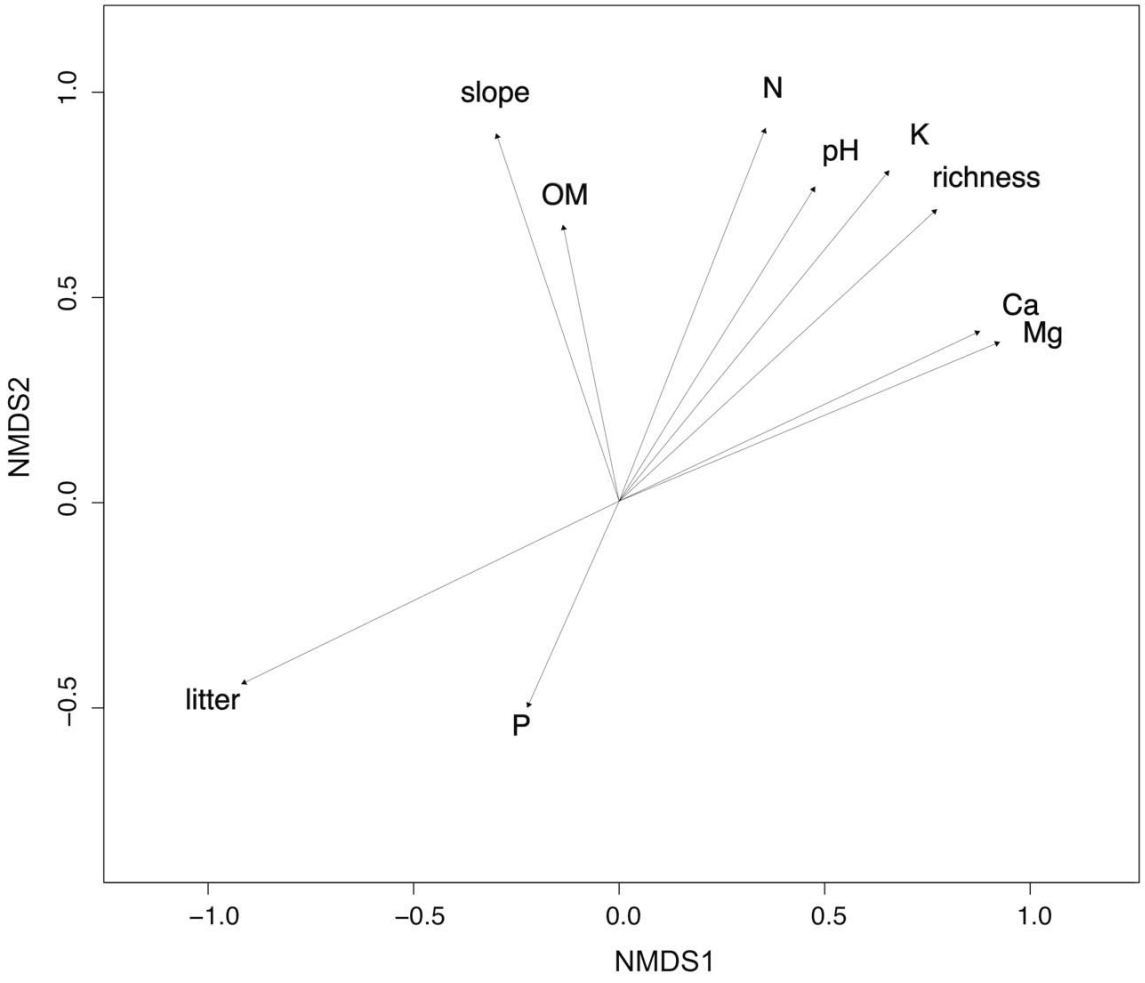
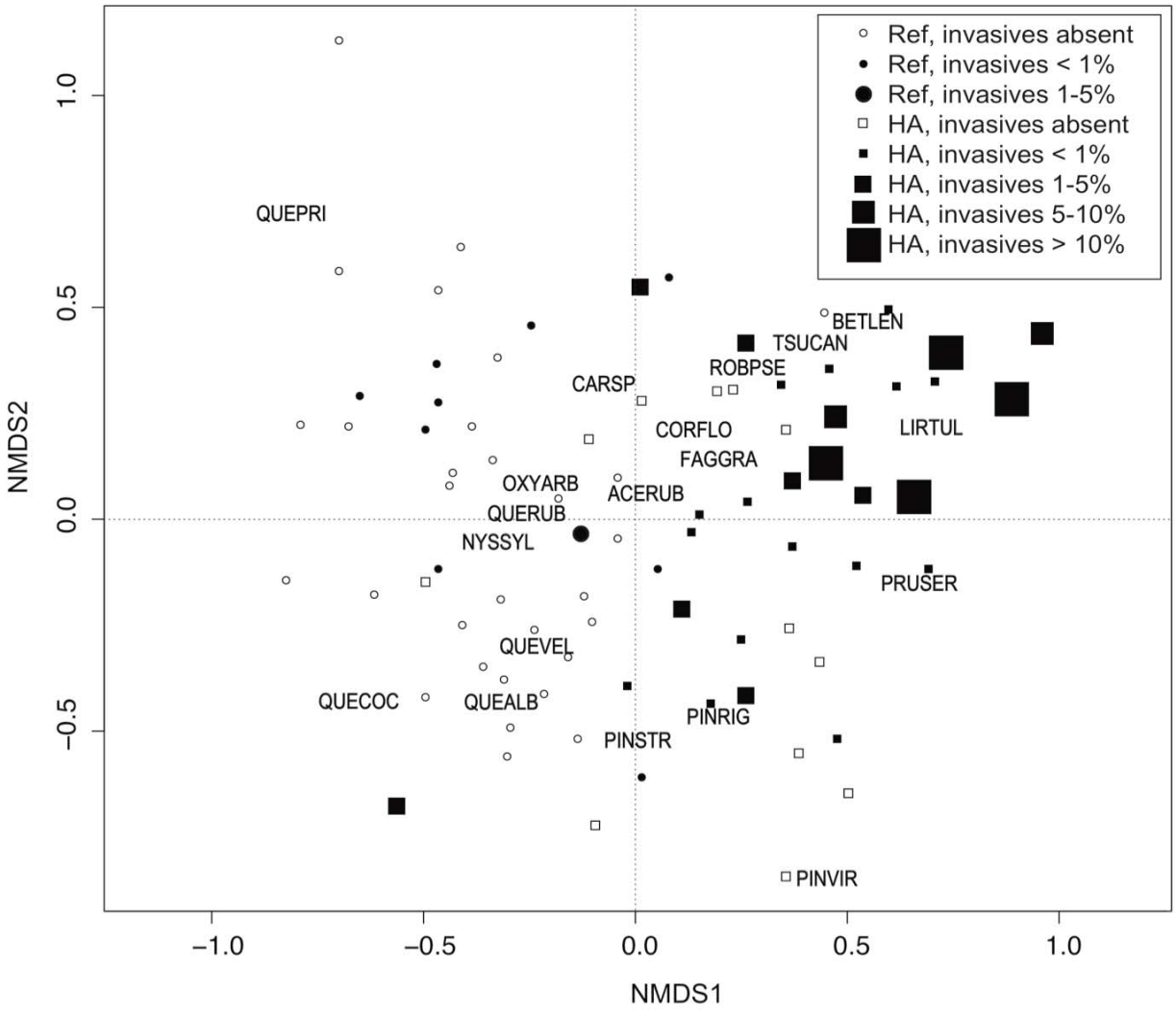


Figure 4. Significant environment vectors correlated with the NMDS overstory ordination. Significance is defined for vectors as having $P < 0.05$ based on permutation tests (See Table 6 for *r* and *P*-values). Environmental variable are defined as follows: P = soil phosphorus, litter = average litter depth, slope = local terrain slope, OM = soil organic matter content, N = total soil nitrogen, pH = soil pH, K = soil exchangeable potassium, richness = average quadrat-level native species richness, Ca = soil exchangeable calcium, Mg = soil exchangeable magnesium.

Appendix 1. Non-metric multidimensional scaling (NMDS) ordination of the overstory species with symbols sized to represent invasive plant cover. The figure shows the same NMDS ordination as Figure 2, but the symbols are sized to represent the abundance (percent cover) of invasive plants in each of the plots. Overstory species centroids are overlain to show their relationship to the ordination solution. Species abbreviations: ACERUB = *Acer rubrum*, BETLEN = *Betula lenta*, CARSP = *Carya* spp., CORFLO = *Cornus florida*, FAGGRA = *Fagus grandifolia*, LIRTUL = *Liriodendron tulipifera*, NYSSYL = *Nyssa sylvatica*, OXYARB = *Oxydendrum arboreum*, PINRIG = *Pinus rigida*, PINSTR = *Pinus strobus*, PINVIR = *Pinus virginiana*, PRUSER = *Prunus serotina*, QUEALB = *Quercus alba*, QUECOC = *Quercus coccinea*, QUEPRI = *Quercus prinus*, QUERUB = *Quercus rubra*, QUEVEL = *Quercus velutina*, ROBPSE = *Robinia pseudoacacia*, TSUCAN = *Tsuga canadensis*.



Appendix 2. Overstory tree species and their average dominance (basal area) in historic agriculture and reference plots. Species abbreviations correspond to those used to represent species centroids in the NMDS ordination (Fig. 3 and Appendix 1). Mean and standard error (SE) for basal area are reported.

Overstory tree species	Species abbreviations	Basal area (m^2ha^{-1}) in historic agriculture plots		Basal area (m^2ha^{-1}) in reference plots	
		Mean	SE	Mean	SE
Acer rubrum	ACERUB	3.85	0.56	3.26	0.44
Betula lenta	BETLEN	0.51	0.17	0.43	0.25
Carya spp.	CARSP	0.56	0.22	0.94	0.40
Cornus florida	CORFLO	0.31	0.09	0.20	0.06
Fagus grandifolia	FAGGRA	0.23	0.22	0.09	0.07
Liriodendron tulipifera	LIRTUL	11.72	1.80	0.92	0.27
Nyssa sylvatica	NYSSYL	0.27	0.14	0.29	0.08
Oxydendrum arboreum	OXYARB	2.10	0.33	3.25	0.35
Pinus rigida	PINRIG	1.02	0.31	0.31	0.14
Pinus strobus	PINSTR	2.70	0.91	1.96	0.75
Pinus virginiana	PINVIR	1.96	0.71	0.36	0.20
Prunus serotina	PRUSER	0.71	0.27	0.03	0.03
Quercus alba	QUEALB	1.88	0.63	4.13	0.85
Quercus coccinea	QUECOC	0.34	0.13	2.97	0.72
Quercus prinus	QUEPRI	0.71	0.53	6.25	1.25
Quercus rubra	QUERUB	0.81	0.38	1.61	0.53
Quercus velutina	QUEVEL	0.86	0.29	1.00	0.33
Robinia pseudoacacia	ROBPSE	0.24	0.12	0.17	0.08
Tsuga canadensis	TSUCAN	0.87	0.36	0.24	0.12

CHAPTER 2

Disentangling the factors related to land-use history driving *Celastrus orbiculatus* invasion in southern Appalachian oak and tulip poplar forests[1]

Abstract

Although historic land use is often implicated in non-native plant invasion of forests, little is known about how land-use legacies might actually facilitate invasion. We conducted a two-year field seeding experiment at the Bent Creek Experimental Forest in western North Carolina, USA, to compare germination and first-year seedling survival of Oriental bittersweet (*Celastrus orbiculatus* Thunb.) in stands dominated by tulip poplar (*Liriodendron tulipifera* L.), which had been cultivated and abandoned a century earlier, and in nearby stands dominated by oaks (*Quercus* spp.) that had never been cultivated. Our aim was to determine why tulip poplar stands had higher abundance of *C. orbiculatus*, as evidenced from previous work. Experiments were conducted at five sites, each with one tulip poplar and one oak stand, by varying litter mass (none, low, or high) and litter type (tulip poplar or oak). Each of the five treatments was assigned to three 1-m^2 plots per stand that were seeded with *C. orbiculatus* in 2008 and 2009. To test for effects of site and soil type, we also performed reciprocal soil translocations using pots. Soil moisture and temperature were measured throughout the 2008 growing season. Germination and survival were consistently higher in tulip poplar stands than in oak stands. Germination was also higher in plots with low litter mass than in those with no litter or high litter mass. Seedling survival was lowest in plots with high litter mass. Soil moisture was higher in tulip poplar stands and under low-mass litter and thus may play a major role in determining establishment success. Differences in germination and survival among the pots were minimal,

[1] Manuscript to be submitted to *Biological Invasions* with co-authors Scott M. Pearson and Monica G. Turner

suggesting that soil type and site conditions unrelated to the forest floor were less important than litter conditions for *C. orbiculatus* establishment. The low litter mass and mesic soil conditions that are characteristic of tulip poplar stands may confer higher invasibility and explain the higher abundance of *C. orbiculatus* in areas with successional overstory communities associated with land-use history.

Introduction

Invasion of intact forests by non-native plants has generally received less attention than invasion of more open or disturbed habitats, perhaps owing to the comparatively slow rates of invasion and smaller pool of potential forest invaders (Martin et al. 2009). Nonetheless, such species pose a considerable threat to forest ecosystems. They may alter forest structure and composition (Richardson 1998), reduce biodiversity (Lugo 2004, Stinson et al. 2007), and affect nutrient cycling (Kourtev et al. 1998, Ehrenfeld et al. 2001, Ashton et al. 2005). Invasive plants tend not to spread uniformly in forest landscapes but seem to respond to heterogeneity that makes certain areas more susceptible to invasion than others (Meekins and McCarthy 2000, Chabrerie et al. 2007). By understanding the factors that influence invasibility of forests, we can improve our understanding of the mechanisms underlying the invasion process and increase our ability to predict future spread of non-native plants.

Historic land use can increase invasive plant abundance in forested landscapes (Lundgren et al. 2004, DeGasperis and Motzkin 2007, Von Holle and Motzkin 2007). However, the actual mechanisms related to land-use history that may facilitate plant invasion are poorly understood. Based on work conducted in 2006 at the Bent Creek Experimental Forest (BCEF) in western North Carolina, USA, we found that forested areas that had previously been cultivated and were

abandoned roughly a century ago had far more non-native invasive plants in their understories than observed in comparable reference forests. The overstories of these historic agricultural areas were frequently dominated by tulip poplar (*Liriodendron tulipifera* L), whereas areas that lacked an agricultural land-use history were typically dominated by oak (*Quercus*) species. There was a strong positive correlation between tulip poplar basal area and the abundance of non-native invasive plants. Tulip poplar dominated stands also had higher cation concentrations, pH, and total nitrogen in their soils, and the leaf litter on the forest floor was thinner than in the oak dominated stands.

In this study we investigated the factors influencing non-native plant invasion at BCEF using a field seeding experiment with Oriental bittersweet (*Celastrus orbiculatus* Thunb), a common forest invader in the study region. A woody twining vine that was introduced in the northeastern U.S. from eastern Asia in 1860, *C. orbiculatus* has spread rapidly throughout eastern North America (Patterson 1973, Dreyer et al. 1987). Seedlings exhibit a wide tolerance for light intensity and are able to persist for long periods in lowlight conditions (Ellsworth et al. 2004b, Leicht and Silander 2006, Leicht-Young et al. 2007), making *C. orbiculatus* a particularly effective understory invader and a considerable threat to forests in the eastern U.S. (Patterson 1973, McNab and Loftis 2002).

We set out to address the following overarching question: Why do areas with greater overstory dominance by tulip poplar (historically cultivated areas) have higher abundances of non-native plants (particularly *C. orbiculatus*) than adjacent stands with high oak dominance (without an agricultural land-use history)? First, we wished to determine whether the tulip poplar stands actually exhibited greater invasibility. Alternatively, higher *C. orbiculatus* abundance could be attributed to greater propagule pressure exerted by reproductive individuals

(often abundant along roads adjacent to historic agricultural areas) that may have become establishment around the time of agricultural abandonment. Propagule pressure often plays a major role in determining the success of invasion by non-native plants (Lonsdale 1999, Lockwood et al. 2005). Secondly, we wished to determine the specific factors that differed between stand types and might influence the differential invasion that was previously observed. Specifically, we considered the roles of soil, leaf litter quantity, leaf litter quality (type of litter), and site conditions (e.g., the light environment related to overstory density and leafing phenology) in determining differential germination and survival of *C. orbiculatus* in the tulip poplar and oak dominated stands. We expected to see higher germination and seedling survival in the richer soils from the *Liriodendron* stands. Several studies have noted the positive correlation between abundance of non-native invasive plants and forest soil nutrient concentrations and pH (Silveri et al. 2001, Cole and Weltzin 2004, Howard et al. 2004, Pande et al. 2007). We also expected germination and survival to decrease with increasing litter mass because litter can act as a physical barrier for emergent seedlings (Facelli and Pickett 1991, Ellsworth et al. 2004a). Similarly, we expected germination and survival to be lower in litter from oak stands due to the toughness and more curled structure of oak leaves compared to those of tulip poplar (Abrams 1990, Van Lear 2004), perhaps making the oak litter a more effective barrier for the germinating seedlings. We did not expect site conditions unrelated to the forest floor to affect germination and survival.

Methods

Study area

The study was conducted at BCEF, a research station managed by the United States Department of Agriculture Forest Service. BCEF is located 15 km southwest of Asheville, NC, USA, and largely covers the 2500-ha Bent Creek watershed. Typical of areas in the Blue Ridge physiographic province, BCEF has steep topography and extensive forest cover. The elevation range is 700 to 1100 meters. The forest is predominantly mixed oak and mixed mesophytic. Common overstory species include *Quercus coccinea, Q. velutina, Q. prinus, Q. alba, Q. rubra, Carya* spp., *Liriodendron tulipifera, Acer rubrum, Oxydendrum arboreum, Pinus rigida, P. echinata, P. strobus,* and *Tsuga canadensis* (McNab 1996). The bedrock geology primarily consists of Precambrian gneisses and schists. Soils are ultisols (associated with intermontane basins) and inceptisols on steeper slopes and are relatively deep, with solums commonly >80 cm (Greenberg and McNab 1998).

Settlement of the Bent Creek basin by European immigrants began in the 1790s. By 1900 over 100 homes were constructed and 23% of the basin (ca. 600 ha) had been cleared for agriculture (Nesbitt and Netboy 1946). Some of the cleared land was used for pasture, but most was cultivated at some time. Residents practiced low-input subsistence agriculture on the basin's steep marginal farmlands, primarily growing corn, wheat, and rye in rotation (Nesbitt and Netboy 1946). Much of the basin was purchased between 1900 and 1910 to expand the holdings of the nearby Biltmore Estate, and most of the cleared areas were abandoned and have since regrown to forest. The US Forest Service has managed the basin since 1925.

Experimental design

The field experiment was initiated in five sites at BCEF (Fig. 1) in March 2008 and repeated at the same sites beginning in March 2009. Within each site, two forest stands were

selected: one stand with oaks (*Quercus* spp.) as the dominant overstory species (hereafter *Q*-stands) and another with tulip poplar (*Liriodendron tulipifera*) as the dominant overstory species (hereafter *L*-stands). All *L*-stands were located in areas that were previously cultivated and abandoned around 1905. The *Q*-stands were located in areas that were not previously cultivated. The paired stands within each site were selected to control for differences in topography to the extent possible (see Table 1). The *Q*-stands were on slightly steeper slopes than the paired *L*-stands (average slope difference = 2.6°, *SE* = 0.36). This difference probably reflects the selection of gentler slopes by early settlers for agriculture, but does not likely represent an ecologically significant difference given the steep topography of the study region. Paired stands were in close proximity (100-400 m apart) to limit differences in bedrock geology.

In each stand, a 20x20-m experimental area was established. Slope and aspect were recorded in each stand. A terrain shape index (TSI) was calculated by averaging slopes from the center of the experimental area in eight sub-cardinal directions to describe the concavity (positive TSI) or convexity (negative TSI) of the local landform (McNab 1989). We identified all trees with stems >5-cm DBH and measured their diameter to compute basal area for each species. Canopy cover was determined using a spherical densiometer by averaging measurements from the grid center and the four vertices. Soil samples were collected using a 5-cm diameter soil corer. The upper 15 cm of mineral soil were sampled after removal of coarse organic material. Soil cores were taken at the grid center and the four vertices and combined as a composite sample. They were dried, sieved, and analyzed at the University of Wisconsin-Madison Soil and Plant Analysis Lab for pH, total nitrogen (organic N, NH_4^+, NO_3^-, and NO_2), organic matter content, exchangeable cations (Ca^{++}, Mg^{++}, and K^+), and plant-available P. We performed soil particle-size analysis using the hydrometer method (Gee and Bauder 1986). In

March 2009, soils were re-sampled as described above, but only to a depth of 5 cm, and were subsequently analyzed for organic matter content.

Plots

Twenty-five 1-m^2 experimental plots were established in each stand within the 20x20-m experimental area, arranged in a five-by-five grid with 5-m spacing between plots. All coarse leaf litter was removed from plots using a yard rake, and a 15-cm high fence was erected around each plot to minimize movement of leaf litter into or out of the plots. Five litter treatments were randomly assigned to the plots (five plots per treatment) to manipulate litter quantity (no litter, low mass, or high mass) and litter type (tulip poplar litter or oak litter). The "no litter" plots were left bare following litter removal. In the low *Liriodendron* litter mass plots (hereafter "low *L*-litter"), we added one kilogram of leaf litter collected from the *L*-stand within that site. (I.e., in *L*-stands, litter was collected from within that stand and added to the *L*-litter plots; in *Q*-stands, litter was moved from the paired *L*-stand.) In the low *Quercus* litter mass plots (hereafter "low *Q*-litter"), we added one kilogram of litter collected from the *Q*-stand within the site. In the high *L*-litter treatment plots, three kilograms of litter from the *L*-stand was added. In the high *Q*-litter plots, three kilograms of litter from the *Q*-stand was added. The two litter masses were chosen to represent realistic extremes of litter mass encountered throughout BCEF, based on preliminary measurements. The low litter mass was more representative of conditions in *Liriodendron* stands whereas the high litter mass was more similar to those in oak-dominated stands.

For each treatment within a stand, three of the five plots were sown with Oriental bittersweet (*Celastrus orbiculatus*) seeds. The other two plots were left unseeded to determine the frequency of establishment by bittersweet seedlings due to seed inputs from parent plants in

the vicinity and to offer a means of correcting germination rates of seeded plots if necessary. The bittersweet seeds sown in experimental plots were collected from several locations at BCEF in November 2007. The fruits were dried at 20°C for several weeks before removing the seeds. Seeds were then placed in plastic bags with moist sand and cold stratified for three months at 5°C before sowing. In each of the seeded plots, we sowed 100 seeds by scattering them evenly across the surface of the plot (on top of the leaf litter where it was present). Seed germination was measured in late June 2008. Bittersweet seedlings were identified by their cotyledons, and a small wire was inserted beside each seedling to mark its location. First-year survival of the seedlings was determined in June 2009.

Soil moisture and temperature were measured for all plots in March, May, June, July, and October 2008. Soil temperature was recorded using a digital soil thermometer inserted to a depth of 5 cm and was measured in the center of each plot. Soil moisture was measured as volumetric water content of the top 12 cm of soil using a Hydrosense Portable Soil Moisture System (Campbell Scientific Australia). Four measurements were recorded and averaged for each 1-m^2 plot. Soil moisture measurements were never taken immediately following a heavy rain event.

Due to low germination rates in 2008 (a drought year), the field experiment was reinitiated in March 2009 using the same set of experimental plots. Leaf litter that had fallen on plots since the previous year was removed from all plots without disturbing any established bittersweet seedlings. Although some decomposition of the original litter undoubtedly occurred, relative differences between low and high litter mass treatments were maintained; all litter was again removed from the no-litter plots. We added a soil scarification treatment in 2009 by establishing five additional plots (three of which were seeded) within each existing experimental grid. As in the no-litter plots, all coarse leaf litter was removed, but in this scarification

treatment, the surface was subsequently scraped using a hand cultivator to remove any partially decomposed organic layer (common in oak-dominated stands) and to scarify the surface of the mineral soil. Seeds for the 2009 planting were collected in November 2008 and processed just as they had been the previous year. The seeds were treated with a fungicide (Captan 50) prior to cold stratification in response to small amounts of mold observed in bags the previous year. Again, 100 seeds were sown in each of the seeded treatment plots. Surviving seedlings from the 2008 planting were small enough and in low enough density as to not warrant concern regarding competition with new seedlings. Seed germination rates were assessed in June 2009.

Pots

To test for independent effects of soils and site conditions, we performed a reciprocal soil translocation. At each of five locations in the 20x20-m grid described above (the four corners and the center), we filled two pots with soil. After removing the organic layer, soil was extracted as a single core and placed in a pot to maintain stratigraphy and structure. For each pair of pots, one was left in that location and the other was moved to the paired stand within the site so that at each of the five locations in a stand, there was one *L*-soil pot and one *Q*-soil pot. All pots were placed in holes so that the soil surface in the pots was even with the ground surface to maintain ambient soil temperature and avoid excessive drying. All pots were sown with 20 *C. orbiculatus* seeds in March 2008, and germination rates were assessed in late June. Soil moisture and temperature measurements were taken in pots prior to sowing seeds in March and again in October 2008 after seedlings were established to avoid disturbance by the instrument probes.

Beginning in March 2009, we repeated the reciprocal soil experiment by adding the same number of pots and placing them in the same arrangement as in 2008. A 5-cm wide strip of

mesh screen was affixed to the rim of each pot in 2009 to avoid possible flushing of seeds due to overflow in heavy rain events (a suspected problem in 2008). We also doubled the number of seeds sown in 2009 to 40 seeds per pot in response to low germination rates in 2008. Seed germination rates in the pots were assessed in June 2009.

Data Analysis

Differences in stand characteristics (topography, overstory composition, canopy cover, soil texture, and soil chemistry) between *L*-stands and *Q*-stands were analyzed using paired t-tests. *Celastrus orbiculatus* germination rates and first-year seedling survival were analyzed using ANOVA with PROC GLM (SAS Institute 2002). For the 2008 seed germination in plots, we first considered the effects of stand type and litter vs. no-litter treatments. Stand type was nested within sites to account for differences among the sites. We then analyzed those plots with litter added to determine effects of litter mass and litter type. Germination rates (percent of seeds that germinated) were arcsine square root transformed prior to analyses. For the 2009 seed germination, analyses were repeated as for the 2008 data, but the plots without litter were subsequently analyzed for an effect of the scarification treatment. Plot soil moisture and temperature data were analyzed using repeated measures ANOVA with PROC GLM. March data were excluded since they were collected at the time of experimental setup and therefore were not expected to reflect treatment effects due to litter manipulation. Germination and seedling survival in the pots were analyzed using ANOVA to test for effects of stand type and soil type. Again, stand type was nested within sites. Soil moisture and temperature in pots were also analyzed using repeated measures ANOVA.

Results

Stand characteristics

With respect to their physiographic characteristics, total basal area, and canopy cover, the paired sites only differed significantly in their slopes ($T = 5.1$, $P = 0.007$), with slightly steeper slopes in the *Q*-stands (Table 1). Soil texture (clay, silt, and sand content) did not differ between stand types. Several soil chemical properties were significantly different between stand types: pH ($T = 3.5$, $P = 0.025$), potassium ($T = 2.9$, $P = 0.044$), calcium ($T = 3.1$, $P = 0.035$), magnesium ($T = 4.6$, $P = 0.010$), and total nitrogen ($T = 3.8$, $P = 0.019$) were all significantly higher in *L*-stands. Although soil organic matter content did not differ in the upper 15 cm of soil ($T = 0.30$, $P = 0.78$), it was significantly greater in the top 5 cm of soil in *L*-stands ($T = 3.9$, $P = 0.018$).

Plots

In 2008 (a below-average rainfall year), the mean germination rate across all seeded plots was 3.1% ($SE = 0.43$, range = 0-39%, $N = 150$ plots). The most variation in germination rates was explained by stand type ($F = 11.5$, $P < 0.0001$, df = 5), with higher germination in *L*-stands (Fig. 2a). There was also higher germination in plots with litter than those without ($F = 6.6$, $P = 0.012$, df = 1). Among plots with litter ($N = 120$), the importance of stand type was even more pronounced ($F = 31.0$, $P < 0.0001$, df = 5). There was no significant effect of litter type ($F = 1.4$, $P = 0.24$, df = 1). However, plots with low litter mass treatments had significantly higher germination rates than those with high litter mass treatments ($F = 12.7$, $P < 0.0001$, df = 1). Among the plots that were not seeded ($N = 100$), only seven plots had *C. orbiculatus* seedlings in

2008, with a mean germination rate of 0.19%. Given the low seed inputs from local propagule sources, germination data for the seeded plots were not adjusted prior to analysis.

In 2009 (an above-average rainfall year), the mean germination rate was 25.0% (*SE* = 1.3, range = 0-81%, *N* = 180 plots). As in 2008, there was a strong effect of stand type ($F = 10.84$, $P < 0.0001$, df = 5), with higher germination in the *L*-stands, though relative differences between stand types were not as great as in 2008 (Fig. 2). Germination was also still significantly higher in the plots with litter added than in the no-litter plots ($F = 43.14$, $P < 0.0001$, df = 1). Among plots with litter, there was again a significant effect of litter mass ($F = 4.37$, $P = 0.039$, df = 1), with higher germination in the low-litter-mass plots, though the effect was not as strong as in 2008. There was again no effect of litter type on germination rates in 2009 ($F = 0.18$, $P = 0.676$, df = 1). Among the plots with no litter, those with the scarification treatment had significantly higher germination than those in which the soil surface was not disturbed ($F = 11.54$, $P = 0.0014$, df = 1). The difference between scarification and no-scarification treatments was greater in the *Q*-stands than in the *L*-stands (Fig. 2b). Among the plots that were not seeded in 2009 (*N* = 120), 16 plots had *C. orbiculatus* seedlings, and the mean germination rate was 1.3%. Seventy-three percent of the seedlings observed in the no-seed plots occurred in two adjacent plots that were positioned below a mature *C. orbiculatus* vine. With the exception of that single location, seed inputs from local propagule sources were very low and did not warrant adjustments to the germination data from the seeded plots.

Mean first-year seedling survival across all plots in which seedlings were present in June 2008 was 34.4% (*SE* = 3.6, *N* = 99 plots). Survival was significantly higher in *L*-stands ($F = 4.8$, $P = 0.0006$, df = 5) (Fig. 3). Survival was also higher in no-litter plots than those with litter, though the difference was only marginally significant ($F = 3.7$, $P = 0.057$, df = 1). Among plots

with litter treatments, there was a significant effect of litter mass (F = 12.3, P = 0.0008, df = 1), with higher survival in the low litter mass treatments. There was no effect of litter type on seedling survival (F = 0.35, P = 0.56).

Soil temperatures varied significantly between stand types (repeated measures ANOVA, F = 7.9, P < 0.001, df = 5), but the direction of effect changed among sites and sampling dates with no clear trend in stand effect (Fig. 4a). Far more variation in soil temperature was explained by differences among sites (F = 77.2, P < 0.0001, df = 4). The presence or absence of litter had the strongest effect on soil temperature (F = 244.5, P < 0.0001, df =1), with higher temperatures in the no-litter plots early in the growing season, and slightly lower temperatures in no-litter plots in October (Fig. 4b). Among the plots with litter treatments, there were also significant effects of litter mass (F = 34.0, P < 0.0001, df = 1) and litter type (F = 11.0, P = 0.001, df = 1); soil temperature was higher in low litter mass treatments and *L*-litter treatments earlier in the growing season and switched directions in October, though differences in mean temperature between treatments at any given sampling date were < 0.67°C (Fig. 4c and 4d).

Soil moisture was consistently and significantly higher in the *L*-stands than in *Q*-stands (repeated measures ANOVA, F = 135.6, P < 0.0001, df = 5). Volumetric water content was on average 5.0 percentage points higher in *L*-stands than in *Q*-stands (Fig. 4e). There was not a significant difference in soil moisture between the litter and no litter treatments (F = 1.3, P = 0.26, df = 1) (Fig. 4f). Litter mass had a modest effect on soil moisture (F = 4.4, P = 0.037, df = 1); moisture was consistently higher in the low-litter-mass plots, but mean differences were modest (<0.89%) and became less pronounced throughout the growing season (Fig. 4g). There was no effect of litter type on soil moisture (F = 0.01, P = 0.93, df = 1) (Fig. 4h).

Pots

In 2008 the mean germination rate across all pots was 2.6% (*SE* = 0.51, *N* = 100). There was a weak significant effect of stand type ($F = 2.6$, $P = 0.028$, df = 5), with germination rates slightly higher in the *Q*-stands (Fig. 5a), but this trend only held for stand pairs in two of the five sites. More of the variation in germination rates was explained by differences among the sites ($F = 3.7$, $P = 0.009$, df = 4). There was no significant effect of soil type ($F = 0.99$, $P = 0.32$, df = 1), though mean germination was slightly higher in *L*-soil (3.1%) than in *Q*-soil (2.0%). In 2009 the mean germination rate for pots was 20.4% (*SE* = 1.4, *N* = 100). Germination was significantly higher in *Q*-stands than in *L*-stands ($F = 6.12$, $P < 0.0001$, df = 5), though the mean difference between stand types was driven largely by a single site in which germination was 34.5% in the *Q*-stand and only 8.0% in the *L*-stand. Germination was also slightly higher in pots with soil taken from the *L*-stands in 2009 ($F = 4.62$, $P = 0.034$, df = 1) (Fig. 5b).

Mean first-year seedling survival for pots in which seedlings were present in June 2008 was 69.8% (*SE* = 7.7, *N* = 29 pots). Survival was not significantly different between stand types ($F = 2.45$, $P = 0.081$, df = 4). There was also no effect of soil type on seedling survival ($F = 0.02$, $P = 0.88$, df = 1) (Fig. 6).

Mean soil temperature in the pots was higher for those in *Q*-stands (repeated measures ANOVA, $F = 27.2$, $P < 0.0001$, df = 5) (Fig. 7a). However, the direction of effect varied considerably among sites, and differences among sites explained far more variation in soil temperature ($F = 732.2$, $P < 0.0001$, df = 4). There was no effect of soil type on temperature ($F = 0.04$, $P = 0.84$, df = 1) (Fig. 7b). Soil moisture was higher in *L*-stands ($F = 2.8$, $P = 0.021$, df = 5) (Fig. 7c), though the effect was only moderately significant and far more variation was explained by differences among sites ($F = 25.5$, $P < 0.0001$, df = 4). There was a strong effect of

soil type (F = 16.7, P <0.0001, df = 1), with higher soil moisture in *L*-soils than in *Q*-soils, and this trend held for both the March and October sampling dates (Fig. 7d).

Discussion

In general, *Celastrus orbiculatus* germination and survival rates were higher in stands dominated by *Liriodendron tulipifera* than those dominated by *Quercus* spp., supporting the notion that higher abundance of *C. orbiculatus* previously observed in tulip poplar stands is due at least in part to greater invasibility and not propagule pressure alone. The higher germination and survival rates in tulip poplar stands may be influenced by a number of factors, but our results suggest that higher soil moisture levels in these stands may play an important role. Soil moisture was consistently higher in tulip poplar stands than in oak stands. Others have noted the positive correlation between soil moisture and invasion by non-native plants in general (Rejmánek 1989, Gelbard and Belnap 2003, Huebner and Tobin 2006, Chytry et al. 2008), and *C. orbiculatus* in particular (Silveri et al. 2001, McNab and Loftis 2002, Leicht-Young et al. 2007). The importance of soil moisture may have been exacerbated during the 2008 growing season due to drought conditions experienced throughout the region. Spring rainfall (total for March-May) at BCEF was 11.6 cm below historic (1971-2000) averages in 2008 and 13.3 cm above historic averages in 2009 (BCEF weather station 31-0724, National Cimate Data Center 2002).

Although variation in soil moisture is typically attributed to differences in local topography (e.g., slope, aspect, terrain shape, and landform position), topographic differences between the paired stands in this study were minimal. Although the *L*-stands had slightly gentler slopes (likely as a result of preferential selection by early settlers as sites for agricultural use) than *Q*-stands, the differences were modest and not likely to explain the observed differences in

soil moisture. The more mesic conditions in the tulip poplar stands may at least in part be a result of the overstory community's effect on soil and litter properties. Tulip poplar leaves have low C:N and decompose quickly (Mudrick et al. 1994, Adams and Angradi 1996, Kominoski et al. 2007), likely resulting in a thinner leaf litter layer, rapid turnover of nutrients, and elevated levels of organic matter in the A horizon. Although there were no detectable differences in soil texture (sand, silt, and clay content) that might explain differences in water holding capacity between the stand types, soil in tulip poplar stands had significantly higher organic matter content in the top 5 cm than in oak stands. Soil moisture measured in the pots was also higher in soils from tulip poplar stands in both March and October regardless of whether the pots resided in *L*-stands or *Q*-stands during the intervening period, suggesting that properties of the soil (e.g., higher organic matter content) rather than site conditions may be responsible for the higher moisture of soils in tulip poplar stands. Others have noted similar effects on forest floor conditions caused by shifts in overstory composition throughout the eastern U.S., where increasing abundance of shade-tolerant tree species in formerly oak-dominated communities (due largely to fire suppression) have resulted in more mesic understory conditions (Nowacki and Abrams 2008, Rogers et al. 2008).

Germination rates of *C. orbiculatus* were higher in the low leaf litter mass treatments than in either the no litter treatments or the high litter mass treatments. First-year seedling survival was also lowest in the high litter mass treatments. These results may reflect a tradeoff between the importance of litter in creating appropriate microsite conditions related to moisture and its influence as a physical barrier limiting seedling establishment. Although soil moisture in the litter and no litter treatments were not significantly different, plots with litter did have slightly higher mean soil moisture in the upper 12 cm of soil early in the growing season, and

these differences were likely more pronounced at the soil surface. Particularly given the dry conditions during the 2008 growing season, the surface of the no-litter plots may have been too dry for substantial germination of the *C. orbiculatus* seeds. The soils under high litter mass treatments were drier than low litter mass plots early in the growing season, perhaps due to interception of precipitation by the thicker leaf litter layer. While leaf litter often promotes infiltration and reduces evaporation from the soil surface, thus maintaining moister soil conditions (Facelli and Pickett 1991, Sayer 2006), dense leaf litter can have the opposite effect by intercepting incoming moisture and reducing infiltration of the soil beneath it (Walsh and Voigt 1977, Facelli and Pickett 1991). The thicker litter layer may also act as a physical barrier (Sydes and Grime 1981, Facelli and Pickett 1991, Sayer 2006), requiring the emergent *C. orbiculatus* seedlings to devote substantial energy stores to hypocotyl growth, as noted by Ellsworth et al. (2004a). Low seedling survival in the high litter mass treatments indicates that many of those that did germinate in 2008 were unable to become established, perhaps owing to the high energy demand required to become established in the thicker litter layer and/or the desiccating conditions within the litter. The no-litter plots, on the other hand, had the lowest germination rate but had the highest seedling survival rate. Given the competing roles of litter in creating moist microsites for germination on one hand, and obstructing seedling growth and reducing survivorship on the other, areas with modest amounts of litter may provide the most appropriate balance between these tradeoffs and the most conducive conditions for establishment by *C. orbiculatus*.

Oak-dominated stands in the study region are often characterized by moder (or “duff mull”) humus forms (McNab 1995), which have thick organic layers and a well-developed layer of fine, partially decomposed litter material (F horizon) between the coarse litter and the mineral

soil (Green et al. 1993, Ponge 2003). Litter layers in tulip poplar stands, on the other hand, tend to be thin and lack an F horizon, typical of the mull humus form. The presence of an F horizon may also contribute to drier soil conditions in oak stands by intercepting precipitation, and it may act as an additional physical barrier for seedling establishment. Results from the scarification treatment are consistent with such a role of the F horizon in conferring resistance to invasion by *C. orbiculatus*. Plots with the scarification treatment had higher germination than the no-litter plots that lacked a scarification treatment, and these differences were most pronounced in the *Q*-stands where the non-scarified plots were more likely to have an F horizon present. McNab and Loftis (2002) noted a higher probability of *C. orbiculatus* occurrence in areas that had experienced scarification of the forest floor (perhaps due to foraging by wild turkeys), underscoring the importance of the organic layer for invasion resistance.

Soils in the tulip poplar stands had higher nutrient levels (especially exchangeable cations and total N), pH, and organic matter (in the upper 5 cm). Nonetheless, soil type had a minimal effect on germination and seedling survival of *C. orbiculatus*, as indicated by the potted soil translocation experiment. Although mean germination and survival was slightly higher in soils taken from the *L*-sites, the only (moderately) significant difference between soil types was for seed germination in 2009. Seed germination in the pots was actually higher in the *Q*-stands than in the *L*-stands, perhaps owing to the later leaf-out of oaks and therefore higher early-season light levels in the *Q*-stands. Regardless of the reason for this relationship, it suggests that site conditions related to the forest canopy and midstory do not explain the higher abundance of *C. orbiculatus* typically observed in tulip poplar stands. The minimal differences in germination and survival between soil types and stand types in the translocated pot experiment (where litter

was excluded) underscores the important role of litter in explaining establishment success by *C. orbiculatus*.

Although soil temperature can have a strong influence on germination (Vegis 1964, Vleeshouwers et al. 1995, Vandelook et al. 2008), the differences between treatments that we observed did not generally correspond to observed differences in seed germination. We expected a positive correlation between spring soil temperature and germination rates. Though soil temperature was higher in no-litter plots early in the growing season, *C. orbiculatus* germination rates were lowest in those plots, perhaps owing to drier surface soil conditions. Furthermore, there were no differences in mean soil temperatures between the *L*-stands and *Q*-stands that could explain the large differences in germination. Mean soil temperatures in the low litter mass treatments were higher than in the high litter mass treatments early in the growing season and could have contributed to the higher germination rates observed in those plots, though mean differences between treatments were small (< 1° C). Overall, our results suggest that soil moisture and litter conditions may be playing a more important role than temperature in determining invasibility.

Although several studies have noted a relationship between land-use history and invasion by non-native plants (Lundgren et al. 2004, DeGasperis and Motzkin 2007, Von Holle and Motzkin 2007), there has been little effort to elucidate the specific factors related to land-use history that facilitate invasion. At BCEF land-use history appears to be influencing invasion indirectly via successional changes in the overstory community (particularly increased dominance by tulip poplar) that in turn affect forest floor conditions, increasing invasibility. It is noteworthy that areas that have experienced non-agricultural, large-scale disturbances such as clear-cuts or windthrow events in the study region also often experience increased tulip poplar

dominance (Clinton and Baker 2000, Elliott et al. 2002). High abundance of *C. orbiculatus* have been observed in such areas at BCEF (McNab and Loftis 2002, personal observations), suggesting that the conditions conducive for its invasion are not exclusively associated with agricultural land-use history, but may be more likely in areas with any large-scale disturbance history and associated successional forest communities.

By elucidating the specific factors that influence invasion of forests by non-native plants, we are better suited to make predictions regarding their spread, identify areas that are most at risk, and implement control measure to minimize their detrimental effects. The results from our study suggest that forest management strategies for controlling the spread of *C. orbiculatus* should be context dependent. For example, forest stands that are particularly susceptible to invasion, such as those dominated by tulip poplar, may warrant special treatment at the time of a timber harvest and/or shortly thereafter to eradicate *C. orbiculatus* seedlings that are already present or may become established due to harvesting activities. In the case of oak dominated stands, our results suggest that measures should be taken to minimized disturbance of the leaf litter layer that may confer resistance to *C. orbiculatus* invasion.

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Table 1. Experimental site/stand characteristics. Stand type refers to stands dominated by *Liriodendron tulipifera* (*L*-stands) or *Quercus* spp. (*Q*-stands), respectively. *L*-stands were all in areas that were previously cultivated, and *Q*-stands were in areas with no agricultural disturbance history. Total basal areas (BA) includes all trees with stems >5-cm DBH. The terrain shape index (TSI) measures the concavity (positive values) or convexity (negative values) of the local landform. Soil texture and chemistry were measured in soil cores sampled to a depth of 15 cm. Organic matter (O.M.) was measured in both the top 15 cm and 5 cm of soil. Results of the paired t-tests are based on differences between paired stands within the five sites.

Site	Stand type	*Lirtul* BA (m^2ha^{-1})	*Q. spp.* BA (m^2ha^{-1})	total BA (m^2ha^{-1})	canopy cover (%)	elev. (m)	slope (°)	aspect (°)	TSI
1	L	26.7	0.0	33.6	87.2	782	17	160	0.00
	Q	0.0	35.7	48.3	88.4	842	19	160	-0.38
2	L	20.2	0.9	34.8	90.4	759	16	290	0.13
	Q	0.2	30.2	43.1	89.8	751	20	295	1.38
3	L	39.8	0.8	44.3	89.6	713	19	110	1.13
	Q	0.0	23.1	36.8	88.8	720	20	110	-0.75
4	L	31.7	1.1	38.5	90.6	744	17	80	1.00
	Q	11.7	30.9	51.9	91.6	747	20	60	-0.63
5	L	20.1	0.8	34.9	91.8	720	13	160	0.63
	Q	0.3	22.6	32.0	90.8	720	16	150	1.63
Paired-t		**6.55****	**10.66*****	**1.18**	**0.09**	**1.02**	**5.10****	**1.12**	**0.51**

*** *P* <0.05, ** *P* <0.01, ****P* <0.001**

Table 1 (cont.)

Site	Stand type	clay (%)	sand (%)	pH	P (ppm)	K (ppm)	Ca (ppm)	Mg (ppm)	total N (mg/L)	O.M. 15cm (%)	O.M. 5cm (%)
1	L	23.6	52.8	4.9	7	50	220	33	0.17	7.2	11.4
	Q	23.4	55.3	4.6	4	34	63	18	0.11	6.6	8.6
2	L	14.1	62.6	5.0	2	38	185	46	0.09	4.8	7.8
	Q	15.1	59.8	4.6	3	24	88	19	0.09	4.2	5.3
3	L	18.0	55.0	5.4	5	74	419	78	0.15	5.7	10.0
	Q	20.3	48.1	4.4	6	29	58	15	0.10	6.5	10.0
4	L	17.2	54.4	5.6	3	54	569	72	0.15	5.4	8.5
	Q	19.1	53.6	4.5	3	34	42	17	0.10	5.2	6.3
5	L	17.3	60.3	4.7	3	38	165	56	0.09	4.3	7.5
	Q	17.2	59.4	4.4	3	34	29	14	0.05	4.5	5.5
Paired-t		**1.89**	**1.15**	**3.5***	**0.27**	**2.90***	**3.12***	**4.59***	**3.81***	**0.30**	**3.85***

*** *P* <0.05, ** *P* <0.01, ****P* <0.001**

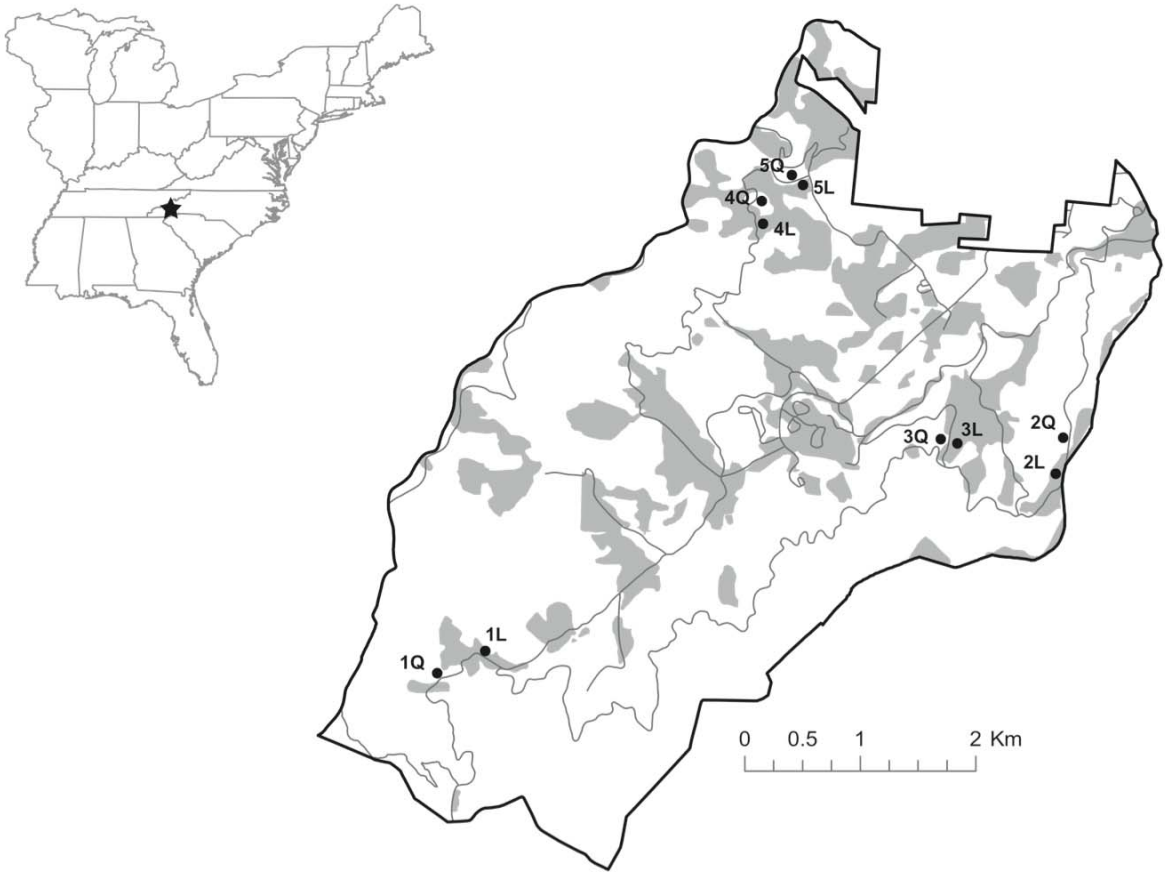

Figure 1. Map of the study area. The inset map on the left shows the location of Bent Creek Experimental Forest (BCEF) in western North Carolina, USA. The larger map shows the BCEF boundary and roads. The gray polygons represent areas that were previously cultivated and abandoned around 1910. The five pairs of experimental stands are represented by black circles (L = *Liriodendron tulipifera* stands, Q = *Quercus* spp. stands).

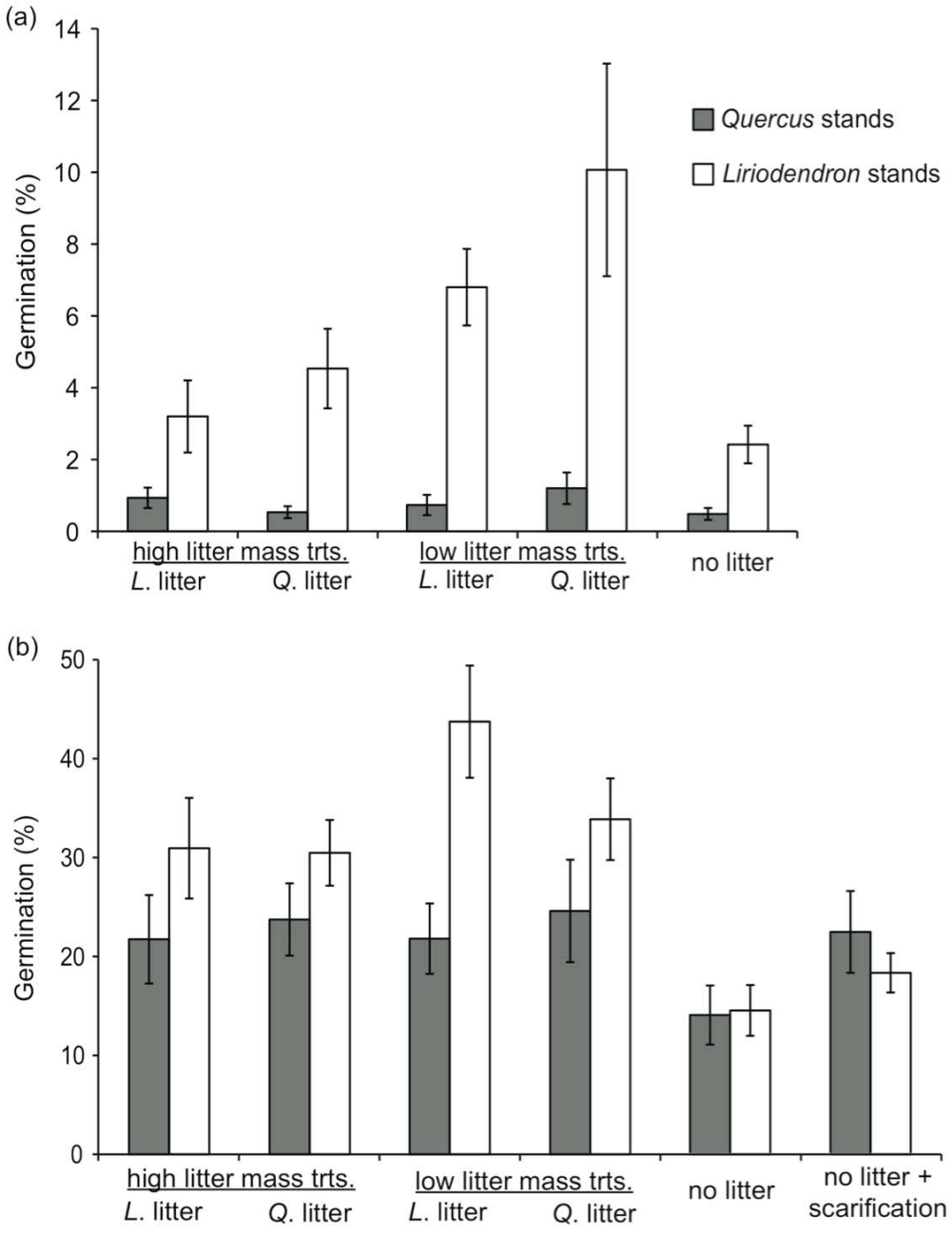

Figure 2. Germination rates in plots sown with *Celastrus orbiculatus* seeds in 2008 (*a*) and 2009 (*b*). Mean percent germination (± 1 *SE*) is shown for the respective treatments. Treatments were the same in 2008 and 2009, with the exception of an additional scarification treatment in 2009. There were significant differences in germination between stand type, no litter vs. litter treatments, and litter mass for both years. There was also a significant effect of scarification among plots without litter in 2009.

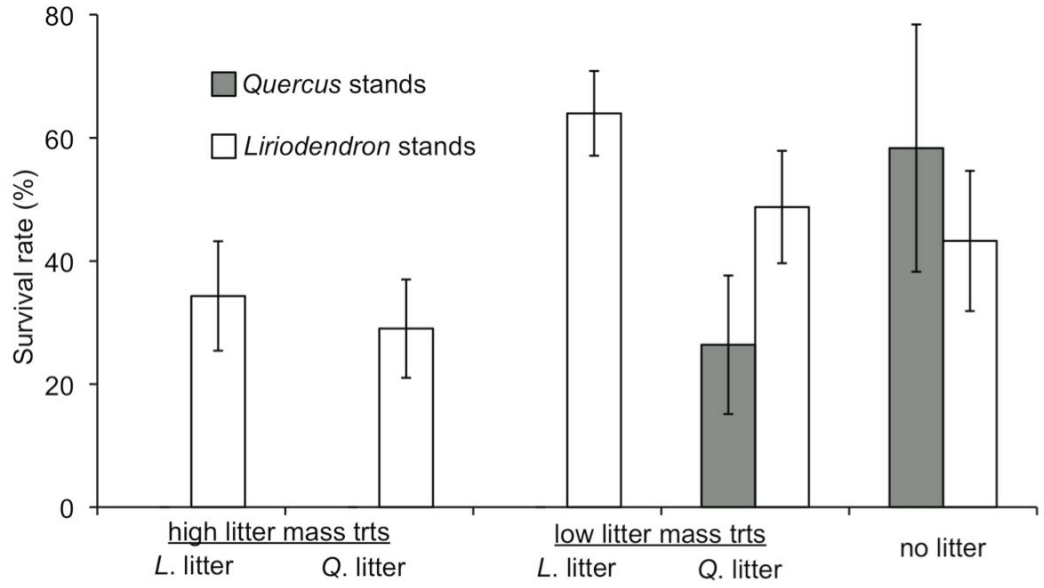

Figure 3. Mean first-year seedling survival (± 1 *SE*) in plots with the respective treatments. Survival rate is based on the percent of seedlings present in plots (*N* = 99) in June 2008 that were still present in June 2009. Three of the treatments in the *Quercus* stands (high *L*-litter, high *Q*-litter, and low *L*-litter) had no surviving seedling in 2009. Seedling survival was significantly higher in *L*-stands than in *Q*-stands, in no-litter plots than those with litter, and in low-litter plots than high-litter plots.

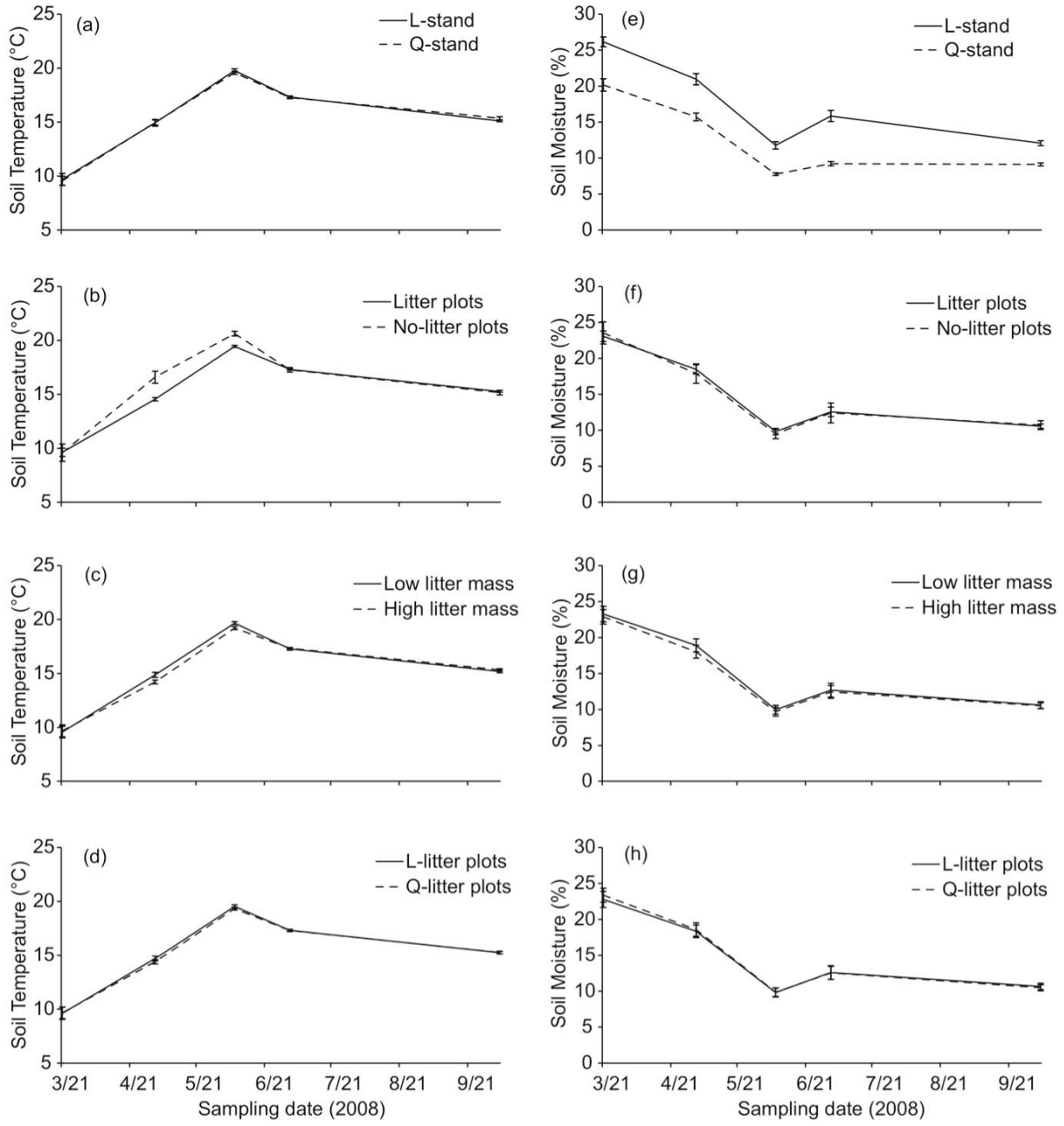

Figure 4. Mean soil temperature (left panel) and soil moisture (right panel) for plots with the respective treatments: stand type (*a* and *e*), litter vs. no litter (*b* and *f*), low vs. high litter mass (*c* and *g*), and litter type (*d* and *h*). Measurements were taken on March 21 (at the time of experimental setup), May 2, June 7, July 2, and October 5, 2008. Soil temperature was recorded at a depth of 5 cm. Soil moisture was measured as volumetric water content in the upper 12 cm of soil. Error bars show ± 2 *SE*.

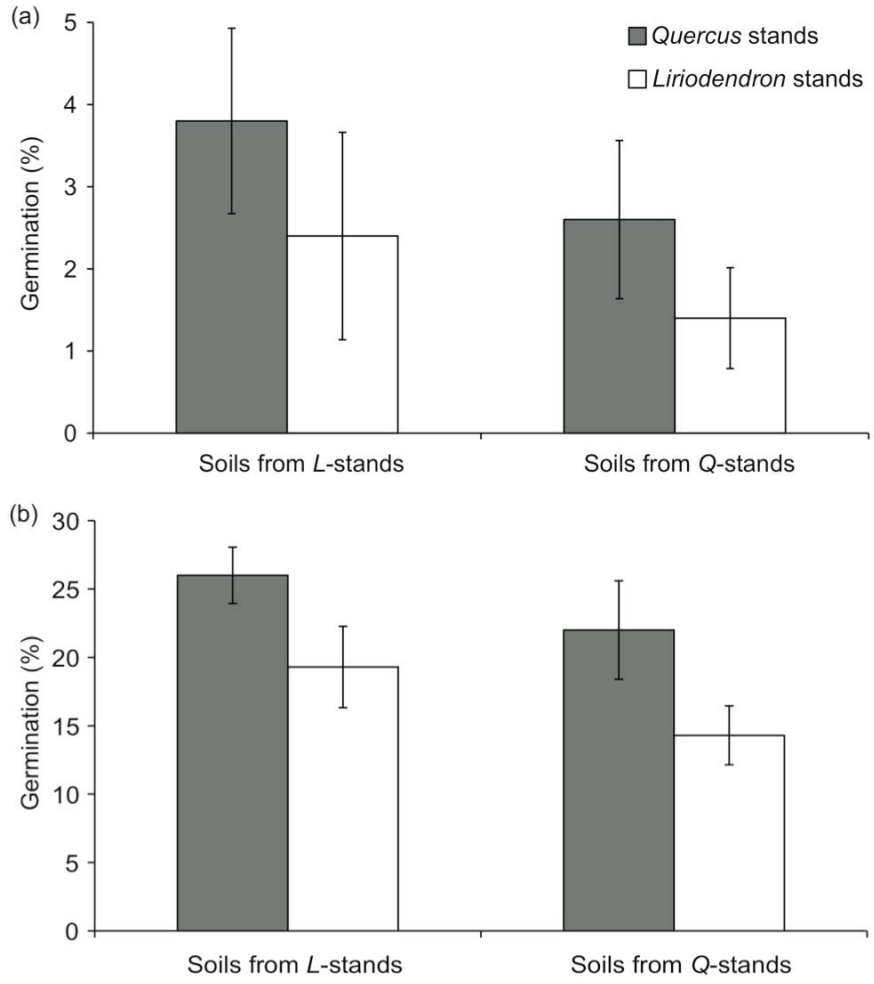

Figure 5. Germination rates in pots sown with *Celastrus orbiculatus* seeds (*N* = 100 pots) in 2008 (*a*) and 2009 (*b*). Mean percent germination (± 1 SE) is shown for pots placed in either *Q*-stands (gray bars) or in *L*-stands (white bars), and in pots with soil taken from either *Q*-stands or *L*-stands.

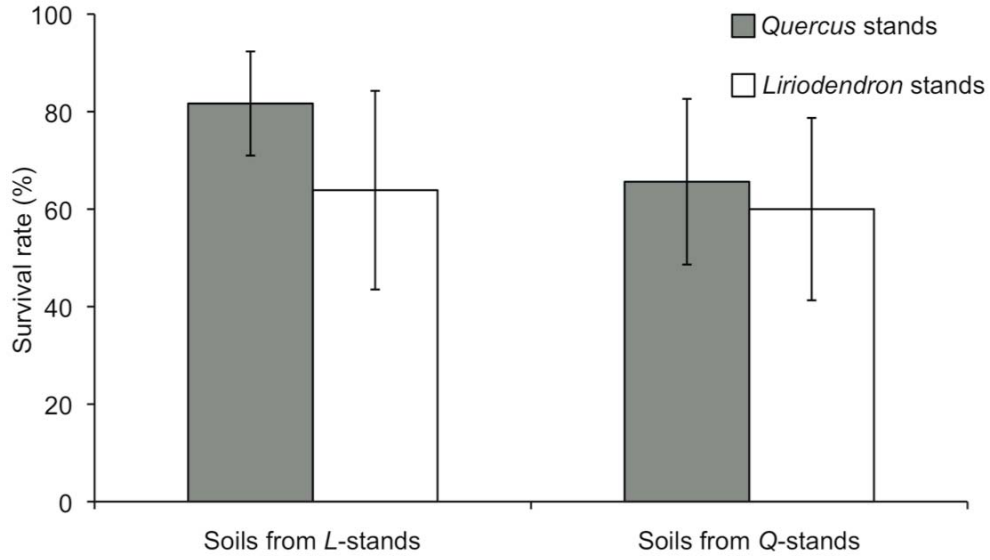

Figure 6. Mean first-year seedling survival (± 1 *SE*) in pots placed either in *Quercus* or *Liriodendron* stands and filled with soil from either *Quercus* or *Liriodendron* stands. Survival rates are based on the percent of seedlings present in pots (N = 29) in June 2008 that were still present in 2009. There were no significant effects of stand type or soil type on seedling survival.

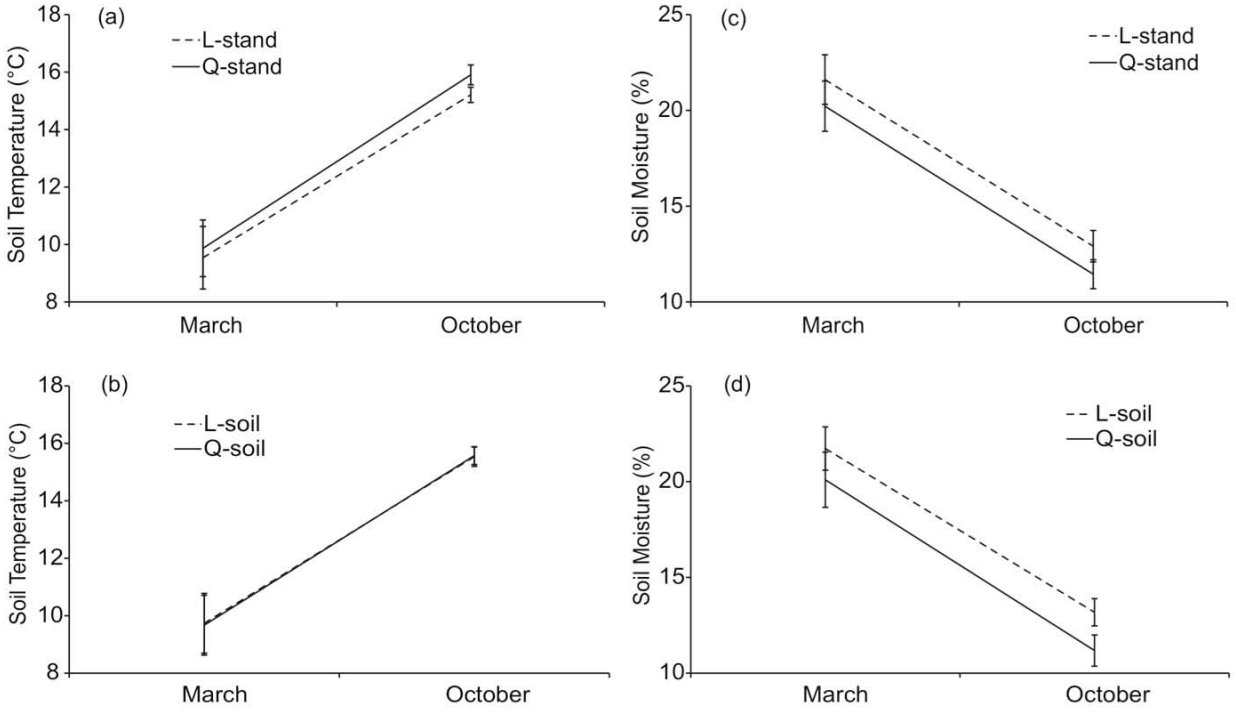

Figure 7. Mean soil temperature (left panel) and soil moisture (right panel) for pots placed either in *Quercus* or *Liriodendron* stands (*a* and *c*) and with soil from either *Quercus* or *Liriodendron* stands (*b* and *d*). Measurements were taken on March 21 (at the time of the experimental setup) and October 5, 2008. Soil temperature was recorded at a depth of 5 cm. Soil moisture was measured as volumetric water content in the upper 12 cm of soil. Error bars show ± 2 *SE*.

CHAPTER 3

Effects of land-use history and the contemporary landscape on non-native plant invasion at local and regional scales in the southern Appalachians[1]

Abstract

Some non-native invasive plant species are well suited for spread in forest-dominated landscapes and may pose a threat to forest communities. By determining what factors explain the distribution of such species, we might advance our understanding of the invasion process and provide a framework for forest managers to identify areas that are particularly susceptible to invasion. We conducted roadside surveys to determine the presence/absence and abundance of 15 non-native plant species known to invade forests in western North Carolina. We used linear and generalized linear models to examine how contemporary land use, landscape context, land-use history, and topography influenced the distribution of the 15 focal species at local and regional scales. The most commonly encountered species were *Microstegium vimineum* (in 84% of plots), *Rosa multiflora* (in 69% of plots), *Lonicera japonica* (in 58% of plots), *Celastrus orbiculatus* (in 53% of plots), *Ligustrum sinense* (in 31% of plots), and *Dioscorea oppositifolia* (in 17% of plots). Results based on AIC model selection varied depending on the scale of analysis. At the regional scale, distance to city center was the most important explanatory variable, with species more likely present and more abundant in watersheds closer to Asheville, NC. Many of the focal species were also more frequently encountered in watersheds at lower elevation and with less continuous forest cover. At the local scale, elevation was still important for explaining the presence/absence of species, but less so for explaining their abundance. Forest cover and land-use history were the most important explanatory variables at the local scale. In

[1] Manuscript to be submitted to *Landscape Ecology* with co-authors Scott M. Pearson and Monica G. Turner

general, species were more likely present and in greater abundance in plots with less forest cover and a higher proportion of area reforested since the 1940s. A notable exception was *M. vimineum*, which had higher abundance in plots with greater forest cover and more residential development. Our results underscore the importance of considering multiple scales to understand the factors driving non-native plant invasion, and they emphasize the need to address both the contemporary landscape and historic land use in facilitating invasion.

Introduction

What factors determine the establishment and spread of non-native invasive plants? This question has long been at the forefront of invasion ecology (Elton 1958, Crawley 1987, Rejmánek 1989, Williamson 1996). Though numerous factors have been implicated, there seems to be no simple or universal answer. Life history traits of non-native species themselves can play a major role in determining their invasion success (Rejmanek and Richardson 1996, Kolar and Lodge 2001, Hamilton et al. 2005). The biotic community (e.g., predators, competitors, and mutualists) in the introduced range may also affect the ability of an invader to become established (Richardson et al. 2000, Shea and Chesson 2002). Likewise, abiotic characteristics of the introduced range influences invasibility. Conclusions regarding the factors that determine invasion success therefore may vary among functional groups or taxa (Rejmanek and Richardson 1996, Tilman 1997, Grotkopp and Rejmanek 2007), geographic regions (Lonsdale 1999, Pysek and Richardson 2006), or scales of analysis (Stohlgren et al. 2002, With 2004, Knight and Reich 2005, Brown et al. 2008).

While no single approach can adequately or universally explain establishment and spread of non-native invasive plants, many studies have recognized the importance of contemporary

land-use patterns. Species may respond to landscape configuration, connectivity, and edge effects associated with habitat fragmentation (Brothers and Spingarn 1992, Hobbs and Huenneke 1992). Roads (Tikka et al. 2001, Forman et al. 2003, Gelbard and Belnap 2003) and residential development (Alston and Richardson 2006, Kowarik 2008) can provide suitable habitat for establishment, growth, and spread of invasive plants. Recent research has also highlighted the influence of historic land use on plant invasions. For example, historically altered forests often have more invasive plants than those without a human disturbance history (Lundgren et al. 2004, Brown et al. 2006, DeGasperis and Motzkin 2007, Von Holle and Motzkin 2007). To ascertain the factors driving invasion in a given region, it may be necessary to consider both the contemporary landscape and land-use history. Furthermore, since their relative importance may be scale-dependent, these factors likely warrant evaluation at both local and regional scales. To our knowledge no previous studies have considered the influence of both contemporary and historic land use on plant invasion by comparing responses at multiple scales and across a suite of non-native invasive species.

Although relatively few non-native plants are shade-tolerant or otherwise adapted for invasion of intact forest (Valladares and Niinemets 2008), such species are likely to pose the greatest threat to native biota in forest-dominated landscapes. Among the vast pool of species introduced for horticultural purposes, a small number are well suited to low-light environments (Martin et al. 2009). Furthermore, shade-tolerant invasive plants typically exhibit slower rates of growth and spread than those in open habitats (Kitajima 1994, Grotkopp et al. 2002, Sanford et al. 2003), often resulting in comparatively low population densities in forests. The relative paucity of forest invaders has led some to describe forests as resistant to non-native plant invasion (Crawley 1987, Rejmánek 1989, Von Holle 2005). However, others have cautioned

against underestimating the invasive potential of non-native plants in forests, citing examples of species well suited to forest invasion and warning of potential long-term effects of these latent invaders (Webb et al. 2000, Martin and Marks 2006, Martin et al. 2009).

Roads can facilitate spread of invasive plants in forest-dominated landscapes by providing favorable growing conditions and effective dispersal corridors (Parendes and Jones 2000, Watkins et al. 2003, Christen and Matlack 2006, Hawbaker et al. 2006). Roadside populations may provide the propagule pressure necessary for invasion of adjacent forest. Most plant species (native and non-native alike) typically experience low germination and seedling survival in the forest understory (Rejmánek 1989, Valladares and Niinemets 2008) and therefore require substantial propagule pressure for successful establishment (Williamson and Fitter 1996, Lonsdale 1999). Given the potential of roads to facilitate invasion of forests, understanding the distribution of roadside populations of forest invaders and the factors influencing their presence and abundance could provide an effective means to identify forests most vulnerable to invasion.

To evaluate the potential risk of invasion in southern Appalachian forests, we determined the distribution and abundance of a suite of forest-adapted non-native invasive plants along roadsides in western North Carolina. We used linear and generalized linear models to address the following overarching question: What is the relative importance of contemporary land use, landscape context, land-use history, and topography in explaining the presence and abundance of non-native invasive plants capable of forest invasion? Because the factors that affect the presence and abundance of invasive plants may vary with scale (Stohlgren et al. 2002, With 2004, Knight and Reich 2005, Brown et al. 2008), we considered both local and regional scales. At the local scale, we expected invasive plants to respond more strongly to the existing biotic community, local land use (e.g., building density), land-use history, and fine-scale environmental

variation (e.g., local landform). At broader scales we expected invasive plants to respond more strongly to landscape context (e.g., distance from the regional city center and regional forest cover) and topographic gradients (e.g., elevation). The interaction of factors at multiple scales may produce complex patterns of invasibility that give rise to heterogeneous distributions of invasive plants, and multi-scale analyses may be necessary to elucidate the factors that facilitate invasion by non-native invasive plants in forested landscapes.

Methods

Study Area

The study was conducted in the French Broad River Basin in Madison, Buncombe, Henderson, and Transylvania Counties of western North Carolina, U.S.A (Fig. 1). As part of the southern Blue Ridge Physiographic Province, the region is characterized by steep terrain, expansive forest, and high biological diversity. Elevation extends from 350 to 1900 meters. The most prominent forest types include northern hardwoods at higher elevations, mixed hardwoods on less fertile lower elevation sites, and mixed mesophytic forests on many lower slopes and cove sites (SAMAB 1996). The bedrock geology of the French Broad Basin is late Precambrian in origin and predominantly metamorphic. Gneisses and schists are common throughout the basin, with interspersed granitic intrusions (Carpenter 1970).

The study region has a rich land-use history. Pre-European human settlement dates back to at least 8000 BC (Ward and Davis 1999). Widespread European settlement began in the late 1700s; land was cleared in the river valleys for agricultural purposes and livestock were grazed in adjacent uplands (Gragson and Bolstad 2006). During the 1800s, there was extensive conversion of forest to agricultural lands, and later a shift toward commercial timber harvesting

throughout the region. World War II marked the beginning of an out-migration period in which many left the region, resulting in widespread agricultural abandonment (Gragson and Bolstad 2006). Continued farm abandonment and a more recent shift away from intensive timber harvesting has resulted in the regeneration of large tracts of forest that characterize the region today. Forest cover has continued to increase throughout the region despite recent population increases associated with exurban development (Wear and Bolstad 1998). The population in the region increased by 28% between 1970 and 1990 (SAMAB 1996), with associated expansions of road networks and more areas in wildland-urban interface (Radeloff et al. 2005). Recent building trends have resulted in development at higher elevations and steeper slopes that were previously cost-inhibitive to develop but provide aesthetics that attract affluent landowners (Turner et al. 2003).

Field sampling

Prior to sampling we established a list of 15 non-native invasive plant species (see Table 1) that were of concern in the region and known to be capable of spread in forested landscapes. Sampling for these focal species was conducted between June and August 2007. We selected 25 second and third order watersheds (see Fig. 1) to represent ranges of forest cover (63-99%) and development intensity that were representative of the study region. Watersheds varied from 700 to 1500 ha, and none contained primary highways. Approximately 25 plots were sampled in each watershed (N=613 plots in total). Plot locations were randomly selected along all navigable roads beforehand using GIS. At each plot location, two 30-m transects were established: one on each side of the road, running parallel to the road at the furthest edge of the right-of-way.

Vegetation sampling was performed in 1-m^2 quadrats placed every 3 meters on both sides of a transect (*N*=40 quadrats per plot). Cover of each focal species was recorded in quadrats using modified Braun-Blanquet cover classes (Braun-Blanquet 1932). Cover classes were later converted to percent cover (using their midpoints) and averaged across all 40 quadrats to estimate invasive cover of plots. The immediate vicinity surrounding each plot was also carefully inspected to detect the presence of focal species that were not otherwise represented in the quadrats. For plots in which such species were detected, they were included in presence/absence analyses but not in cover estimates.

GIS-derived data

Watershed-level variables

The same set of GIS-derived explanatory variables was used in all watershed-level models. We included two topographic variables derived from digital elevation models: minimum elevation and mean aspect. Minimum elevation was taken as elevation at the lowest point in a watershed and was chosen to minimize correlation with other explanatory variables (see Table 2). Mean aspect was derived from 30-m digital elevation models (DEMs) and was calculated by converting degrees azimuth (θ) for all cells within a watershed to an index of insolation (*I*) adapted from Beers et al. (1966): $I = \cos(22.5° - \theta) + 1$. The index results in a range of values between 0 at 202.5° (SSW, considered to have the highest insolation) and 2 at 22.5° (NNE, with the lowest insolation), and increases as compass direction changes in either direction from SSW to NNE. Insolation index values were then averaged across all raster cells in a watershed to describe the watershed's dominant aspect. Forest cover was included as an explanatory variable, and was calculated as the proportion of a watershed in forest based on the

2001 National Land Cover Dataset (NLCD). Forest regrowth was included as a land-use history variable and was calculated by digitally extracting the non-forest areas from 1940s USGS 7.5-minute quadrangle maps for the study region and overlaying the 2001 NLCD forest cover to determine areas that have regrown to forest since the 1940s. We then calculated the proportion of each watershed represented by these regrown areas. Finally, we used distance to city center as a landscape context variable in the watershed-level models. It was calculated as the distance from the centroid of each watershed to Asheville, NC. We excluded edge density, road density, and building density as explanatory variables due to high (negative) correlations with forest cover (see Table 2).

Plot-level variables

All plot-level models also were fitted using a set of explanatory variables generated from GIS-based data. We included two topographic variables: elevation and distance to the nearest stream. Plot elevation was extracted from 30-m DEMs. Distance to stream was meant to describe the landform position of plot locations; those that were closer to streams were assumed to be in more mesic, concave landform positions than those that were further from streams. The stream network used to calculate the distances was generated using the flow accumulation extension in ArcMAP 9.1 (ESRI 2006) with 30-m DEMs. Stream were defined as having a flow accumulation >100 pixels. We calculated the local terrain shape at each plot using the curvature extension in ArcMAP; the terrain shape was correlated with distance to stream (see Table 3), but did not perform as well for capturing landform position, so was excluded from model selection.

We included three local landscape context variables in the plot-level models: forest cover, forest regrowth, and number of developed parcels. These variables were calculated based

on a 126-m radius around the center of each plot, resulting in a 5-ha circular area meant to capture the local land-use/land-cover context while limiting overlap with adjacent plots. Forest cover was measured as the proportion of the 5-ha area in forest, based on the 2001 NLCD. Forest regrowth was measured as the proportion of the area regrown since the 1940s, calculated as described for the watershed-level analyses. The number of developed parcels around each plot was used as a proxy for building density since exact building locations were not available. Developed parcels were defined as those with at least one maintained building according to county property records. For each plot, we tallied the number of developed parcels contained within or intersected by the 126-m radius.

Data Analysis

Analyses were performed for both the regional (watershed-level) and local (plot-level) scales. Linear and generalized linear models were used to determine which variables best explained the presence/absence, abundance, and richness of the focal invasive species at the respective scales. All models were fitted using R version 2.6.2 (R Development Core Team 2008). We used AIC model selection based on second-order AIC (AIC_c) which reduces over-parameterization of models given small sample sizes (Burnham and Anderson 1998). All possible models were considered as candidate models (32 candidates per model set). Akaike weights (w_i) were calculated for all candidate models. We estimated the relative variable importance of each explanatory variable in the respective model sets by summing the Akaike weights of all those candidate models in which that variable was included (Burnham and Anderson 1998). Relative variable importance provides a method for ranking the importance of the respective explanatory variables across multiple models in a model set. Given the number of

model sets we wished to compare and contrast, we defined a single "best" model in each set as the one with the fewest parameters in which $\Delta_i < 1$ (sensu Lebreton et al. 1992). We deemed this method most effective at selecting parsimonious models that still included all significant variables. We have included all comparable best models (those with $\Delta_i < 2$) from watershed-level model selection (Appendix 1) and plot-level model selection (Appendix 2) for reference.

Watershed-level analyses

Linear regression models were used to explain focal species total cover, focal species richness, and frequency of occurrence for the six most common invasive plant species. For the total cover model set, the response variable was the summed percent cover of all focal species averaged across all plots in a watershed. For the focal species richness model set, the response variable was the number of focal species present in each watershed. Frequency of occurrence refers to the proportion of plots in which a species was present in each watershed and indicates the regional abundance of that species. All percent cover and frequency values were arcsine square root transformed to improve normality. Generalized linear (logistic regression) models were used for modeling watershed-level presence/absence of the nine less commonly encountered focal species, those present in 24-72% of watersheds.

Plot-level analyses

Linear mixed effects models were used for plot-level analyses of focal species total cover, focal species richness, and abundance (percent cover) for each of the six most commonly encountered focal species. The linear mixed models were fitted using the *lme* function (Pinheiro and Bates 2000) with maximum likelihood parameter estimation. We used generalized linear

mixed effects models (GLMMs) to analyze presence/absence for each of the six most common focal species. Logistic GLMMs were fitted using the *lmer* function (Bates and Sarkar 2006) with parameter estimation based on the Laplace approximation. For all mixed effects models, *watershed* was included as a random effect. Models for total cover, focal species richness, and presence/absence included all plots (N=613). The species abundance (percent cover) models only included plots in which the respective species were present ($52 < N < 502$). Percent cover values were arcsine square root transformed to improve normality. The nine less common focal species did not occur in enough plots to warrant plot-level modeling.

Results

The six most commonly encountered focal invasive species were each present in >95% of watersheds and >16% of plots (see Table 1). Japanese stiltgrass (*Microstegium vimineum*) was the most common focal species, occurring in all watersheds and in 84% of plots. Oriental bittersweet (*Celastrus orbiculatus*), Japanese honeysuckle (*Lonicera japonica*), and multiflora rose (*Rosa multiflora*) were the next most common species, occurring in 53, 58, and 69% of plots, respectively. Japanese honeysuckle also had a higher mean percent cover (4.8%) than any other focal species. Chinese privet (*Ligustrum sinense*) was present in 31% of plots. Although only in 17% of plots, Chinese yam (*Dioscorea oppositifolia*) occurred in every watershed. The mean aggregate cover for all focal species was 15.8%.

Watershed-level model selection results

The model that best explained watershed-level focal species total cover included minimum elevation and distance to city center, with higher invasive cover in watersheds at lower

elevation and closer to Asheville, NC. The best model for focal species richness included only distance to Asheville, with more species encountered in watersheds closer to Asheville (Table 4). The other explanatory variables had considerably lower importance for total cover and focal species richness models (Fig. 2a).

Among the plot frequency models for the six most common species, forest cover was one of the most important explanatory variables (Fig. 2b) and was included in four of the best models (*C. orbiculatus*, *L. sinense*, *L. japonica*, and *R. multiflora*) (Table 4). These species were encountered more frequently in watersheds with lower forest cover. Elevation was included in three of the models (*L. sinense*, *L. japonica*, and *M. vimineum*), with species more frequently encountered in watersheds at lower elevation. Distance to city center was also included in three of the models (*C. orbiculatus*, *L. sinense*, and *L. japonica*), with species encountered more frequently in watersheds closer to Asheville. Mean aspect was included in the best model for *M. vimineum*, with higher plot frequency in watersheds with more south-southwesterly aspects (higher insolation). Land-use history (forest regrowth) was not included in any of the plot frequency best models (Table 4).

Among the watershed-level presence/absence models, distance to city center was the most important explanatory variable (Fig. 2c). In the best models for *Ailanthus altissima*, *Berberis thunbergii*, *Elaeagnus umbellata*, and *Paulownia tomentosa*, species were more likely present in watersheds closer to Asheville (Table 4). One species, *Alliaria petiolata*, was more likely present in watersheds further from Asheville. Forest cover was included in one of the models (*Albizia julibrissin*), with a higher likelihood of presence in watersheds with less forest cover. Land-use history (forest regrowth) was only included in the model for *E. umbellata*, with a greater likelihood of presence in watersheds with less forest regrowth since the 1940s.

Elevation and mean aspect were not included in any of the presence/absence best models. Models for three species (*Miscanthus sinenis*, *Polygonum cuspidatum*, and *Pueraria montana*) included only the intercept term (Table 4).

Plot-level model selection results

The best plot-level models for focal species total cover and focal species richness included elevation, forest cover, and forest regrowth as explanatory variables (Table 5). Both total cover and richness were higher at lower elevations, in plots with less forest cover in the 5-ha area surrounding them, and in plots with more forest regrowth since the 1940s in the surrounding area. The number of developed parcels in the area surrounding plots was also included as an important explanatory variable in the focal species richness best model, with more species in plots with more developed parcels (Table 5). Distance to stream had a low variable importance for total cover and focal species richness models (Fig. 3a).

Among the plot-level presence/absence models for the six most commonly encountered focal species, elevation was one of the most important variables (Fig. 3b) and was included in five of the best models (*D. oppositifolia*, *L. sinense*, *L. japonica*, *M. vimineum*, and *R. multiflora*) (Table 5). In all models, species were more likely present in plots at lower elevations. Forest cover was also an important variable (Fig. 3b). In four of the presence/absence best models (*C. orbiculatus*, *L. sinense*, *L. japonica*, and *R. multiflora*), species presence was negatively correlated with forest cover. The best model for *M. vimineum*, however, showed a positive relationship between species presence and forest cover. Land-use history (forest regrowth) was included in three of the presence/absence best models (*L. sinense*, *L. japonica*, and *R. multiflora*), with greater likelihood of presence in plots with a higher proportion of surrounding area that had

regrown to forest since the 1940s. Distance to stream was included as an important explanatory variable in three of the presence/absence best models (Table 5). In the *C. orbiculatus* model, there was a positive relationship between distance to stream and likelihood of presence. In the *D. oppositifolia* and *M. vimineum* models, there was a negative relationship, indicating that plots closer to streams had a greater likelihood of species presence. The number of developed parcels surrounding a plot was included in two of the best models (*C. orbiculatus* and *L. sinense*), with greater likelihood of presence in plots with more developed parcels in their vicinity.

Among the plot-level abundance (percent cover) models for the six most common focal species, forest cover and forest regrowth were the two most important variables (Fig. 3c). Forest cover was included in four of the percent cover best models (Table 5). Just as in the presence/absence models for *L. sinense, L. japonica*, and *R. multiflora*, there was a negative relationship between species cover and proportion of forest cover around each plot, and for *M. vimineum* there was a positive relationship. Land-use history (forest regrowth) was included in the cover models for *C. orbiculatus, L. sinense, L. japonica*, and *R. multiflora*. In all four models, percent cover was greater in plots with more forest regrowth since the 1940s in the surrounding 5-ha area. The number of developed parcels was included in the *C. orbiculatus* and *M. vimineum* best models, with greater cover in plots with more developed parcels around them. Elevation was included only in the *L. japonica* best model, with greater cover in plots at lower elevation. Distance to stream was not included in any of the plot-level cover best models.

Discussion

The distribution of non-native invasive plants that we observed in western North Carolina was influenced by a number of factors related to contemporary land use, landscape context, historic land use, and topography. The relative importance of factors varied depending on the scale of analysis. While some factors were more important for explaining patterns of invasion at either local or regional scales, others influenced invasion at both scales. Our results underscore the importance of considering plant invasion at multiple scales to elucidate the factors driving invasion and to predict future spread of non-native invasive plants. The importance of considering multiple scales to explain ecological processes is well accepted (Holling 1996, Peterson et al. 1998, Steffan-Dewenter et al. 2002, Leibold et al. 2004) and has been demonstrated for invasion by non-native species (Stohlgren et al. 2002, With 2004, Knight and Reich 2005). We considered three explanatory variables at both the watershed- and plot-level scales: elevation (topography), forest cover (contemporary land use and land cover), and forest regrowth (land-use history).

Elevation was an important explanatory variable at both the watershed and local scales. At the watershed scale, elevation was more important in explaining focal species total cover and abundance (plot frequency) of the more common species; it was not included in any of the presence/absence best models for the less common species. At the plot scale, on the other hand, elevation was more important among the presence/absence models than the abundance (cover) models. These results underscore the importance of distinguishing between regional and local abundance, and they suggest that elevation plays a major role in determining where non-native plants occur across the landscape but may be overshadowed by other factors that influence invasive abundance at finer scales.

Although forest cover was an important explanatory variable at both the watershed and plot scales, its importance was particularly apparent in the plot-level models, suggesting that the focal species responded more strongly to land cover patterns at the local scale than at the watershed scale. Land-use history was considerably more important in explaining patterns of invasion at the local scale than at the watershed scale, suggesting that focal species were responding to local site conditions influenced by land-use legacies rather than to broader-scale patterns produced by historic land use.

Some factors only warrant consideration at a specific scale but may contribute substantial explanatory power at that scale. Distance to city center (Asheville, NC) was considered only at the regional scale (among watersheds) and was the most important variable at that scale. With the exception of *Alliaria petiolata*, species were more common closer to Asheville. Others have noted a negative relationship between plant invasion and distance to urban areas (Alston and Richardson 2006, Kowarik 2008, Albright *in review*). The city center may act as the regional site of introduction for many species. Particularly in the case of escaped cultivars, the likelihood of introduction may be higher near urban centers with more initial propagule sources such as nurseries and more potential establishment sites such as lawns and gardens (Reichard and White 2001). This would suggest that the local abundance of an invasive species is related to its residence time (Rejmanek 2000, Wilson et al. 2007), and we would expect a continued outward expansion surrounding the city center fueled by increasing propagule pressure at the invasion front. We found that several of the most commonly cultivated focal species (*C. orbiculatus, L. sinense, L. japonica, A. altissima, B. thunbergii,* and *P. tomentosa*) were more prevalent closer to Asheville, lending support to the city-center-as-propagule-source concept. Alternatively, other factors associated with proximity to the city may actually be facilitating invasion. Higher road

density, development, and fragmentation closer to urban areas might provide more suitable habitat for invasives due to perpetual disturbance (Hobbs and Huenneke 1992) and/or elevated levels of resources (Davis et al. 2000). A denser transportation network and higher volume of traffic might also facilitate a more rapid spread of propagules closer to the city center (Forman and Alexander 1998, von der Lippe and Kowarik 2007). The positive relationship between *A. petiolata* presence and distance to Asheville is likely due the species' more northern distribution. It is more common north or the study region in Tennessee (Welk et al. 2002) and primarily occurred in the northernmost watersheds that we sampled.

Results from our study underscore the importance of considering both the contemporary landscape and land-use history to understand patterns of plant invasion, particularly at the local scale. Focal species were more common in plots with a greater proportion of surrounding area that had regrown to forest since the 1940s. Several studies have demonstrated a positive relationship between land-use history and non-native plant invasion in forested regions (Lundgren et al. 2004, DeGasperis and Motzkin 2007, Von Holle and Motzkin 2007), but the mechanisms underlying land-use history's influence on invasion are poorly understood. The species might have become established around the time of land abandonment and persisted in the regrown areas. Alternatively, the species might be responding to persistent changes in site conditions caused by the former land use or those generated by subsequent forest succession.

Certain variables may be more important for establishment of invasive plants while others may be more important for determining their abundance and potential for spread via increased propagule pressure (Lonsdale 1999). Our plot-level model results offer insight into such differences among variables by comparing their effects on both focal species presence/absence (establishment) and abundance. For example, elevation was important for

explaining presence/absence for five of the six species, whereas it was included in the abundance (cover) model only for *L. japonica*. Invasives were more common at lower elevations, a pattern that is commonly observed in mountainous regions (Wilson et al. 1992, Stohlgren et al. 2002, Pauchard and Alaback 2004). Elevation may influence invasibility due to associated climatic conditions. Colder conditions and a shorter growing season at higher elevations may preclude establishment of many species. In the study region, likely source populations are also at lower elevations for many species, perhaps related to the higher development densities (Crawley 1987). Regardless of the reasons for elevation's influence on establishment, other local-scale factors seem to play a more important role in determining the abundance of species once they have become established. Similarly, distance to stream was included in the presence/absence models for *C. orbiculatus*, *Dioscorea oppositifolia*, and *M. vimineum* but not in the abundance models. Both *D. oppositifolia* and *M. vimineum* were more likely present in plots closer to streams, suggesting they favor more mesic conditions associated with lower slopes and drainages for establishment. Presence/absence of *C. orbiculatus*, on the other hand, showed a positive relationship with distance to stream. The abundance of *C. orbiculatus* was influenced most by land-use history (forest regrowth), which was not important for explaining its presence/absence. While other factors are more important for determining where *C. orbiculatus* becomes established, land-use history seems to affect the local conditions that facilitate rapid growth and reproduction. Alternatively, disturbance associated with historic land use could have facilitated earlier establishment, giving invasive populations in such areas more time to proliferate.

Although the focal species were similar in their ability to invade forest landscapes, many responded idiosyncratically to the factors considered, suggesting the need to consider them

independently for management purposes. However, some species could be grouped according to their similarity in responses to certain variables. With limited resources available for invasive control and eradication, knowing which species can be grouped and targeted simultaneously can improve efficiency of management practices (Buckley et al. 2006). Among the species we considered, *L. japonica* and *L. sinense* had remarkably similar responses to the explanatory variables at both local and regional scales. *Rosa multiflora* also showed similar responses to factors at the local scale, suggesting that these three species could be grouped for management purposes. *Microstegium vimineum*, on the other hand, demonstrated unique responses to the factors and may warrant individual attention for management purposes. For example, it was the only species that showed a positive correlation with forest cover at the plot level. Due to its high shade tolerance (Winter et al. 1982, Horton and Neufeld 1998) this annual C4 grass may warrant special attention as a threat to forest understory communities in the eastern US (Barden 1987, Leicht et al. 2005). It is also noteworthy that *M. vimineum* abundance was higher in areas with both greater forest cover and more development. Though often thought of as mutually exclusive, this combination of factors is indicative of current trends in exurban and rural development in the region where homes are frequently constructed with minimal forest clearing (Wear and Bolstad 1998, Turner et al. 2003).

At first glance, the negative relationship between many of the shade-tolerant focal species and forest cover (with the abovementioned exception of *M. vimineum*) may seem counterintuitive. However, while the focal species are capable of spread in forested landscapes, they still respond favorably to disturbance and forest edge conditions. In the forest-dominated study region, areas with comparatively lower proportions of forest cover tend to have high fragmentation and edge density, providing favorable conditions for the establishment, growth,

and spread of many invasive plants (Brothers and Spingarn 1992, With 2002, Hobbs and Yates 2003).

Invasion of forests by non-native plants may proceed more slowly than in open or disturbed habitats, but this pace does not necessarily imply resistance to invasion (Martin et al. 2009). The potential long-term impacts of plant invasions in forest communities should not be overlooked or underestimated. Through improved understanding of the factors that influence establishment and spread of these forest invaders, more effective management strategies can be implemented to curb their spread and minimize their detrimental impacts on forest communities. Our results illustrate the importance of considering more than one spatial scale to effectively explain invasion across a forested landscape, and they underscore the important influence of historic land use on invasibility. Finally, the study highlights the efficacy of using road networks to track invasion in forest-dominated regions and identify areas of likely spread into adjacent forest.

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Table 1: Focal non-native invasive plant species. The percent of plots (*N*= 613) and watersheds (*N*= 25) in which the species were present are given as measures of their regional prevalence. Mean percent cover is the average cover for the species across all plots. The mean percent cover for all focal species (in aggregate) is the average cover across all plots; cover is summed across species in a plot and could therefore exceed 100% given overlapping species covers.

Species name	Common name	Growth form	Escaped cultivar? (Y/N)	Non-anthropogenic Dispersal mechanisms	% plots in which present	% watersheds in which present	Mean % cover
Ailanthus altissima	tree of heaven	deciduous tree	Y	wind, water	6.5	52	0.37
Albizia julibrissin	silktree/mimosa	deciduous tree	Y	mammals, water	5.1	64	0.04
Alliaria petiolata	garlic mustard	biennial forb	?	gravity, water	2.9	24	0.02
Berberis thunbergii	Japanese barberry	shrub	Y	birds, mammals	3.1	36	0.004
Celastrus orbiculatus	Oriental bittersweet	woody vine	Y	birds	52.5	100	2.54
Dioscorea oppositifolia	Chinese yam	herbaceous vine	Y	water	16.6	100	0.32
Elaeagnus umbellata	autumn olive	shrub	Y	birds, mammals	5.1	32	0.25
Ligustrum sinense	Chinese privet	shrub	Y	birds, mammals	31.2	96	0.71
Lonicera japonica	Japanese honeysuckle	woody vine	Y	birds, mammals	58.1	96	4.77
Microstegium vimineum	Japanese stiltgrass	annual grass	N	gravity, water	84.0	100	2.75
Miscanthus sinensis	Chinese silvergrass	perennial grass	Y	wind	14.2	56	0.38
Paulownia tomentosa	princesstree	deciduous tree	Y	wind, water	6.0	72	0.23
Polygonum cuspidatum	Japanese knotweed	perennial forb	Y	wind, water	6.2	48	0.34
Pueraria montana	kudzu	woody vine	Y	wind, water, animals	2.0	32	0.22
Rosa multiflora	multiflora rose	shrub	Y	birds, mammals	68.5	100	2.88
All focal species	*n/a*	*n/a*	*n/a*	*n/a*	*n/a*	*n/a*	15.82

Table 2. Correlation table for watershed-level explanatory variables. All variables were derived from GIS-based data and were calculated for each of the 25 watersheds. Forest regrowth refers to the proportion of a watershed that has regrown to forest since the 1940s. "Ashe. dist." refers to the distance from a watershed's centroid to the regional city center, Asheville, NC. Pearson's correlation values significant at $P < 0.05$ are shown ($N = 25$ watersheds); non-significant correlations are denoted by "ns."

	Edge density	Road density	Forest regrow†	Ashe. dist.†	Min. elev.†	Max. elev.	Elev. range	Mean elev.	Mean aspect†	Building density
Forest cover†	-0.793***	-0.693***	ns	ns	0.486*	0.737***	0.708***	0.769***	ns	-0.681***
Edge density		0.452*	ns	ns	-0.560*	-0.720***	-0.662***	-0.771***	ns	ns
Road density			ns	-0.412*	ns	-0.429*	-0.403*	-0.484*	ns	0.876***
Forest				ns	ns	ns	ns	ns	ns	ns
Ashe. dist.†					ns	ns	ns	ns	ns	-0.533**
Min. elev.†						0.658***	0.427*	0.821***	ns	ns
Max. elev.							0.962***	0.925***	ns	-0.394*
Elev. range								0.813***	ns	-0.400*
Mean elev.									ns	-0.467*
Mean aspect†										ns

† Explanatory variables included in the model selection process.
*P<0.5, **P<0.01, **P<0.001

Table 3. Correlation table for plot-level explanatory variables. All variables were derived from GIS-based data. Developed parcels, forest cover, and forest regrowth (since the 1940s) are measured within a 5-ha area surrounding each plot. Pearson's correlation values significant at $P < 0.05$ are shown ($N = 613$ plots); non-significant correlations are denoted by "ns."

	Terrain shape	Distance to stream†	Developed parcels†	Forest cover†	Forest regrow†
Elevation†	**-0.171*** **	**0.266*** **	**-0.318*** **	**0.406*** **	**-0.189*** **
Terrain shape		**-0.561*** **	**-0.238*** **	ns	**0.229*** **
Distance to stream†			ns	**0.150*** **	**-0.307*** **
Developed parcels†				**-0.411*** **	**-0.092***
Forest cover†					**0.175*** **

† Explanatory variables included in the model selection process.
*P<0.5, **P<0.01, ***P<0.001

Table 4. Watershed-level model selection results for focal species total cover, focal species richness, plot frequency (proportion of plots in which present) for the six most commonly encountered focal species, and presence/absence (logistic regression) for the nine less common focal species (present in 24-72% of the watersheds). For models in a given set with an AIC_c difference (Δ_i) less than one, the model with the fewest parameters was considered the best model and is shown here. Intercept and model coefficients for variables included in the best model are shown. Akaike model weights (w_i) are also given. For all models, N = 25 watersheds. The number of parameters in a model (K) includes the intercept and error terms.

Model set (response variables)	**Intercept and model coefficients for explanatory variables* in the best model for each model set**						***K***	Δ_i	w_i
	intercept	elev	aspect	ashdist	forest	regrow			
Focal spp. total cover	0.55	-0.0004	---	-0.006	---	---	4	0.00	0.307
Focal spp. richness	13.24	---	---	-0.13	---	---	3	0.00	0.319
Plot frequency models									
Celastrus orbiculatus	2.91	---	---	-0.04	-1.03	---	4	0.00	0.495
Dioscorea oppositifolia	0.40	---	---	---	---	---	2	0.00	0.183
Ligustrum sinense	2.65	-0.002	---	-0.01	-0.68	---	5	0.00	0.255
Lonicera japonica	3.37	-0.002	---	-0.008	-0.67	---	5	0.00	0.401
Microstegium vimineum	2.49	-0.001	-0.53	---	---	---	4	0.00	0.214
Rosa multiflora	2.78	---	---	---	-1.57	---	3	0.72	0.163
Presence/absence models									
Ailanthus altissima	3.35	---	---	-0.13	---	---	3	0.00	0.355
Albizia julibrissin	16.23	---	---	---	-13.50	---	3	0.00	0.370
Alliaria petiolata	-4.79	---	---	0.13	---	---	3	0.00	0.157
Berberis thunbergii	2.37	---	---	-0.13	---	---	3	0.00	0.162
Elaeagnus umbellata	9.76	---	---	-0.21	---	-15.66	4	0.73	0.211
Miscanthus sinensis	0.24	---	---	---	---	---	2	0.00	0.181
Paulownia tomentosa	5.50	---	---	-0.17	---	---	3	0.00	0.299
Polygonum cuspidatum	-0.08	---	---	---	---	---	2	0.00	0.198
Pueraria montana	-0.75	---	---	---	---	---	2	0.00	0.255

* elev= minimum elevation of watersheds, aspect= mean aspect, or northeasterliness of watershed orientation; ashdist= distance from watershed centroid to city center, Asheville, NC; forest= proportion of watershed in forest cover; regrow= proportion of watershed regrown to forest since the 1940s

Table 5. Plot-level mixed effects model selection results for focal species total cover, focal species richness, and both presence/absence and percent cover for the six most common species. The species cover models only include plots in which the respective species were present ($52 < n < 502$). For models in a given set with an AIC_c difference (Δ_i) less than one, the model with the fewest parameters was considered the best model and is shown here. Akaike model weights (w_i) are also given. The number of parameters in a model (K) includes the intercept, random effect (watershed), and error terms.

Model set (response variables)		**Intercept and model coefficients for explanatory variables* in the best model for each model set**						***n***	***K***	Δ_i	w_i
		intercept	elev	strdist	dparc	forest	regrow				
Focal spp. total cover		3.74	-0.50	---	---	-0.13	0.18	613	6	0.15	0.299
Focal spp. richness		34.20	-4.62	---	0.19	-0.85	1.21	613	7	0.00	0.441
Celastrus orbiculatus	Pres/Abs	0.29	---	0.18	0.36	-1.43	---	613	6	0.27	0.160
	Cover	0.07	---	---	0.02	---	0.12	265	5	0.00	0.204
Dioscorea oppositifolia	Pres/Abs	15.63	-2.43	-0.37	---	---	---	613	5	0.72	0.123
	Cover	0.11	---	---	---	---	---	88	3	0.00	0.190
Ligustrum sinense	Pres/Abs	34.90	-5.37	---	0.32	-2.36	2.20	613	7	0.00	0.422
	Cover	0.17	---	---	---	-0.12	0.12	127	5	0.00	0.194
Lonicera japonica	Pres/Abs	90.27	-13.25	---	---	-2.85	1.68	613	6	0.00	0.551
	Cover	2.16	-0.28	---	---	-0.18	0.18	338	6	0.82	0.198
Microstegium vimineum	Pres/Abs	46.34	-6.67	-0.47	---	2.16	---	613	6	0.45	0.293
	Cover	0.01	---	---	0.03	0.08	---	502	5	0.11	0.254
Rosa multiflora	Pres/Abs	41.19	-5.95	---	---	-1.45	1.96	613	6	0.46	0.314
	Cover	0.20	---	---	---	-0.07	0.10	341	5	0.00	0.193

* elev= elevation of plot, strdist= distance from plot center to nearest stream; dparc= number of developed parcels within 126 m of plot; forest= proportion of 5-ha area around plot in forest cover; regrow= proportion of 5-ha area around plot regrown to forest since the 1940s

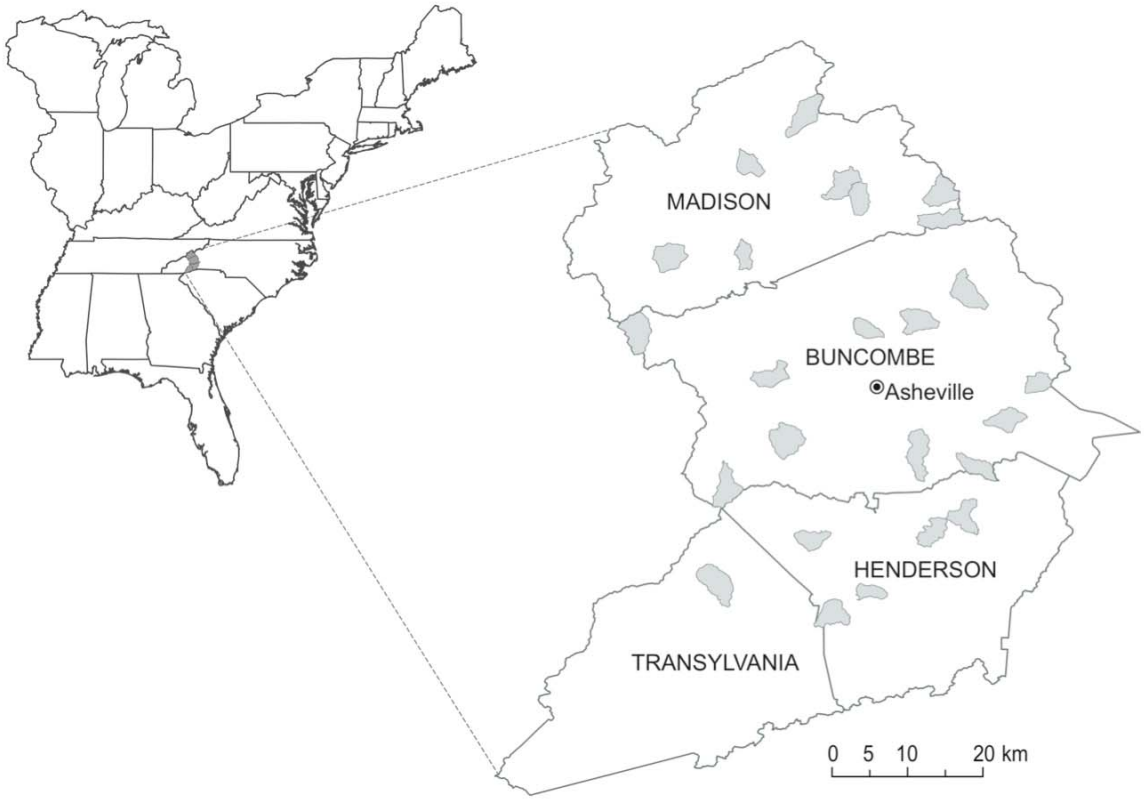

Figure 1. Map of the study area showing the four counties in western North Carolina, U.S.A, and the 25 watersheds (shaded polygons) in which non-native invasive plant sampling was conducted.

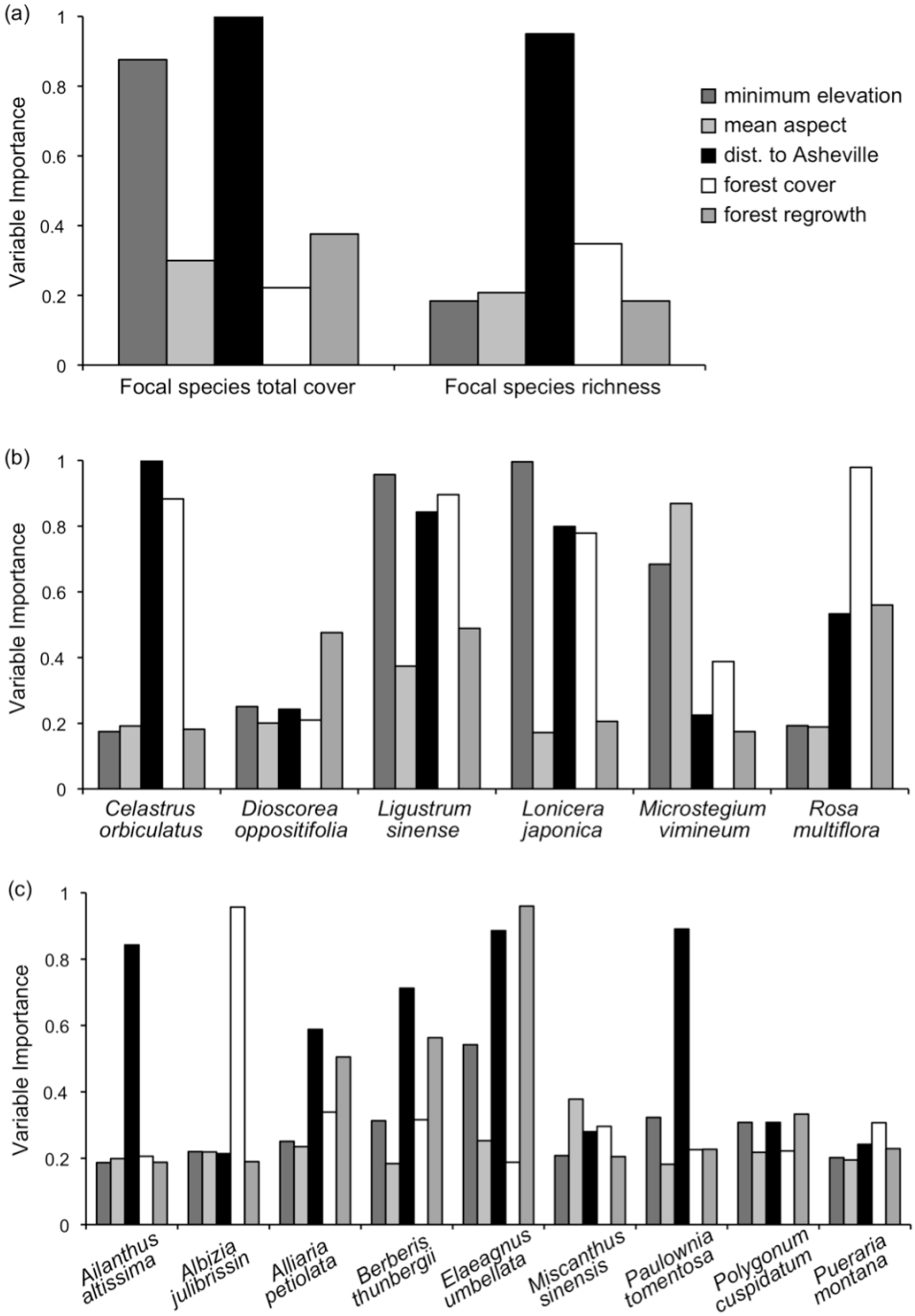

Figure 2. Watershed-level variable importance for each model set: focal species total cover and focal species richness (*a*), plot frequency of the six most common focal species (*b*), and presence/absence of the nine less common focal species (*c*). Relative variable importance is calculated by summing the model Akaike weights (w_i) of all candidate models within a model set in which that explanatory variable is included. Variable weights can range from 0 to 1.

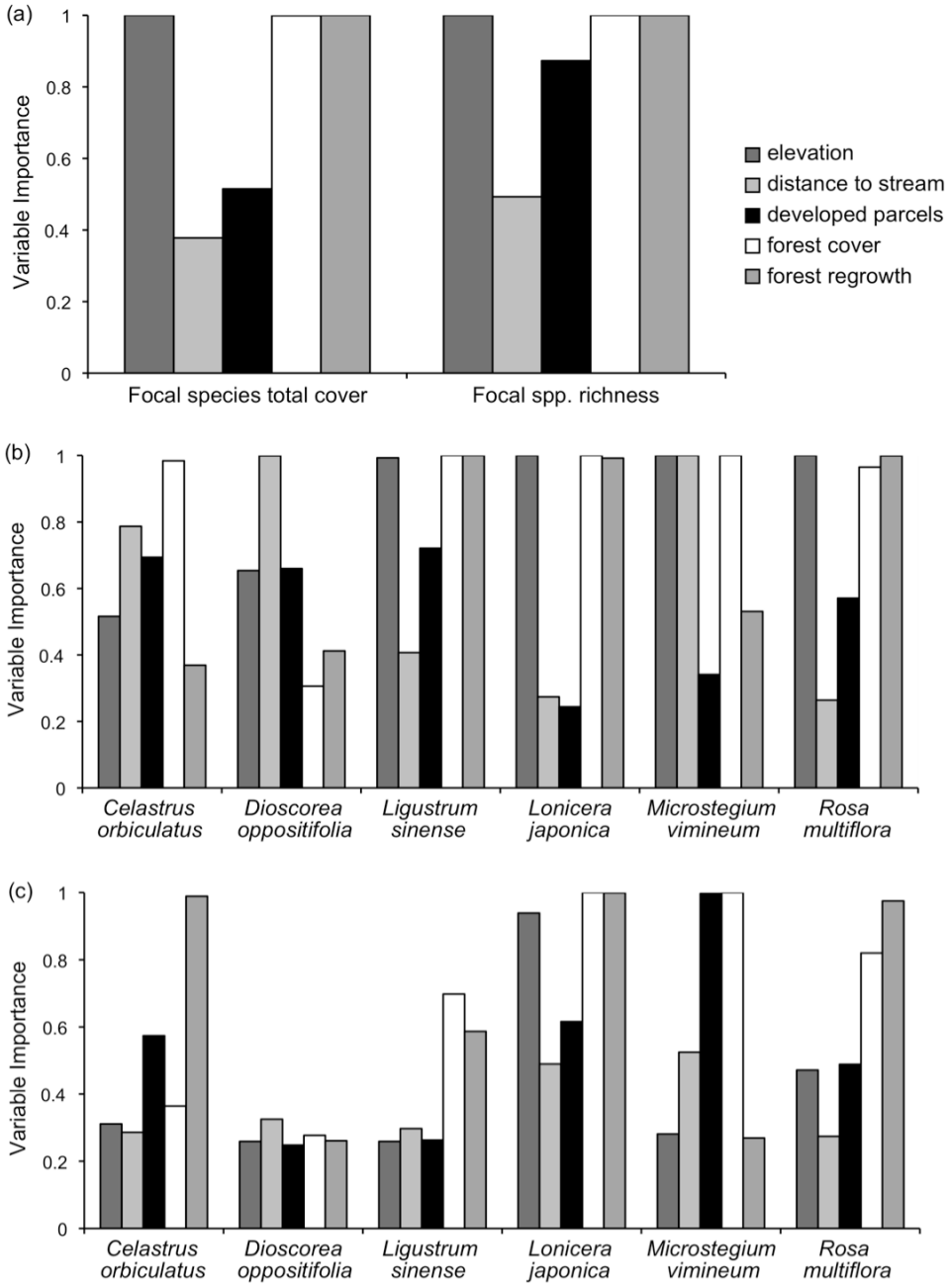

Figure 3. Plot-level variable importance for each model set: focal species total cover and focal species richness (*a*), presence/absence of the six most common focal species (*b*), and abundance (percent cover) of the six most common focal species (*c*). Relative variable importance is calculated by summing the model Akaike weights (w_i) of all candidate models within a model set in which that explanatory variable is included. Variable weights can range from 0 to 1.

Appendix 1. Watershed-level model selection results for focal species total cover, focal species richness, plot frequency for the six most common focal species, and presence/absence (logistic) models for the nine less common focal species. Comparable best models (with $\Delta_i < 2$) are shown. For all models, $N = 25$ watersheds. The number of parameters in a model (K) includes the intercept and error terms.

Model set	Explanatory variables included in the best candidate models (and direction of effect)*	*K*	Δ_i	w_i
Focal spp. total cover	elevmin(-) ashedist(-)	4	0.00	0.307
	elevmin(-), ashedist(-), reforest(+)	5	1.17	0.171
	elevmin(-), aspmean(-), ashedist(-)	5	1.52	0.143
Focal spp. richness	ashedist(-)	3	0.00	0.319
	ashedist(-), forest(-)	4	1.19	0.176
Plot frequency models				
Celastrus orbiculatus	ashedist(-), forest(-)	4	0.00	0.495
Dioscorea oppositifolia	intercept only	2	0.00	0.183
	reforest(+)	3	0.19	0.166
Ligustrum sinense	elevmin(-), ashedist(-), forest(-)	5	0.00	0.255
	elevmin(-), ashedist(-), forest(-), reforest(-)	6	0.42	0.206
	elevmin(-), aspmean(+), ashedist(-), forest(-), reforest(-)	7	1.28	0.134
	elevmin(-), aspmean(+), ashedist(-), forest(-)	6	1.64	0.112
Lonicera japonica	elevmin(-), ashedist(-), forest(-)	5	0.00	0.401
Microstegium vimineum	elevmin(-), aspmean(-)	4	0.00	0.214
	elevmin(-), aspmean(-), forest(+)	5	0.23	0.191
	aspmean(-)	3	1.19	0.118
Rosa multiflora	ashedist(-), forest(-), reforest(+)	5	0.00	0.233
	forest(-)	3	0.72	0.163
	forest(-), reforest(+)	4	1.07	0.136
	ashedist(-), forest(-)	4	1.46	0.112
Presence/Absence Models				
Ailanthus altissima	ashedist(-)	3	0.00	0.355
Albizia julibrissin	forest(-)	3	0.00	0.370
Alliaria petiolata	ashedist(+)	3	0.00	0.157
	ashedist(+), reforest(+)	4	0.71	0.110
	forest(+), reforest(+)	4	1.36	0.080
	reforest(+)	3	1.60	0.071
	elevmin(-), ashedist(+)	4	1.72	0.066
Berberis thunbergii	ashedist(-)	3	0.00	0.162
	ashedist(-), reforest(-)	4	0.52	0.125
	elevmin(-), ashedist(-), reforest(-)	5	0.74	0.112
Elaeagnus umbellata	elevmin(-), ashedist(-), reforest(-)	5	0.00	0.304
	ashedist(-), reforest(-)	4	0.73	0.211
	elevmin(-), aspmean(-), ashedist(-), reforest(-)	6	1.84	0.121
Miscanthus sinense	intercept only	2	0.00	0.181
	aspmean(-)	3	0.78	0.122
	forest(-)	3	1.36	0.091
	ashedist(-)	3	1.66	0.079
Paulownia tomentosa	ashedist(-)	3	0.00	0.299
	elevmin(+), ashedist(-)	4	1.51	0.140
Polygonum cuspidatum	intercept only	2	0.00	0.198
	reforest(+)	3	1.64	0.088
	elevmin(+)	3	1.78	0.082
	ashedist(-)	3	1.79	0.081
Pueraria montana	intercept only	2	0.00	0.255
	forest(-)	3	1.72	0.108

*elevmin= minimum elevation of watersheds, aspmean= mean aspect (northeasterliness); ashedist= distance to city center (Asheville, NC); forest= proportion of watershed in forest cover; reforest= proportion of watershed regrown to forest since 1940s

Appendix 2. Plot-level mixed effects model selection results. Response variables include focal species total cover, focal species richness, presence/absence, and percent cover for the six most common focal species. The species cover models only include plots in which the respective species were present ($52 < N < 502$). Candidate models with $\Delta_i < 2$ were considered comparable "best" candidate models and included here. The number of parameters in a model (K) includes the intercept, random effect (watershed), and error terms.

Model set	Explanatory variables included in the best candidate models (and direction of effect)*	*N*	*K*	Δ_i	w_i
Focal spp. total cover	elev(-), dparcels(+), forest(-), reforest(+)	613	7	0.00	0.323
	elev(-), forest(-), reforest(+)	613	6	0.15	0.299
	elev(-), streamdist(+), dparcels(+), forest(-), reforest(+)	613	8	1.04	0.192
	elev(-), streamdist(+), forest(-), reforest(+)	613	7	1.10	0.186
Focal spp. richness	elev(-), dparcels(+), forest(-), reforest(+)	613	7	0.00	0.441
	elev(-), streamdist(+), dparcels(+), forest(-), reforest(+)	613	8	0.04	0.432
Presence/absence models					
Celastrus orbiculatus	elev(+), streamdist(+), dparcels(+), forest(-)	613	7	0.00	0.183
	streamdist(+), dparcels(+), forest(-)	613	6	0.27	0.160
	streamdist(+), dparcels(+), forest(-), reforest(+)	613	7	1.13	0.104
	elev(-), streamdist(+), dparcels(+), forest(-), reforest(+)	613	8	1.26	0.097
	elev(-), streamdist(+), forest(-)	613	6	1.50	0.087
Dioscorea oppositifolia	elev(-), streamdist(-), dparcels(+)	613	6	0.00	0.177
	elev(-), streamdist(-)	613	5	0.72	0.123
	elev(-), streamdist(-), dparcels(+), reforest(+)	613	7	0.98	0.109
	streamdist(-), dparcels(+)	613	5	1.03	0.106
	streamdist(-), dparcels(+), reforest(+)	613	6	1.45	0.086
	elev(-), streamdist(-), reforest(+)	613	6	1.97	0.066
Ligustrum sinense	elev(-), dparcels(+), forest(-), reforest(+)	613	7	0.00	0.422
	elev(-), streamdist(-), dparcels(+), forest(-), reforest(+)	613	8	0.74	0.292
	elev(-), forest(-), reforest(+)	613	6	1.84	0.169
Lonicera japonica	elev(-), forest(-), reforest(+)	613	6	0.00	0.551
Microstegium vimineum	elev(-), streamdist(-), forest(+), reforest(+)	613	7	0.00	0.366
	elev(-), streamdist(-), forest(+)	613	6	0.45	0.293
	elev(-), streamdist(-), dparcels(+), forest(+)	613	7	1.46	0.177
	elev(-), streamdist(-), dparcels(+), forest(+), reforest(+)	613	8	1.60	0.164
Rosa multiflora	elev(-), dparcels(+), forest(-), reforest(+)	613	7	0.00	0.396
	elev(-), forest(-), reforest(+)	613	6	0.46	0.314
Species cover models					
Celastrus orbiculatus	dparcels(+), reforest(+)	265	5	0.00	0.204
	forest(-), reforest(+)	265	5	1.41	0.101
	reforest(+)	265	4	1.47	0.098
	dparcels(+), forest(-), reforest(+)	265	6	1.69	0.088
	elev(-), dparcels(+), reforest(+)	265	6	1.82	0.082
	streamdist(+), dparcels(+), reforest(+)	265	6	1.87	0.080
Dioscorea oppositifolia	intercept only	88	3	0.00	0.190
	streamdist(+)	88	4	1.25	0.101
	forest(-)	88	4	1.70	0.081
	reforest(-)	88	4	1.92	0.073
	elev(-)	88	4	1.94	0.072
Ligustrum sinense	forest(-), reforest(+)	127	5	0.00	0.194
	streamdist(+), forest(-), reforest(+)	127	6	1.67	0.084
	forest(-)	127	4	1.67	0.084
	intercept only	127	3	1.91	0.075

*elev= elevation of plot, streamdist= distance from plot center to nearest stream; dparcels= number of developed parcels within 126 m of plot; forest= proportion of 5-ha area around plot in forest cover; reforest= proportion of 5-ha area around plot regrown to forest since 1940s

Appendix 2 (cont.)

Model set	Explanatory variables included in the best candidate models (and direction of effect)*	*N*	*K*	Δ_i	w_i
Species cover models (cont.)					
Lonicera japonica	elev(-), streamdist(+), dparcels(-), forest(-), reforest(+)	338	8	0.00	0.298
	elev(-), dparcels(-), forest(-), reforest(+)	338	7	0.16	0.276
	elev(-), forest(-), reforest(+)	338	6	0.82	0.198
	elev(-), streamdist(+), forest(-), reforest(+)	338	7	1.17	0.166
Microstegium vimineum	streamdist(+), dparcels(+), forest(+)	502	6	0.00	0.269
	dparcels(+), forest(+)	502	5	0.11	0.254
	elev(-), streamdist(+), dparcels(+), forest(+)	502	7	1.75	0.113
	streamdist(+), dparcels(+), forest(+), reforest(+)	502	7	1.97	0.101
Rosa multiflora	forest(-), reforest(+)	341	5	0.00	0.193
	dparcels(+), forest(-), reforest(+)	341	6	0.42	0.156
	elev(-), forest(-), reforest(+)	341	6	0.79	0.130
	elev(-), dparcels(+), forest(-), reforest(+)	341	7	1.16	0.108
	streamdist(+), forest(-), reforest(+)	341	6	1.93	0.073

*elev= elevation of plot, streamdist= distance from plot center to nearest stream; dparcels= number of developed parcels within 126 m of plot; forest= proportion of 5-ha area around plot in forest cover; reforest= proportion of 5-ha area around plot regrown to forest since 1940s

Appendix 3. Focal non-native invasive species cover by plots. Watershed (WS) and plot identification is given. GPS coordinates were recorded at the start of each plot, and transects ran from this point toward the lower part of the watershed, parallel to the road. Percent (%) cover values are given. Percent cover was calculated by taking the midpoint of the cover class recorded for a given species in each quadrat and averaging values across all quadrats in a plot (*n* = 40 quadrats per plot). Cover classes were 1 = trace, 2 =0.1-1%, 3 =1-5%, 4 =5-10%, 5 =10-25%, 6 =25-50%, 7 =50-75%, 8 >75%. Therefore, the corresponding percent cover estimates based on cover class midpoints were 0.05%, 0.55%, 3%, 7.5%, 17.5%, 37.5%, 62.5%, 87.5%, respectively. Species abbreviations are as follows: AIAL= *Ailanthus altissima*, ALJU= *Albizia julibrissin*, ALPE= *Alliaria petiolata*, BETH= *Berberis thunbergii*, CEOR= *Celastrus orbiculatus*, DIOP= *Dioscorea oppositifolia*, ELUM= *Elaeagnus umbellata*, LISI= *Ligustrum sinense*, LOJA= *Lonicera japonica*, MISI= *Miscanthus sinensis*, MIVI= *Microstegium vimineum*, PATO= *Paulownia tomentosa*, POCU= *Polygonum cuspidatum*, PUMO= *Pueraria montana*, ROMO= *Rosa multiflora*. Note that the last seven focal species are shown in the latter part of the table.

WS	Plot	Latitude	Longitude	AIAL	ALJU	ALPE	BETH	CEOR	DIOP	ELUM	LISI
1	1	35.854027	-82.556350	0	0	0	0	0	0	0	0
1	2	35.855572	-82.555486	0	0	0	0	0	0	0	0
1	3	35.857100	-82.554955	0	0	0	0	0	0	0	0
1	4	35.858635	-82.554606	0	0	0	0	0	0	0	0
1	5	35.860587	-82.553963	0	0	0	0	0.001	0	0	0
1	6	35.866461	-82.548797	0	0	0	0	1.076	0	0	0
1	7	35.864949	-82.550106	0	0	0	0	0.090	0	0	0
1	8	35.862315	-82.552541	0	0	0	0	0	0	0	0
1	9	35.858994	-82.551897	0	0	0	0	0.439	1.125	0	0
1	10	35.849097	-82.548153	0	0	0	0	0	0	0	0
1	11	35.847284	-82.548620	0	0	0	0	0	0	0	0
1	12	35.842171	-82.544569	0	0	0	0	0.001	0	0	0
1	13	35.839387	-82.549564	0	0	0	0	0.225	0	0	0
1	14	35.835273	-82.548904	0	0	0	0	0.001	0	0	0
1	15	35.830461	-82.548738	0	0	0	0	0	0	0	1.563
1	16	35.835342	-82.557991	0	0	0	0	2.150	0	0	0
1	17	35.840900	-82.559338	0	0	0	0	0	0	0	6.013
1	18	35.842611	-82.557589	0	0	0	0	0	0	0	0
1	19	35.846061	-82.557610	0	0	0	0	0.500	0	0	0
1	20	35.855813	-82.562412	0	0	0	0	0	2.250	0	0
1	21	35.849928	-82.557712	0	0	0	0	0	0	0	0
1	22	35.844955	-82.554145	0	0	0	0	0	0	0	0
1	23	35.844237	-82.550905	0	0	0	0	0.188	0	0	0
1	24	35.853029	-82.550030	0	0	0	0	1.125	0.850	0	0.775
1	25	35.833132	-82.557396	0	0	0	0	0	0	0	0
2	1	35.871295	-82.562530	0	0	0	0	0	0	0	0
2	2	35.873263	-82.561296	0	0	0	0	0	0	0	0
2	3	35.873864	-82.561741	0	0	0	0	0	0	0	0
2	4	35.874701	-82.564069	0	0	0	0	0	0	0	0.075
2	5	35.875211	-82.566011	0	0	0	0	0	0	0	0
2	6	35.880103	-82.571536	0	0	0	0	0	0.625	0	0
2	7	35.876327	-82.572346	0	0	0	0	0	2.151	0	0
2	8	35.874910	-82.572180	0	0	0	0	0	0	0	0
2	9	35.873730	-82.575935	0	0	0	0	0.075	0	0	0
2	10	35.871000	-82.579127	0	0	0	0	0	0	0	0
2	11	35.868462	-82.581713	0	0	0.338	0	1.750	0	0	0
2	12	35.867636	-82.580302	0	0	0	0	0	0	0	0

WS	Plot	Latitude	Longitude	AIAL	ALJU	ALPE	BETH	CEOR	DIOP	ELUM	LISI
2	13	35.866145	-82.577555	0	0	0	0	0	0	0	0
2	14	35.858104	-82.578832	0	0	0	0	0	0	0	0
2	15	35.858560	-82.579932	0	0	0	0	0	0	0	0
2	16	35.860512	-82.582303	0	0	0	0	0	0	0	0
2	17	35.861295	-82.583671	0	0	0	0	0	0	0	0
2	18	35.859793	-82.586927	0	0	0	0	0	0.150	0	1.650
2	19	35.858951	-82.591648	0	0	0	0	0	0.263	0	2.375
2	20	35.856081	-82.593187	0	0	0	0	0	0	0	0
2	21	35.854193	-82.595778	0	0	0	0	0	0	0	0
2	22	35.850985	-82.590070	0	0	0	0	0	0	0	0
2	23	35.852686	-82.593944	0	0	0	0	0	0	0	0
2	24	35.852895	-82.598283	0	0	0	0	0	0	0	0
2	25	35.851784	-82.601454	0	0	0	0	0	0	0	0
3	1	35.957040	-82.622740	0	0	0	0	0	0	0	0
3	2	35.956272	-82.624424	0	0	0	0	0	0	0	0
3	3	35.954416	-82.629960	0	0	0	0	0	0	0	0
3	4	35.954288	-82.631135	0	0	0	0	0	0	0	0
3	5	35.952936	-82.634391	0	0	0	0	0	0	0	0
3	6	35.952024	-82.637808	0	0	0	0	0	0	0	0
3	7	35.939240	-82.650576	0	0	0	0	0	0	0	0
3	8	35.943897	-82.646670	0	0	0.938	0	0	0	0	0
3	9	35.945646	-82.646279	0	0	0	0	0	0	0	0
3	10	35.949331	-82.644718	0	0	0	0	0	0	0	0
3	11	35.951981	-82.647196	0	0	0.263	0	0	0	0	0
3	12	35.952088	-82.637932	0	0	0	0	0	0.425	0	0
3	13	35.951257	-82.640142	0	0	0	0	0	0	0	0
3	14	35.952512	-82.644299	0	0	0	0	0	0	0	0
3	15	35.978208	-82.624666	0	0	0	0	0	0	0	0
3	16	35.976405	-82.626366	0	0	0	0	0	0	0	0
3	17	35.974490	-82.628882	0	0	0	0	0	0	0	0
3	18	35.970622	-82.632068	0	0	0	0	0	0	0	0
3	19	35.968235	-82.633039	0	0	0	0	0	0	0	0
3	20	35.966454	-82.634354	0	0	0	0	0	0	0	0
3	21	35.959293	-82.636145	0	0	0	0	0	0	0	0
3	22	35.956707	-82.638769	0	0	0	0	0	0.689	0	0
3	23	35.956825	-82.641558	0	0	0	0	0	0	0	0
3	24	35.954513	-82.642722	0	0	0	0	0	0	0	0
3	25	35.953520	-82.646729	0	0	0	0	0	0	0	0
4	1	35.315707	-82.534307	0	0	0	0	3.100	0	0	0
4	2	35.313385	-82.538395	0	0	0	0	0	0	0	0.263
4	3	35.311094	-82.539666	0	0	0	0	0	0	0	0.075
4	4	35.309275	-82.540138	0	0	0	0	0.188	0	0	0
4	5	35.295618	-82.530413	0	0	0	0	0.075	0	0	0
4	6	35.296154	-82.531593	0	0	0	0	0.013	0	0	0
4	7	35.301910	-82.531593	0	0	0	0	3.140	0	0	0
4	8	35.300322	-82.524442	0	0	0	0	6.775	0.075	0	0
4	9	35.300118	-82.521696	0	0	0	0	0	0	0	0
4	10	35.301459	-82.520258	0	0	0	0	0	0	0	0
4	11	35.303364	-82.519067	0	0	0	0	5.163	0	0	0
4	12	35.302978	-82.522447	0	0	0	0	0.738	0	0	0
4	13	35.305574	-82.529356	0	0	0	0	0.425	0	0	0.075
4	14	35.305987	-82.535627	0	0	0	0	0	2.613	0	0.075
4	15	35.306051	-82.538363	0	0	0	0	0	0.188	0	0
4	16	35.307017	-82.541512	0	0	0	0	0	0	0	0
4	17	35.306840	-82.546603	0	0	0	0	0	0	0	0.188
4	18	35.305172	-82.549194	0.813	0	0	0	0	0	0	0
4	19	35.314087	-82.553946	0	0	0	0	0.613	0	0	0.950

WS	Plot	Latitude	Longitude	AIAL	ALJU	ALPE	BETH	CEOR	DIOP	ELUM	LISI
4	20	35.310826	-82.555062	0	0	0	0	0.438	0	0	0.250
4	21	35.308337	-82.552949	0	0	0	0	0.200	0	0	0.088
4	22	35.307108	-82.554875	0	0	0	0	1.663	0	0	0.788
4	23	35.313524	-82.553029	0	0	0	0	0	0	0	0
4	24	35.308181	-82.551704	0	0	0	0	0	0	0	0
4	25	35.300403	-82.552498	0	0	0	0	0	0	0	0
5	1	35.321898	-82.774923	0	0	0	0	0	0	0	0
5	2	35.322509	-82.773292	0	0	0	0	0	0	0	0
5	3	35.321195	-82.770615	0	0	0	0	0.013	0	0	0
5	4	35.319441	-82.768314	0	0	0	0	0	0	0	0
5	5	35.318245	-82.766195	0	0	0	0	0	0	0	0
5	6	35.320745	-82.761571	0	0	0	0	0	0	0	0
5	7	35.318990	-82.757022	0	0	0	0	0	0	0	0
5	8	35.317301	-82.758438	0	0	0	0	0	0	0	0
5	9	35.316904	-82.755911	0	0	0	0	0	0	0	0
5	10	35.315702	-82.751727	0	0	0	0	0	0	0	0
5	11	35.315037	-82.749372	0	0	0	0	0	0	0	0
5	12	35.311673	-82.748230	0	0	0	0	0	0	0	0
5	13	35.310128	-82.747130	0	0	0	0	6.313	0	5.125	3.125
5	14	35.308052	-82.744957	0	0	0	0	0	0	43.900	0
5	15	35.305992	-82.742602	0	0	0	0	0	0	3.825	0
5	16	35.305236	-82.740301	0	0	0	0	0	0	33.513	0
5	17	35.303804	-82.738740	0	0	0	0	0	0	0.600	0
5	18	35.300902	-82.737967	0	0	0	0	0	0.075	39.088	0
5	19	35.297356	-82.738804	0	0	0	0	0	0	0.338	0
5	20	35.295022	-82.740006	0	0	0	0	0	0	0	0
5	21	35.291643	-82.738627	0	0	0	0	0	0	0	0
5	22	35.289293	-82.736921	0	0	0	0	0.013	0	0	0.075
6	1	35.669051	-82.475315	0	0	0	0	1.375	0	0	0
6	2	35.670081	-82.473309	10.60	0	0	0	0	0	0	0
6	3	35.669786	-82.471629	0	0	0	0	0	0	0	0
6	4	35.674587	-82.467027	0	0	0	0	0	0	0	0
6	5	35.678514	-82.470889	0	0	0	0	40.925	0	0	0
6	6	35.674190	-82.472895	0	0	0	0	10.376	0	0	14.81
6	7	35.676534	-82.473040	0	0	0	0	3.100	0	0	0
6	8	35.679104	-82.472836	0	0	0	0	8.888	0	0	0
6	9	35.680295	-82.476624	0	0	0	0	0.075	0	0	0
6	10	35.680686	-82.479236	19.57	0	0	0	1.088	0	0	2.313
6	11	35.671240	-82.486038	0	0	0	0	0.100	0.438	0	0
6	12	35.674254	-82.484021	19.06	0	0	0	0.438	9.289	0	0
6	13	35.680311	-82.485550	0	0	0	0	2.775	0	0	0
6	14	35.681958	-82.484998	0	0	0	0	21.538	0	0	0
6	15	35.679200	-82.482669	0	0	0	0	15.525	0	0	0
6	16	35.683787	-82.481167	0	0	0	0	0	0	0	0.438
6	17	35.687065	-82.482739	0	0	0	0	2.700	0	0	0.938
6	18	35.686356	-82.472037	1.125	0	0	0	0.338	0	0	0
6	19	35.691378	-82.469950	1.213	0	0	0	0.225	0	0	0.350
6	20	35.690112	-82.472885	0	0	0	0	0.075	0	0	0
6	21	35.689698	-82.478630	0	0	0	0	1.025	0	0	0
6	22	35.689875	-82.498285	0	0	0	0	18.488	0	0	0.013
6	23	35.690315	-82.497218	0	0	0	0	15.525	0	0	0
6	24	35.689285	-82.485378	0	0	0	0	14.250	0	0	4.500
6	25	35.692300	-82.492953	0	0	0	0	10.875	0	0	3.638
7	1	35.891567	-82.714702	0	0	0	0	0.088	0	0	0
7	2	35.893997	-82.713967	0	0	0.438	0	0	0	0	0
7	3	35.893670	-82.707047	0	0	0.665	0	0	0	0	0
7	4	35.895429	-82.708946	0	0	2.275	0	0	0	0	0

WS	Plot	Latitude	Longitude	AIAL	ALJU	ALPE	BETH	CEOR	DIOP	ELUM	LISI
7	5	35.896760	-82.710437	0	0	0.938	0	0	0	0	0
7	6	35.899372	-82.706736	0	0	0	0	0	0	0	0
7	7	35.902988	-82.705969	0	0	7.151	0	0	0	0	0
7	8	35.894759	-82.693802	0	0	0.263	0	0	0	0	0
7	9	35.896035	-82.697793	0	0	0	0	0	0	0	0
7	10	35.888187	-82.695084	0	0	0	0	0	0	0	0
7	11	35.890258	-82.697665	0	0	0	0	0	0	0	0
7	12	35.893879	-82.698941	0	0	0	0	0	0	0	0
7	13	35.895869	-82.700062	0	0	0	0	0	0	0	0
7	14	35.900815	-82.700964	0	0	0	0	0	0	0	0
7	15	35.903905	-82.697525	0	0	0	0	0	0	0	0.938
7	16	35.902253	-82.700781	0	0	0	0	0	7.050	0	0.438
7	17	35.903959	-82.705781	0	0	0	0	0	0	0	0
7	18	35.906228	-82.706671	0	0	0	0	0	0	0	0
7	19	35.909522	-82.708876	0	0	0	0	0	0	0	0
7	20	35.911490	-82.711387	0	0	0	0	0	0	0	0
7	21	35.913159	-82.714139	0	0	0.188	0	0	0	0	0
7	22	35.915465	-82.716934	0	0	0.150	0	0	0	0	0
7	23	35.914108	-82.719530	0	0	0	0	0	0	0	0
8	1	35.866338	-82.454115	0	0	0	0	0	0	0	0
8	2	35.862679	-82.450563	0	0	0	0	0	0	0	0
8	3	35.875340	-82.432678	0	0	0	0	0	0	0	0
8	4	35.873076	-82.435591	0	0	0	0	0	0	0	0
8	5	35.868865	-82.435709	0	0	0	0	0	0	0	18.25
8	6	35.869321	-82.437142	0	0	0	0	0	0.188	0	1.638
8	7	35.870635	-82.438654	0	0	0	0	0	0	0	0
8	8	35.871252	-82.441648	0	0	0	0	0	0	0	0.075
8	9	35.870887	-82.445741	0	0	0	0	0	0	0	0
8	10	35.861805	-82.430527	0	0	0	0	0	0	0	0
8	11	35.864106	-82.431745	0	0	0	0	0	0	0	0
8	12	35.863699	-82.434234	0	0	0	0	0	0	0	0
8	13	35.865464	-82.435725	0	0	0	0	0	0	0	0
8	14	35.863624	-82.439395	0	0	0	0	0	0	0	0
8	15	35.864149	-82.441599	0	0	0	0	0	0	0	0
8	16	35.862277	-82.447221	0	0	0	0	0	0	0	0
8	17	35.858458	-82.450585	0	0	0	0	0	0	0	0
8	18	35.855545	-82.452575	0	0	0	0	0	0	0	0.075
8	19	35.849955	-82.455783	0	0	0	0	0	0	0	0.188
8	20	35.842906	-82.456668	0	0	0	0	0	0	0	0
8	21	35.849091	-82.428719	0	0	0	0	0	0	0	0
8	22	35.847021	-82.433687	0	0	0	0	0	0	0	0
8	23	35.844955	-82.440580	0	0	0	0	0	0	0	0
8	24	35.842981	-82.448144	0	0	0	0	0.013	0	0	0
8	25	35.841039	-82.455772	0	0	0	0	0	0	0	0
9	1	35.822849	-82.427824	0	0	0	0	0	0.263	0	0
9	2	35.825504	-82.430479	0	0	0	0	0	0	0	0
9	3	35.817710	-82.420083	0	0	0	0	0	0	0	0
9	4	35.818568	-82.422078	0	0	0	0	0	0	0	0
9	5	35.820225	-82.424637	0	0	0	0	0	0	0	0
9	6	35.821486	-82.426316	0	0	0	0	0	0	0	0
9	7	35.825703	-82.434170	0	0	0.075	0	0	0	0	0
9	8	35.822951	-82.434535	0	0	0	0	0	0	0	0
9	9	35.824361	-82.433816	0	0	0	0	2.263	0	0	0
9	10	35.823058	-82.438311	0	0	0	0	0	0.950	0	0
9	11	35.821320	-82.442876	0	0	0	0	0	0	0	0
9	12	35.822559	-82.446529	0	0	0	0	0	0.850	0	0
9	13	35.823122	-82.449474	0	0	0	0	0	0	0	0

WS	Plot	Latitude	Longitude	AIAL	ALJU	ALPE	BETH	CEOR	DIOP	ELUM	LISI
9	14	35.822210	-82.454013	0	0	0	0	0	0	0	0.075
9	15	35.821626	-82.455788	0	0	0	0	0.189	0.013	0	0
9	16	35.818552	-82.457328	0	0	0	0	0.013	0	0	0
9	17	35.820757	-82.457451	0	0	0	0	0	0.088	0	0
9	18	35.822414	-82.460702	0	0	0	0	0	0.075	0	0
9	19	35.824297	-82.465557	0	0	0	0	0	0	0	0
9	20	35.825107	-82.468094	0	0	0	0	0	0	0	0
9	21	35.826008	-82.471259	0	0	0	0	0	0	0	0
10	1	35.584980	-82.301776	0	0	0	0	0	0	0	0
10	2	35.590773	-82.303305	0	0	0	0	0.188	0	0	0
10	3	35.587420	-82.303830	0	0	0	0	0	0	0	0
10	4	35.584947	-82.302924	0	0	0	0	0	0	0	0
10	5	35.586450	-82.304700	0	0	0	0	0	0	0	0
10	6	35.587984	-82.307156	0	0	0	0	0	0	0	0
10	7	35.589207	-82.307387	0	0	0	0	0	0	0	0
10	8	35.590044	-82.309463	0	0	0	0	0	0	0	0
10	9	35.592098	-82.310332	0	0	0	0	0	0	0	0
10	10	35.593075	-82.309978	0	0	0	0	0	0	0	0
10	11	35.594657	-82.310472	0	0	0	0	0	0	0	0
10	12	35.595714	-82.313454	0	0	0	0	0	0	0	0
10	13	35.597484	-82.301894	0	0	0	0	0	4.213	0	0
10	14	35.597683	-82.304753	0	0	0	0	0.013	0	0	0
10	15	35.596878	-82.304126	0	0	0	0	0.075	0.075	0	0
10	16	35.594759	-82.305268	0	8.625	0	0	0.013	3.113	3.825	0
10	17	35.595242	-82.324403	0	0	0	0	25.875	0	0	0
10	18	35.593750	-82.322708	0	0	0	0	0	0	0	0
10	19	35.591181	-82.321630	0	0	0	0	0	0	0	0
10	20	35.606931	-82.303219	0	0	0	0	0	0	0	0
10	21	35.605080	-82.309114	2.138	0	0	0	0.938	0	0	0
10	22	35.603519	-82.311373	0	0	0	0	0.163	0	0	0.513
10	23	35.598798	-82.311453	0	0	0	0	0.163	0.725	0	0
10	24	35.601159	-82.315632	0	0	0	0	0	0	0	0
10	25	35.599458	-82.319999	0	0	0	0	0.275	2.938	0	0.338
11	1	35.542595	-82.332557	0	0	0	0	0	0	0	0
11	2	35.544376	-82.335271	0	0	0	0	0	0	0	0
11	3	35.542145	-82.339043	0	0	0	0	0	0	0	0
11	4	35.544296	-82.338576	0	0	0	0	0	0	0	0
11	5	35.547890	-82.330068	0	0	0	0	0	0	0	0
11	6	35.550470	-82.330293	0	0	0	0	0.013	0	0	0
11	7	35.552911	-82.328094	0	0	0	0	0	0	0	0
11	8	35.550132	-82.332004	0	0	0	0	0	0	0	0
11	9	35.544607	-82.335169	0	0	0	0	0	0	0	0
11	10	35.547547	-82.334418	0	0	0	0	5.851	0	0	0
11	11	35.548990	-82.341129	0	0	0	0	0	0	0	0
11	12	35.546576	-82.341494	0	0	0	0	0	0	0	0
11	13	35.545417	-82.342959	0	0	0	0	10.975	11.413	0	0
11	14	35.556618	-82.346263	0	0	0	0	0.075	0	0	0
11	15	35.553260	-82.348242	0	0	0	0	0	0	0	0
11	16	35.550556	-82.348350	0	0	0	0	0	0	0	0
11	17	35.546190	-82.347540	0	0	0	0	0.075	0	0	0
11	18	35.544629	-82.348301	0	0	0	0	6.488	0	0	0
11	19	35.537172	-82.355350	0	0	0	0	0	0	0	0
11	20	35.541490	-82.356740	0	0	0	0	0	0	0	0
11	21	35.551549	-82.353854	3.513	0	0	0	1.375	0	0	0
11	22	35.551023	-82.354294	0	0	0	0	0.013	0	0	0
11	23	35.546608	-82.351536	0	0	0	0	34.900	0	0	0
11	24	35.543003	-82.359057	0	0	0	0	0.450	0	0	0

WS	Plot	Latitude	Longitude	AIAL	ALJU	ALPE	BETH	CEOR	DIOP	ELUM	LISI
11	25	35.542080	-82.371621	0	0	0	0	9.838	0	0	0.375
11	26	35.541909	-82.379034	0	0	0	0	14.000	0	0	0
12	1	35.419890	-82.416768	11.87	0	0	0	0	0	0	0
12	2	35.417562	-82.413281	6.813	0	0	0	18.625	0	0	0
12	3	35.415099	-82.410792	0	0	0	0	0.450	0	0	0
12	4	35.432222	-82.397048	2.413	0	0	0	0	0	0	0
12	5	35.430366	-82.397322	0.775	0	0	0	0	0	0	2.188
12	6	35.427695	-82.399693	0.150	0	0	0	0	0	0	0
12	7	35.428344	-82.401576	0	0	0	0	0.001	0	0	0
12	8	35.425817	-82.402144	0	0	0	0	0	0	0	0
12	9	35.421982	-82.405127	0	0	0	0	0	0	0	0
12	10	35.417202	-82.402681	0	0	0	0	0	0	0	0
12	11	35.418060	-82.405379	0	0	0	0	0	0	0	0
12	12	35.416220	-82.406758	0	0	0	0	0	0	0	1.063
12	13	35.414895	-82.408319	0	0	0	0	0	3.963	0	0
12	14	35.410851	-82.409965	0	0	0	0	0	0	0	0
12	15	35.406591	-82.425581	0	0	0	0	0	0	0	0
12	16	35.409381	-82.427942	0.988	0	0	0	0	0	0	0
12	17	35.409649	-82.423870	0	0	0	0	0	0.150	0	0
12	18	35.406028	-82.417283	11.88	0	0	0	0	0	0	0
12	19	35.406237	-82.412669	0.075	0	0	0	0.738	0	0	0
12	20	35.405910	-82.407192	4.375	0	0	0	0.438	2.100	0	0
12	21	35.402541	-82.405545	6.438	0	0	0	0	0	0	0
12	22	35.400170	-82.402707	23.12	0	0	0	8.150	1.575	0	0.075
12	23	35.396968	-82.403630	0	0	0	0	0	4.600	0	1.975
12	24	35.393770	-82.399875	0	0	0	0	0.025	0	0	0
12	25	35.392987	-82.397096	0	0	0	0	0	0	0	0
13	1	35.397552	-82.440258	0	0	0	0	8.088	0	0.188	0
13	2	35.397295	-82.441878	0	0	0	0	5.500	0	0.075	0
13	3	35.392858	-82.442592	0	0	0	0	1.125	0	0	0
13	4	35.390310	-82.444276	0	0	0	0	0.075	4.250	0	0
13	5	35.384806	-82.442619	7.813	0	0	0	1.828	0	0	0
13	6	35.388309	-82.441535	0	0	0	0	0	0	0	0
13	7	35.389511	-82.444239	0	0	0	0	0	0	0	0
13	8	35.385783	-82.447248	0	0	0	0	0	5.275	0.438	0
13	9	35.384350	-82.449662	0	0	0	0	2.388	0	0	0
13	10	35.381958	-82.450247	0	0	0	0	3.700	0.188	0	0
13	11	35.380021	-82.447844	0	0	0	0	0.663	0.313	0	0
13	12	35.380960	-82.454597	0	0	0	0	14.800	0	0	0
13	13	35.378358	-82.450574	0	0	0	0	0	0	0	0
13	14	35.378203	-82.452597	0	0	0	0	0.438	0	0	0
13	15	35.378267	-82.453981	0	0	0	0	0	0	0	0.513
13	16	35.380483	-82.460117	0	0	0	0	1.013	0	0	0
13	17	35.387510	-82.454791	0	0	0	0	0	0	0	0
13	18	35.385525	-82.454029	0	0	0	0	0	0.200	0	4.375
13	19	35.385981	-82.463427	0	0	0	0	0.075	0.075	0	0
13	20	35.387102	-82.464570	0	0	0	0	5.313	20.938	0	0.075
13	21	35.383004	-82.465514	0	0	0	0	0	0	0	0
13	22	35.379791	-82.462129	0	0	0	0	5.188	0	0.625	0
13	23	35.383642	-82.469822	0	0	0	0	6.314	0	0	0
13	24	35.384426	-82.469221	0	0	0	0	1.114	0	0.375	0
13	25	35.380134	-82.470975	0	0	0	0	9.500	0.403	0	0.188
14	1	35.261473	-82.602355	0	0	0	0	0	0	0	0
14	2	35.260588	-82.608138	0	0	0	0	0	0	0	0.001
14	3	35.259869	-82.615015	0	0	0	0	0	0	0	0
14	4	35.260883	-82.615616	0	0	0	0	0	0	0	0.075
14	5	35.262911	-82.614355	0	0	0	0	0	0	0	0

WS	Plot	Latitude	Longitude	AIAL	ALJU	ALPE	BETH	CEOR	DIOP	ELUM	LISI
14	6	35.265325	-82.613749	0	0	0	0	0	0	0	0
14	7	35.265046	-82.611410	0	0	0	0	0	0	0	0
14	8	35.267884	-82.608728	0	0	0	0	0	0	0	0
14	9	35.270346	-82.609275	0	0	0	0	0	0	0	0
14	10	35.271274	-82.609270	0	0	0	0	0	1.025	0	0
14	11	35.272073	-82.606802	0	0	0	0	0	3.628	0	0
14	12	35.272803	-82.604780	0	0	0	0	0	0.089	0	0
14	13	35.276982	-82.609554	0	0	0	0	0	0	0	0
14	14	35.278366	-82.607521	0	0	0	0	0	0	0	8.750
14	15	35.274450	-82.606759	0	0	0	0	0	0	0	0
14	16	35.275061	-82.601298	0	0	0	0	0	0	0	0.938
14	17	35.278398	-82.604410	0	0	0	0	0	0	0	0
14	18	35.276451	-82.601829	0	0	0	0	0	0	0	0
14	19	35.271322	-82.601330	0	0	0	0	0	0	0	0
14	20	35.269659	-82.596095	0	0	0	0	0	0	0	0
14	21	35.271580	-82.598149	0	0	0	0	0	0	0	0
14	22	35.273843	-82.597082	0	0	0	0	0	0	0	0
14	23	35.274562	-82.600402	0	0	0	0	0	0	0	0
14	24	35.278784	-82.600322	0	0	0	0	0	0	0	0.075
14	25	35.283178	-82.599823	0	0	0	0	0	0	0	0
14	26	35.289550	-82.599555	0	0	0	0	0	0	0	0
15	1	35.369974	-82.633774	0	0	0	0	0	11.650	0	0
15	2	35.371562	-82.629499	0	0	0	0	0	0.375	0	0
15	3	35.375934	-82.629697	0	0	0	0	0	0	0	0
15	4	35.375258	-82.626688	0	0	0	1.025	0.025	0	0	0
15	5	35.374646	-82.624451	0	0	0	0.388	0	0	0	0
15	6	35.375065	-82.623378	0	0	0	0	0	0	0	0
15	7	35.374673	-82.619521	0	0	0	0	2.388	0	0	0.075
15	8	35.372688	-82.623029	0	0	0	0	1.375	0	0	0
15	9	35.372849	-82.614226	0	0	0	0	5.200	0	0	10.35
15	10	35.375773	-82.614527	0	0	0	0	1.675	0	0	1.575
15	11	35.382156	-82.615219	0	0	0	0	0	0	0	0.025
15	12	35.382162	-82.615219	0	0	0	0	3.588	0	0	3.400
15	13	35.389516	-82.619639	0	0	0	0.450	0.363	0	0	0.788
15	14	35.383497	-82.632358	0	0	0	0	0	0	0	0
15	15	35.382468	-82.628190	0	0	0	0	0	0	0	0
15	16	35.382451	-82.624440	0	0	0	0	0	0	0	0
15	17	35.384071	-82.628034	0	0	0	0	0	0	0	0
15	18	35.386346	-82.629086	0	0	0	0	0	0	0	0
15	19	35.385252	-82.624263	0	0	0	0	0	0	0	0
15	20	35.385423	-82.617043	0	0	0	0	0.013	0	0	0
15	21	35.384656	-82.615289	0	0	0	0	0.413	0	0	1.350
15	22	35.386056	-82.610976	0	0	0	0.075	0.700	0	0	0
15	23	35.386877	-82.607022	0	0	0	0	2.376	0	0	1.475
15	24	35.387682	-82.599844	0	0	0	0	0.075	0	0	0
15	25	35.389436	-82.602205	0	0	0	0	5.150	0	0	0.450
15	26	35.389726	-82.597404	0	0	0	0.075	5.013	0	0	0
16	1	35.753481	-82.707245	0	0	0	0	1.075	0	0	0.463
16	2	35.757070	-82.708114	0	0.188	0	0	0	0	0	0
16	3	35.761163	-82.709144	0	0	0	0	0.451	0	0	1.788
16	4	35.763749	-82.711489	0	0	0	0	0.001	0	0	0
16	5	35.759752	-82.711811	0.263	0	0	0	0.663	0	0	0
16	6	35.766651	-82.713339	0	0	0	0	0.625	0.150	0	0.438
16	7	35.769639	-82.714192	0	0	0.075	0	2.575	0	0	0
16	8	35.772847	-82.716987	0	0	0	0	0	0	0	0.075
16	9	35.778034	-82.724771	0	2.625	0	0	0.075	0	0	0
16	10	35.776516	-82.721939	0	0	0	0	0	0	0	0

WS	Plot	Latitude	Longitude	AIAL	ALJU	ALPE	BETH	CEOR	DIOP	ELUM	LISI
16	11	35.774150	-82.720555	0	0	0	0	0	0	0	0
16	12	35.775803	-82.718559	0	0	0	0	0	0	0	0
16	13	35.778206	-82.716424	0	0	0	0	0	2.325	0	0.188
16	14	35.781966	-82.715002	25.00	0	0.013	0	0	0	0	0
16	15	35.784600	-82.716617	0	0	0	0	0	0	0	0
16	16	35.784144	-82.708206	6.563	0	0	0	0	0	0	0
16	17	35.782803	-82.705427	0	0	0	0	0.076	0	0	0.188
16	18	35.781757	-82.704504	0	0	0	0	0.925	0	0	0.600
16	19	35.782793	-82.709461	0	0	0	0	0.075	0	0	0
16	20	35.785008	-82.711183	0	1.875	0	0	0	0	0	0
16	21	35.787385	-82.714734	0	0	0	0	0	0	0	0
16	22	35.790072	-82.715871	0	0	0	0	0	0	0	0
16	23	35.792373	-82.716306	0	0	0	0	0	3.025	0	0
17	1	35.657405	-82.543582	0	0	0	0	2.838	0	0	0
17	2	35.658520	-82.542949	0	0	0	0	0.201	0	0	0
17	3	35.661412	-82.539339	0	0	0	0	8.025	0	0	0
17	4	35.664341	-82.537226	0	0	0	0	5.150	0	0	1.413
17	5	35.664067	-82.532376	0	0	0	0	1.138	0	0	0
17	6	35.664673	-82.533653	0	0	0	0	2.801	0	0	0
17	7	35.666304	-82.533996	0	0	0	0	2.756	0	0	0.013
17	8	35.667956	-82.529753	0	0	0	0	4.253	0	0	0.075
17	9	35.667543	-82.532414	0	0	0	0	3.588	0	0	0.263
17	10	35.668225	-82.535825	0	0	0	0.075	0.801	0	0	0
17	11	35.669104	-82.540750	0	0	0	0	15.800	0	0	7.863
17	12	35.673037	-82.540884	0	0	0	0	0.188	0	0	3.638
17	13	35.674565	-82.543325	0	0	0	0	34.088	0	0	15.32
17	14	35.676545	-82.545245	0	0	0	0	23.688	0	0	9.800
17	15	35.673975	-82.545642	0	0	0	0	5.738	0	0	1.726
17	16	35.673251	-82.549628	0	0	0	0	4.563	1.213	0	0
17	17	35.671862	-82.553340	0	0	0	0	7.150	0	0	0
17	18	35.674265	-82.553179	0	0	0	0	2.413	0	0	0
17	19	35.675241	-82.563270	0	0	0	0	1.713	0	0	0
17	20	35.675043	-82.558077	0	0	0	0	8.488	0	0	8.001
17	21	35.676357	-82.555776	0	0	0	0	10.788	0	0	16.26
17	22	35.679957	-82.557868	0	0	0	0	9.175	0	0	29.10
17	23	35.682414	-82.559359	0	0	0	0	19.275	0	0	6.125
18	1	35.526942	-82.483796	0	0	0	0	19.901	0	0	0
18	2	35.526867	-82.478721	0	0	0	0	14.938	0	0	0
18	3	35.524625	-82.480213	0	0	0	0	14.225	0	0	0
18	4	35.521143	-82.479360	0	0	0	0	8.489	0	0	0
18	5	35.524238	-82.474210	0	0	0	0	13.513	0	0	0
18	6	35.522323	-82.475326	3.525	0	0	0	10.425	0	0	0
18	7	35.520296	-82.472198	0	0	0	0	4.363	0	0	0
18	8	35.517656	-82.467676	0	0	0	0	3.750	0	0	0
18	9	35.516251	-82.471029	0	0	0	0	10.663	0	0	0
18	10	35.512447	-82.467236	0	0	0	0	15.425	0.638	0	0.263
18	11	35.512383	-82.460809	0	0	0	0	8.625	0	0	0
18	12	35.507872	-82.466544	0	0	0	0	5.713	1.563	0	0
18	13	35.501681	-82.468373	0	0	0	0	7.301	0	0	0
18	14	35.498741	-82.471560	0	0	0	0	4.325	0	0	0
18	15	35.499229	-82.477096	18.45	0	0	0	5.388	0	0	0
18	16	35.496778	-82.482369	0	0	0	0	10.225	0	0	0
18	17	35.498317	-82.479880	0	0	0	0	4.500	0	0	0
18	18	35.493532	-82.475653	0	0	0	0	14.463	0.188	0	0
18	19	35.489718	-82.476790	0	0	0	0	20.225	0	0	0.188
18	20	35.485883	-82.471581	0	0	0	0	0.526	0	0	0.438
18	21	35.489879	-82.486682	0	0	0	0	2.963	0	0	4.325

WS	Plot	Latitude	Longitude	AIAL	ALJU	ALPE	BETH	CEOR	DIOP	ELUM	LISI
18	22	35.483721	-82.482787	0	0	0	0	15.963	0	0	1.013
18	23	35.481956	-82.475728	0	0	0	0	27.600	0	0	0
18	24	35.471560	-82.474124	0	0	0	0	12.980	0	0	0
18	25	35.465010	-82.471871	0	0	0	0	5.025	0	0	13.50
19	1	35.472751	-82.382559	0	0	0	0	1.065	0	0	0
19	2	35.474687	-82.383948	0	0	0	0	1.800	1.839	0	0
19	3	35.478372	-82.384688	0	0	0	0	2.188	0	0	0
19	4	35.480180	-82.384206	2.375	0	0	0	2.388	0	0	17.85
19	5	35.480588	-82.387998	0	0	0	0	0	0	0	0
19	6	35.482873	-82.384152	0	0.375	0	0	13.650	0	0	0
19	7	35.479236	-82.389055	0	0	0	0	7.025	0	0	0
19	8	35.477461	-82.396871	8.750	0	0	0	0	0	0	0
19	9	35.479665	-82.395567	0	0	0	0	17.588	0	0	1.200
19	10	35.481285	-82.392408	0	0	0	0	0	0	0	0
19	11	35.482723	-82.396951	0	0	0	0	0.288	1.463	0	0.075
19	12	35.488817	-82.394929	0	0	0	0	1.715	0	0	0
19	13	35.490394	-82.398555	0	0	0	0	0	0	0	0
19	14	35.488157	-82.400014	0	0	0	0	3.138	0	0	0.513
19	15	35.485218	-82.402369	0	0	0	0	0.013	0.188	0	0.450
19	16	35.486172	-82.404848	0	0	0	0	0.788	0	0	1.788
19	17	35.491714	-82.406291	0	0	0	0	0.350	0	0	0
19	18	35.489032	-82.408168	0	0	0	0	0.989	0.075	0	0
19	19	35.489751	-82.409048	0	0	0	0	0.150	0	0	0.175
19	20	35.485234	-82.410320	0	0	0	0.438	19.613	0	0	22.32
19	21	35.494037	-82.408968	0	0	0	0	0	0	0	0.150
19	22	35.489096	-82.417154	0	0	0	0	4.213	0	0	0.075
19	23	35.490534	-82.413436	0	0	0	0	0.538	0	0	0.013
19	24	35.493361	-82.412605	0	0	0	0	0	0	0	16.67
19	25	35.494117	-82.416886	0	0	0	0	13.653	0	0	3.013
20	1	35.770556	-82.823616	0	0	0	0	0	0.188	0	0
20	2	35.765369	-82.825407	0	0	0	0	0	0	0	0
20	3	35.767729	-82.823787	0	0	0	0	0	0	0	0
20	4	35.772895	-82.822774	0	0	0	0	0	16.438	0	0
20	5	35.775239	-82.820934	0	0	0	0	0	0	0	0
20	6	35.778313	-82.818756	0	0	0	0	0	0	0	0
20	7	35.780540	-82.816449	0	0	0	0	0	0	0	0
20	8	35.783243	-82.815650	0	0	0	0	0	2.463	0	0
20	9	35.784692	-82.813364	0	0	0	0	0	0	0	0
20	10	35.759522	-82.816840	0	0	0	0	0	0	0	0
20	11	35.760825	-82.815317	0	0	0	0	0	0.263	0	0
20	12	35.763615	-82.813450	0	0	0	0	0	0	0	0
20	13	35.766383	-82.811519	0	0	0	0	0	0	0	0.938
20	14	35.767826	-82.810500	0	0	0	0	0	0	0	0
20	15	35.770138	-82.808295	0	0	0	0	0	0	0	0
20	16	35.772745	-82.807404	0	0	0	0	0	0	0	0
20	17	35.774521	-82.807737	0	0	0	0	0	0.225	0	0
20	18	35.776286	-82.807061	0	0	0	0	0	0.075	0	0
20	19	35.777788	-82.807297	0	0	0	0	0	0	0	0
20	20	35.780711	-82.808193	0	0	0	0	0	0.188	0	0
20	21	35.782192	-82.808890	0	0	0	0	0	0.001	0	0
20	22	35.784198	-82.809915	0	0	0	0	0	0	0	0
20	23	35.786365	-82.811868	0	0	0	0	0	0.513	0	0
21	1	35.435387	-82.730908	0	0	0	0	0	0	0	0
21	2	35.438719	-82.728204	0	0	0	0	0	0	0	0
21	3	35.442227	-82.726960	0	0	0	0	0	0	0	0
21	4	35.447533	-82.726750	0	0	0	0	1.251	0	0	0
21	5	35.445516	-82.724154	0	0	0	0	0	0	0	0

WS	Plot	Latitude	Longitude	AIAL	ALJU	ALPE	BETH	CEOR	DIOP	ELUM	LISI
21	6	35.448949	-82.720817	0	0	0	0	0	0	0	0
21	7	35.450048	-82.719342	0	0	0	0	0	0	0	0
21	8	35.451234	-82.724095	0	0	0	0	0	0	0	0
21	9	35.454120	-82.727748	0	0	0	0	0	0	0	0
21	10	35.451969	-82.730366	0	0	0	0	0	0	0	0
21	11	35.451990	-82.734577	0	0	0	0	0	0	0	0
21	12	35.454147	-82.734127	0	0	0	0	0.001	0	0	0
21	13	35.458106	-82.728360	0	0	0	0	33.453	0	0	0
21	14	35.457301	-82.734143	0	0	0	0	1.876	0	0	0.338
21	15	35.452575	-82.742956	0	0	0	0	18.163	0	0	0.588
21	16	35.453970	-82.741229	0	0	0	0	0.600	0	0	0
21	17	35.458712	-82.736862	0	0.075	0	0	0.150	0	0	0
21	18	35.462392	-82.735993	0	0	0	0	0	0.188	0	1.125
21	19	35.465906	-82.738016	0	0	0	0	6.575	0	0	0
21	20	35.469607	-82.740247	0	0	0	0	18.438	0	0	0.200
21	21	35.469693	-82.744485	0	0	0	0	1.428	0	0	1.038
21	22	35.472735	-82.740628	0	0	0	0	31.425	0.150	0	0.438
21	23	35.478056	-82.744598	0	0	0	0	14.988	0	0	12.02
21	24	35.481940	-82.740972	0	0	0	0	3.613	0	0	3.525
21	25	35.484359	-82.740623	8.750	0	0	0	1.788	0	0	0
22	1	35.660924	-82.859005	0	0	0	0	0	0	0	0
22	2	35.660350	-82.860196	0	0	0	0	12.950	0	0	0
22	3	35.655420	-82.864283	0	0	0	0	0	0	0	0
22	4	35.656745	-82.861161	0	0	0	0	0	0	0	0
22	5	35.658638	-82.860904	0	0	0	0	0.450	0	0	0
22	6	35.659153	-82.859488	0	0	0	0	0	0	0	0
22	7	35.658944	-82.855958	0	0	0	0	2.425	0	0	0
22	8	35.658016	-82.855293	0	0	0	0	0.740	0	0	0
22	9	35.655940	-82.850851	0	0	0	0	0	0	0	0
22	10	35.659588	-82.849140	0	0	0	0	1.013	0	0	0
22	11	35.662002	-82.847326	0	0	0	0	0	0	0	0
22	12	35.664942	-82.845368	0	0	0	0	0	0	0	0
22	13	35.667307	-82.842804	0	0	0	0	0	0	0	0
22	14	35.672184	-82.854408	0	0	0	0	0.275	0	0	0
22	15	35.669239	-82.855336	0	0	0	0	20.625	0	0	0
22	16	35.669255	-82.851457	0	0	0	0	0	0	0	0
22	17	35.669029	-82.848314	0	0	0	0	6.375	0	0	0
22	18	35.668654	-82.844489	0	0	0	0	11.250	0	0	0
22	19	35.682655	-82.854676	0	0	0	0	0.438	2.763	0	0
22	20	35.680069	-82.852374	0	0	0	0	0	0.438	0	0
22	21	35.678750	-82.851511	0	0	0	0	0	0	0	0
22	22	35.675724	-82.849161	0	0	0	0	0.513	16.438	0	0
22	23	35.673106	-82.846844	0	0	0	0	0.013	0	0	0
22	24	35.670295	-82.843663	0	0	0	0	0.088	0	0	0
22	25	35.669426	-82.840760	0	0	0	0	5.313	0	0	0
23	1	35.519346	-82.678310	0	0	0	0	9.675	3.563	0	2.575
23	2	35.516487	-82.673948	0	0	0	0	11.713	0	0	16.83
23	3	35.512710	-82.670789	0	0	0	0	0.338	0	0	0.013
23	4	35.515478	-82.669593	0	0	0	0	0.638	0	0	0.013
23	5	35.520145	-82.668423	0	0	0	0	31.838	0.263	0	31.97
23	6	35.521529	-82.672559	0	9.775	0	0	4.763	0	0	0.438
23	7	35.522940	-82.667388	0	0	0	0	0.600	0	0	1.088
23	8	35.525810	-82.662560	0	0	0	0	35.838	0	5.350	8.113
23	9	35.504771	-82.664057	0	0	0	0	0.938	0	0	0
23	10	35.512378	-82.662726	0	0	0	0	6.300	0	0	0
23	11	35.510430	-82.665124	0	0	0	0	0	0	0	0
23	12	35.508644	-82.662383	0	0	0	0	24.900	0	0	0

WS	Plot	Latitude	Longitude	AIAL	ALJU	ALPE	BETH	CEOR	DIOP	ELUM	LISI
23	13	35.503097	-82.661133	0	0	0	0	0	0	0	0
23	14	35.506493	-82.660098	0	0	0	0	2.463	0.263	0	0
23	15	35.511589	-82.656863	0	0	0	0	32.463	0	0	1.388
23	16	35.508891	-82.654969	0	0	0	0	4.338	0	0	16.82
23	17	35.508134	-82.651745	0	0	0	0	5.778	0	0	0
23	18	35.514309	-82.658150	0	0	0	0	1.713	0	0	0
23	19	35.512340	-82.652614	0	0	0	0	3.628	0	0	3.913
23	20	35.513451	-82.648881	0	0	0	0	0.438	0	0	0
23	21	35.517077	-82.652148	0	0	0	0	1.738	0	0	0
23	22	35.524453	-82.653059	0	1.013	0	0	1.025	0	0.438	0
23	23	35.523144	-82.657431	0	0	0	0	20.438	0	0.938	0
23	24	35.528149	-82.654620	0	0	0	0	4.088	0.163	0	1.975
23	25	35.532698	-82.652008	0	1.275	0	0	20.214	0	0	2.375
24	1	35.602489	-82.694585	0	0	0	0	8.675	0.188	0	0
24	2	35.605552	-82.691383	0	1.375	0	0	4.663	0.013	0	0
24	3	35.605053	-82.685922	0	0	0	0	0	0	0	0
24	4	35.600821	-82.690047	0	0	0	0	0.075	0	0	0
24	5	35.600896	-82.687687	0	0	0	0	0.626	0	0	0
24	6	35.597774	-82.693121	0	0.075	0	0	14.000	0	0	0
24	7	35.598546	-82.687204	0	0	0	0	0.863	0	0	0
24	8	35.601239	-82.684318	0	0	0	0	10.550	0	0	0
24	9	35.603836	-82.682237	0	0	0	0	7.053	0	0	0.188
24	10	35.609581	-82.677725	0	0	0	0	11.588	0.850	0	6.063
24	11	35.605997	-82.679367	0	0	0	0	0.375	0	0	0.488
24	12	35.596862	-82.676395	0	0	0	0	3.176	0	0	0
24	13	35.599329	-82.676303	0	0	0	0	2.300	0	0	0
24	14	35.602489	-82.675182	0	0	0	0	30.513	0	0	0
24	15	35.605761	-82.674211	0	0	0	0	6.153	0.275	0	0
24	16	35.603031	-82.664362	0	0	0	0.188	8.425	0	0	0
24	17	35.607902	-82.669979	0	0.075	0	0	13.200	0	0	0
24	18	35.611158	-82.669212	0	0	0	0	4.338	9.014	0	0.151
24	19	35.608873	-82.664690	0	0	0	0	12.214	0	0	0
24	20	35.607827	-82.662098	0	0	0	0	0	0	0	0
24	21	35.612821	-82.661879	0	0	0	0	27.338	0	0	0
24	22	35.615369	-82.669464	0	0	0	0	4.138	1.825	0	0
24	23	35.621892	-82.665532	0	0	0	0	0.625	2.463	0	4.063
24	24	35.620814	-82.658998	0	0	0	0	0.075	0	0	0
24	25	35.625374	-82.665033	0	0	0	0	0.825	0	0	4.775
25	1	35.701994	-82.390004	0	0	0	0	0	0	0	0
25	2	35.700771	-82.396157	0	0	0	0	0	0	0	0
25	3	35.700148	-82.399151	0	0	0	0	0	0	0	0
25	4	35.700722	-82.402359	0	0	0	0	0	0	0	0
25	5	35.704579	-82.402949	0	0	0	0	0	0	0	0
25	6	35.707707	-82.401002	0	0	0	0	0	0	0	0
25	7	35.704654	-82.400814	0	0	0	0	0	0	0	0
25	8	35.706865	-82.399365	0	0	0	0	0	0	0	0
25	9	35.708120	-82.395718	0	0	0	0	0	0	0	0
25	10	35.711462	-82.396420	0	0	0	0	0	0	0	0
25	11	35.714804	-82.395836	0	0	0	0	0	0	0	0
25	12	35.716075	-82.398266	0	0	0	0	0	0	0	0
25	13	35.720501	-82.401763	0	0	0	0	0	0	0	0
25	14	35.721257	-82.403501	0	0	0	0	0	0	0	0
25	15	35.724648	-82.405234	0	0	0	0	0	0.026	0	0
25	16	35.727099	-82.408453	0	0	0	0	0	0	0	0
25	17	35.730259	-82.409096	0	0	0	0	0	0	0	0
25	18	35.733059	-82.407884	0	0	0	0	0	3.638	0	15.00
25	19	35.736959	-82.408694	0	0	0	0	0	1.750	0	0

25	20	35.739695	-82.408898	0	0	0	0	0	0	0	0
25	21	35.740859	-82.412873	0	0	0	0	0	0	0	0
25	22	35.743434	-82.413737	0	0	0	0	0	4.038	0	0
25	23	35.747210	-82.412267	21.87	0	0	0	0	0	0	1.375
25	24	35.749662	-82.411151	0	0	0	0	0	0	0	0
25	25	35.751684	-82.409370	0	0	0	0	0	0.338	0	0

Appendix 3 (continued).

WS	Plot	Latitude	Longitude	LOJA	MISI	MIVI	PATO	POCU	PUMO	ROMU
1	1	35.854027	-82.556350	0	0	0.179	0	0	0	1.450
1	2	35.855572	-82.555486	0	0	0.365	0	0	0	0.014
1	3	35.857100	-82.554955	0	0	0.008	0	0	0	0
1	4	35.858635	-82.554606	0	0	0.026	0	0	0	1.013
1	5	35.860587	-82.553963	0	0	0	0	0	0	0.189
1	6	35.866461	-82.548797	0	0	7.559	0	0	0	0.438
1	7	35.864949	-82.550106	0	0	0.049	0	0	0	0
1	8	35.862315	-82.552541	0	0	0.389	0	0	0	0
1	9	35.858994	-82.551897	8.150	0	0	0	0	0	9.675
1	10	35.849097	-82.548153	3.290	0	0	0	0	0	0.001
1	11	35.847284	-82.548620	32.763	0	0	0	0	0	0
1	12	35.842171	-82.544569	9.226	0	0	0	0	0	6.339
1	13	35.839387	-82.549564	44.425	0	3.368	0	0	0	1.375
1	14	35.835273	-82.548904	0.019	0	0.131	0	0	0	0
1	15	35.830461	-82.548738	21.000	0	0	0	0	0	2.513
1	16	35.835342	-82.557991	17.075	0	0	0	0	0	2.088
1	17	35.840900	-82.559338	17.063	4.175	0	0	0	0	5.913
1	18	35.842611	-82.557589	26.250	0	0	0	0	0	5.200
1	19	35.846061	-82.557610	0	0	2.653	0	0	0	13.463
1	20	35.855813	-82.562412	0	0.938	2.176	0	0	0	1.876
1	21	35.849928	-82.557712	0	0	0.001	0	0	0	0.438
1	22	35.844955	-82.554145	0.013	0	8.179	0	0	0	3.150
1	23	35.844237	-82.550905	7.950	0	0.583	0	0	0	4.425
1	24	35.853029	-82.550030	29.963	0	0	0	0	0	1.375
1	25	35.833132	-82.557396	0.750	0	0	0	0	0	0
2	1	35.871295	-82.562530	0	0	0	0	0	0	0
2	2	35.873263	-82.561296	0	0	0.396	0	0	0	0
2	3	35.873864	-82.561741	0	0	1.393	0	0	0	0
2	4	35.874701	-82.564069	0	0	7.265	0	2.688	0	0
2	5	35.875211	-82.566011	0	0	2.038	0	0	0	0
2	6	35.880103	-82.571536	0	0	1.691	0	0	0	0
2	7	35.876327	-82.572346	0	0	1.239	0	0.513	0	14.126
2	8	35.874910	-82.572180	0	0	0	0	0	0	0
2	9	35.873730	-82.575935	0	0	0.269	0	5.100	0	0
2	10	35.871000	-82.579127	0	0	0	0	0	0	0
2	11	35.868462	-82.581713	6.013	0	0.275	0	5.438	0	0
2	12	35.867636	-82.580302	0	0	0.463	0	0.875	0	0
2	13	35.866145	-82.577555	0	0	0.041	0	0	0	0
2	14	35.858104	-82.578832	0	0.188	0.040	0	0	0	5.000
2	15	35.858560	-82.579932	9.150	0	0.468	0	0	0	16.575
2	16	35.860512	-82.582303	0	0	0.040	0	14.263	0	0
2	17	35.861295	-82.583671	0	0	1.441	0	5.750	0	2.514
2	18	35.859793	-82.586927	0	0	2.393	0	32.750	0	0
2	19	35.858951	-82.591648	0	0	0.626	0	0	0	1.888
2	20	35.856081	-82.593187	28.000	5.750	0.964	0	0	0	0
2	21	35.854193	-82.595778	16.563	0	0	0	16.438	12.075	0

WS	Plot	Latitude	Longitude	LOJA	MISI	MIVI	PATO	POCU	PUMO	ROMU
2	22	35.850985	-82.590070	0	0	1.639	0	0	14.625	0
2	23	35.852686	-82.593944	1.450	0.438	0.134	0	0	0	0
2	24	35.852895	-82.598283	13.904	0.015	4.403	0	0	0	0
2	25	35.851784	-82.601454	11.476	0	4.089	0	0	0	0
3	1	35.957040	-82.622740	0	0	0.155	0	0	0	0
3	2	35.956272	-82.624424	0	0	0.001	0	0	0	0
3	3	35.954416	-82.629960	0	0	6.419	0	0	0	0
3	4	35.954288	-82.631135	0	0	2.091	0	0	0	0
3	5	35.952936	-82.634391	0	0	0.053	0	0	0	0
3	6	35.952024	-82.637808	0	0	0.355	0	0	0	0
3	7	35.939240	-82.650576	0	0	0	0	0	0	0.075
3	8	35.943897	-82.646670	0	0	0.041	0	0	0	0
3	9	35.945646	-82.646279	0	0	0	0	0	0	0
3	10	35.949331	-82.644718	0	0	0.001	0	0	0	0
3	11	35.951981	-82.647196	0	0	0.428	0	0	0	0
3	12	35.952088	-82.637932	0	0	0.133	0	0	0	0
3	13	35.951257	-82.640142	0	0	0.043	0	0	0	0
3	14	35.952512	-82.644299	0	0	0	0	0	0	0
3	15	35.978208	-82.624666	0	0	0	0	0	0	0
3	16	35.976405	-82.626366	0	0	0.006	0	0	0	0
3	17	35.974490	-82.628882	0	0	0	0	32.213	0	0
3	18	35.970622	-82.632068	0	0	0.370	0	0	0	0
3	19	35.968235	-82.633039	0	0	0.203	0	0	0	0
3	20	35.966454	-82.634354	0	0	0.245	0	0	0	0
3	21	35.959293	-82.636145	0	0	0	0	0	0	0
3	22	35.956707	-82.638769	0	0	0.478	0	0	0	0
3	23	35.956825	-82.641558	0	0	0.104	0	0	0	0
3	24	35.954513	-82.642722	0	0	0	0	0	0	0
3	25	35.953520	-82.646729	0	0	0	0	0	0	0
4	1	35.315707	-82.534307	16.750	0	0.391	0	0	0	0.625
4	2	35.313385	-82.538395	6.563	0	0.133	0	0	0	3.526
4	3	35.311094	-82.539666	12.113	0	0.368	0	0	0	2.500
4	4	35.309275	-82.540138	17.563	0	0	0	0	0	6.963
4	5	35.295618	-82.530413	0	0	0	0	0	0	0
4	6	35.296154	-82.531593	0	0	0	0	0	0	2.375
4	7	35.301910	-82.531593	0	0	0	0	0	0	3.400
4	8	35.300322	-82.524442	0	0	0	0	0	0	1.375
4	9	35.300118	-82.521696	0	0	2.614	0	0	0	0
4	10	35.301459	-82.520258	0	0	0.315	0	0	0	0
4	11	35.303364	-82.519067	6.788	0	0.289	0	0	0	2.163
4	12	35.302978	-82.522447	0.175	0	4.788	0	0	0	1.613
4	13	35.305574	-82.529356	2.538	0	0.564	0	0	0	0.012
4	14	35.305987	-82.535627	8.763	0	1.238	0	0	0	7.738
4	15	35.306051	-82.538363	4.388	0	0.226	0	0	0	0.150
4	16	35.307017	-82.541512	4.300	0	0.003	0	0	0	9.113
4	17	35.306840	-82.546603	2.450	0	0.014	0	0	0	2.212
4	18	35.305172	-82.549194	3.400	0	0.126	0	0	0	1.450
4	19	35.314087	-82.553946	0	0	2.653	0	0	0	6.075
4	20	35.310826	-82.555062	1.138	0	3.701	0	0	0	8.463
4	21	35.308337	-82.552949	0.025	0	0.178	0	0	0	5.050
4	22	35.307108	-82.554875	7.526	0	0.709	0	0	0	11.225
4	23	35.313524	-82.553029	1.401	0	2.693	0	0	0	12.538
4	24	35.308181	-82.551704	0.313	0	0.443	0	0	0	0
4	25	35.300403	-82.552498	7.313	0	1.189	0	0	15.800	48.825
5	1	35.321898	-82.774923	0	0	4.164	0	0	0	0
5	2	35.322509	-82.773292	0	0	0.618	0	0	0	0
5	3	35.321195	-82.770615	0	0	1.228	0	0	0	0

WS	Plot	Latitude	Longitude	LOJA	MISI	MIVI	PATO	POCU	PUMO	ROMU
5	4	35.319441	-82.768314	0	0	2.863	0	0	0	0
5	5	35.318245	-82.766195	0	0	0.076	0	0	0	0
5	6	35.320745	-82.761571	0	0	0.153	0	0	0	0
5	7	35.318990	-82.757022	0	0	0.950	0	0	0	0
5	8	35.317301	-82.758438	0	0	0.393	0	0	0	0
5	9	35.316904	-82.755911	0	0	0.601	0	0	0	0
5	10	35.315702	-82.751727	0	0	0.993	0	0	0	0
5	11	35.315037	-82.749372	0	0	3.643	0	0	0	0
5	12	35.311673	-82.748230	6.225	0	0.588	0	0	0	2.075
5	13	35.310128	-82.747130	0.088	0	1.500	0	0	0	0
5	14	35.308052	-82.744957	3.288	0	0.188	0	0	0	3.613
5	15	35.305992	-82.742602	0.151	0	0.415	0	0	0	0
5	16	35.305236	-82.740301	0.275	0	2.003	0	0	0	3.338
5	17	35.303804	-82.738740	0.046	0	0.566	0	0	0	0
5	18	35.300902	-82.737967	0.165	0	1.614	0	0	0	4.375
5	19	35.297356	-82.738804	0.130	0	0	0	0	0	0
5	20	35.295022	-82.740006	0	0	0.153	0	0	0	0
5	21	35.291643	-82.738627	0.013	0	1.791	0	0	0	0
5	22	35.289293	-82.736921	0.746	0	1.845	0	0	0	0
6	1	35.669051	-82.475315	0	0	0	0	0	0	0
6	2	35.670081	-82.473309	0	0	2.050	0	0	0	0
6	3	35.669786	-82.471629	0	0	1.101	0	0	0	0
6	4	35.674587	-82.467027	0	0	6.201	0	0	0	0
6	5	35.678514	-82.470889	0	0	0.401	0	0	0	40.863
6	6	35.674190	-82.472895	2.088	0	0.838	0	0	0	41.625
6	7	35.676534	-82.473040	0	0	17.375	0	0	0	5.375
6	8	35.679104	-82.472836	0.014	0	0.406	0	0	0	15.851
6	9	35.680295	-82.476624	8.913	0	0.014	0	0	0	5.400
6	10	35.680686	-82.479236	4.838	0	5.156	0	0	0	1.639
6	11	35.671240	-82.486038	1.813	0	3.856	0	0	0	0
6	12	35.674254	-82.484021	0.088	0	15.513	0	0	0	1.825
6	13	35.680311	-82.485550	0	0	4.123	0	0	0	0
6	14	35.681958	-82.484998	0	0	15.313	0	0	0	8.750
6	15	35.679200	-82.482669	11.388	0	2.759	0.088	0	0	0
6	16	35.683787	-82.481167	19.513	0	0.028	0	0	0	0.012
6	17	35.687065	-82.482739	21.875	0	0	0	0	0	0.438
6	18	35.686356	-82.472037	0	0	22.739	0	0	0	0
6	19	35.691378	-82.469950	0	0	31.928	0	0	0	0
6	20	35.690112	-82.472885	0.088	0	7.116	0	0	0	0
6	21	35.689698	-82.478630	11.214	0	13.600	0	0	0	4.588
6	22	35.689875	-82.498285	5.225	0	3.118	0	0	0	0
6	23	35.690315	-82.497218	12.063	0	1.291	0	0	0	5.538
6	24	35.689285	-82.485378	11.500	0	2.475	0	0	0	18.650
6	25	35.692300	-82.492953	11.475	0	0.400	0	0	0	16.800
7	1	35.891567	-82.714702	0	0	1.483	0	0	0	0
7	2	35.893997	-82.713967	1.825	0	0.254	0	0	0	0
7	3	35.893670	-82.707047	0	0	7.401	0	0	0	0
7	4	35.895429	-82.708946	0	0	0.126	0	0	0	0
7	5	35.896760	-82.710437	0	0	0.026	0	0	0	0
7	6	35.899372	-82.706736	11.325	0	0.063	0	0	0	0
7	7	35.902988	-82.705969	9.726	0	0.403	0	0	0	0
7	8	35.894759	-82.693802	0	0	0.075	0	0	0	0
7	9	35.896035	-82.697793	15.150	0	0.025	0	0	0	0
7	10	35.888187	-82.695084	0	0	0	0	0	0	0
7	11	35.890258	-82.697665	1.300	0	0	0	0	0	0
7	12	35.893879	-82.698941	22.913	0	0.126	0	0	0	0
7	13	35.895869	-82.700062	1.238	0	0.276	0	0	0	0

WS	Plot	Latitude	Longitude	LOJA	MISI	MIVI	PATO	POCU	PUMO	ROMU
7	14	35.900815	-82.700964	33.538	0	0	0	0	0	0
7	15	35.903905	-82.697525	47.075	0	0.300	0	0	0	2.650
7	16	35.902253	-82.700781	35.700	0	0.190	0	0	0	0
7	17	35.903959	-82.705781	3.001	0	0	0	0	0	0
7	18	35.906228	-82.706671	0	0	0	0	0	0	0
7	19	35.909522	-82.708876	0.588	0	0	0	0	0	0
7	20	35.911490	-82.711387	5.426	0	1.053	0	0	0	0
7	21	35.913159	-82.714139	8.725	0	0.176	0	0	0	0
7	22	35.915465	-82.716934	1.775	0	0.714	0	0	0	0
7	23	35.914108	-82.719530	3.425	0	0.078	0	0	0	0
8	1	35.866338	-82.454115	0.075	0	0.004	0	0	0	9.900
8	2	35.862679	-82.450563	0.263	0	0.388	0	0	0	2.150
8	3	35.875340	-82.432678	0	0	0.013	0	0	0	0
8	4	35.873076	-82.435591	0	0	0.139	0	0	0	0.188
8	5	35.868865	-82.435709	0	0	0.140	0	0	0	0
8	6	35.869321	-82.437142	0.275	0	16.663	0	0	0	0
8	7	35.870635	-82.438654	19.768	0	0.178	0	0	0	4.375
8	8	35.871252	-82.441648	0	0	0.013	0	0	0	0.450
8	9	35.870887	-82.445741	9.778	0	0.138	0	0	0	1.089
8	10	35.861805	-82.430527	0	0	0	0	0	0	0
8	11	35.864106	-82.431745	0	0	0	0	0	0	0
8	12	35.863699	-82.434234	0	0	0	0	0	0	0
8	13	35.865464	-82.435725	0	0	11.951	0	0	0	3.113
8	14	35.863624	-82.439395	0	0	11.150	0	0	0	0
8	15	35.864149	-82.441599	9.675	0	0.600	0	0	0	7.662
8	16	35.862277	-82.447221	0	0	0.014	0	0	0	1.450
8	17	35.858458	-82.450585	0	0.013	0.400	0	0	0	2.700
8	18	35.855545	-82.452575	30.188	0	0.139	0	0	0	2.576
8	19	35.849955	-82.455783	18.650	0	0.139	0	0	0	8.888
8	20	35.842906	-82.456668	21.750	0	0.026	0	0	0	2.338
8	21	35.849091	-82.428719	0.029	0.075	0.990	0	0	0	0
8	22	35.847021	-82.433687	0	0	0.250	0	0	0	0.075
8	23	35.844955	-82.440580	0	0	3.825	0	0	0	0
8	24	35.842981	-82.448144	8.025	1.375	0.364	0	0	0	2.562
8	25	35.841039	-82.455772	5.675	0	0.075	0	0	0	0
9	1	35.822849	-82.427824	0	0	3.250	0	2.500	0	0
9	2	35.825504	-82.430479	0	0	15.213	0	0	0	3.450
9	3	35.817710	-82.420083	0	0	0.026	0	0	0	0
9	4	35.818568	-82.422078	0	0	0.075	0	0	0	0
9	5	35.820225	-82.424637	0	0	0.379	0	0	0	5.125
9	6	35.821486	-82.426316	0	0	0.154	0	0	0	0
9	7	35.825703	-82.434170	0	0	3.789	0	0	0	0.225
9	8	35.822951	-82.434535	0	8.913	0.226	0.875	0	0	0.075
9	9	35.824361	-82.433816	3.400	7.538	3.426	0	0	0	7.813
9	10	35.823058	-82.438311	2.788	0	0.306	0	0.263	0	0.075
9	11	35.821320	-82.442876	0	0	0.515	0	0	0	5.838
9	12	35.822559	-82.446529	0	0	4.653	0	0	0	0.188
9	13	35.823122	-82.449474	24.775	0	0.129	0	0	0	2.375
9	14	35.822210	-82.454013	0	0	3.613	0	0.875	0	8.525
9	15	35.821626	-82.455788	0	0	0.829	0	0	0	2.075
9	16	35.818552	-82.457328	0.450	0	0.401	0	0	0	11.088
9	17	35.820757	-82.457451	0	0	4.625	0	22.413	0	0.075
9	18	35.822414	-82.460702	15.825	0	2.575	0	0	0	1.013
9	19	35.824297	-82.465557	42.275	0	0	0	0	0	1.063
9	20	35.825107	-82.468094	6.089	0.001	0.075	0	0	0	0.513
9	21	35.826008	-82.471259	8.350	0	0	0	0	0	0
10	1	35.584980	-82.301776	0	0	0	0	0	0	0

WS	Plot	Latitude	Longitude	LOJA	MISI	MIVI	PATO	POCU	PUMO	ROMU
10	2	35.590773	-82.303305	0	0	0.563	0	0	0	0
10	3	35.587420	-82.303830	0	0	0	0	0	0	0
10	4	35.584947	-82.302924	2.901	0	11.875	0	0	0	0
10	5	35.586450	-82.304700	0	0	2.626	0	0	0	0
10	6	35.587984	-82.307156	0	0	7.414	0	0	0	0
10	7	35.589207	-82.307387	4.563	0	5.251	0	0	0	3.137
10	8	35.590044	-82.309463	0	0	4.228	0	0	0	0
10	9	35.592098	-82.310332	0.075	0	2.768	0	0	0	0
10	10	35.593075	-82.309978	4.900	0	2.776	21.21	0	0	5.200
10	11	35.594657	-82.310472	0	0	4.554	3.525	0	0	0
10	12	35.595714	-82.313454	0	0.938	1.013	0	0	0	0
10	13	35.597484	-82.301894	0.338	0	0.865	0	6.063	0	0.150
10	14	35.597683	-82.304753	0	3.438	1.479	0	0	0	0
10	15	35.596878	-82.304126	0.150	0	13.779	0	0.513	0	0
10	16	35.594759	-82.305268	3.325	0	5.565	0	1.138	0	0
10	17	35.595242	-82.324403	6.388	12.43	10.815	0	0	0	23.213
10	18	35.593750	-82.322708	0	3.388	6.505	0	0	0	3.575
10	19	35.591181	-82.321630	0	0.088	8.029	0	0	0	4.213
10	20	35.606931	-82.303219	0.118	0	4.918	0	0	0	0
10	21	35.605080	-82.309114	0	0	2.980	0	0	0	3.750
10	22	35.603519	-82.311373	2.238	5.638	0.571	0	0	0	22.963
10	23	35.598798	-82.311453	0.081	0	33.375	0	0	2.025	0.290
10	24	35.601159	-82.315632	0.538	0	1.901	0	0	0	8.137
10	25	35.599458	-82.319999	0.676	0	3.178	0	0	0	6.925
11	1	35.542595	-82.332557	0	0	2.753	0	0	0	0
11	2	35.544376	-82.335271	0	0	0.148	0	0	0	0
11	3	35.542145	-82.339043	0	0	5.001	0	0	0	0.075
11	4	35.544296	-82.338576	0	0	7.691	0	0	0	0
11	5	35.547890	-82.330068	0	0	2.628	0	0	0	0
11	6	35.550470	-82.330293	0	0	3.691	0	0	0	0
11	7	35.552911	-82.328094	8.613	0	11.000	0	0	0	1.138
11	8	35.550132	-82.332004	0.475	0	2.404	0	0	0	4.375
11	9	35.544607	-82.335169	0	0	1.029	0	0	0	0
11	10	35.547547	-82.334418	0.614	0	3.228	0	0	0	0
11	11	35.548990	-82.341129	0.700	0	0.025	0	0	0	0
11	12	35.546576	-82.341494	0	0	24.904	0	0	0	2.888
11	13	35.545417	-82.342959	1.050	0	2.251	0	0	0	57.038
11	14	35.556618	-82.346263	0	0	2.075	0	0	0	0
11	15	35.553260	-82.348242	0	0	1.841	0	0	0	0
11	16	35.550556	-82.348350	0	0	8.376	8.125	0	0	0
11	17	35.546190	-82.347540	0.263	0	0.814	0	0	0	0.087
11	18	35.544629	-82.348301	1.150	0	0.076	0	0	0	2.025
11	19	35.537172	-82.355350	19.238	0	0.025	0	0	0	7.325
11	20	35.541490	-82.356740	0	0	3.800	0	0	0	0
11	21	35.551549	-82.353854	0	0	4.283	0	0	0	2.475
11	22	35.551023	-82.354294	0	0	4.114	0	0	0	0.075
11	23	35.546608	-82.351536	0	0	1.450	0	0	0	18.950
11	24	35.543003	-82.359057	3.050	0	0.363	0	0	0	0.275
11	25	35.542080	-82.371621	13.113	0	0	0	0	0	3.700
11	26	35.541909	-82.379034	6.625	0	0.926	0	0	0	4.238
12	1	35.419890	-82.416768	15.250	0	0.864	0	0	0	13.125
12	2	35.417562	-82.413281	23.125	0	3.550	0	0	0	0
12	3	35.415099	-82.410792	0.275	0	0.996	0	0	0	0.075
12	4	35.432222	-82.397048	0	0	12.213	0	0	0	1.375
12	5	35.430366	-82.397322	0	0	0.839	0	0	0	4.188
12	6	35.427695	-82.399693	0	0	0.038	0	0	0	0
12	7	35.428344	-82.401576	0	0	20.638	0	0	0	0

WS	Plot	Latitude	Longitude	LOJA	MISI	MIVI	PATO	POCU	PUMO	ROMU
12	8	35.425817	-82.402144	0.338	0	0.100	0	0	0	2.463
12	9	35.421982	-82.405127	0	0	2.875	0	0	0	0.438
12	10	35.417202	-82.402681	0.088	0	0.479	0	0	0	3.325
12	11	35.418060	-82.405379	0	0	11.514	0	0	0	2.000
12	12	35.416220	-82.406758	4.525	0	14.288	0	0	0	0.338
12	13	35.414895	-82.408319	0.375	0	12.214	0	0	0	19.100
12	14	35.410851	-82.409965	0.563	0.513	1.076	0	0	28.875	0.675
12	15	35.406591	-82.425581	0	0	0.276	0	0	0	0
12	16	35.409381	-82.427942	1.188	0	7.025	0	0	0	0.937
12	17	35.409649	-82.423870	1.164	0	0.568	0	0	0	0
12	18	35.406028	-82.417283	0	0	3.155	0	0	0	0.012
12	19	35.406237	-82.412669	0	0	10.164	0	0	0	3.825
12	20	35.405910	-82.407192	37.538	0	0.113	0	0	0	11.175
12	21	35.402541	-82.405545	17.550	0	7.488	0	0	0	3.900
12	22	35.400170	-82.402707	5.525	0	5.963	0	0	0	15.900
12	23	35.396968	-82.403630	47.788	0.775	3.689	0	0	0	4.763
12	24	35.393770	-82.399875	0	0	1.938	0	0	0	0
12	25	35.392987	-82.397096	4.488	0	0.151	0	0	0	2.562
13	1	35.397552	-82.440258	1.513	0	1.665	0	0	0	1.213
13	2	35.397295	-82.441878	0	0	2.163	7.500	0	0	0
13	3	35.392858	-82.442592	4.388	0	10.150	0	0	0	13.925
13	4	35.390310	-82.444276	25.750	0	15.438	0	0	0	13.525
13	5	35.384806	-82.442619	0	0	17.863	0	0	0	11.838
13	6	35.388309	-82.441535	0.075	0	0.389	0	0	0	0
13	7	35.389511	-82.444239	3.614	0	2.488	0	0	0	18.338
13	8	35.385783	-82.447248	15.675	0.088	2.850	0	0	0	2.262
13	9	35.384350	-82.449662	21.525	0	0.113	0	0	0	4.213
13	10	35.381958	-82.450247	6.476	0	6.389	0	0	0	3.650
13	11	35.380021	-82.447844	4.413	0	15.814	0	0	0	0
13	12	35.380960	-82.454597	0.188	0	2.775	0	0	0	0
13	13	35.378358	-82.450574	2.139	0	0.288	0	0	0	1.375
13	14	35.378203	-82.452597	5.900	0	0.013	0	0	0	0
13	15	35.378267	-82.453981	0.088	0	3.038	0	0	0	0
13	16	35.380483	-82.460117	0.714	0	0.055	0	0	0	0
13	17	35.387510	-82.454791	0	0	4.876	0	0	0	4.388
13	18	35.385525	-82.454029	2.975	0.950	4.153	0	0	0	6.900
13	19	35.385981	-82.463427	5.913	2.375	0.038	0	0	0	1.450
13	20	35.387102	-82.464570	1.463	0	6.963	0	0	0	2.100
13	21	35.383004	-82.465514	1.238	0	3.150	0	0	0	4.263
13	22	35.379791	-82.462129	3.925	0	3.616	0	0	0	3.137
13	23	35.383642	-82.469822	0	0	0.428	0	0	0	0
13	24	35.384426	-82.469221	2.850	0	0	0	0	0	1.375
13	25	35.380134	-82.470975	9.375	0	0.250	0	0	0	2.425
14	1	35.261473	-82.602355	0	2.013	3.606	0	0	0	10.938
14	2	35.260588	-82.608138	0.788	0.713	0	0	0	0	0
14	3	35.259869	-82.615015	2.525	13.75	3.829	0	0	22.775	1.013
14	4	35.260883	-82.615616	0	15.67	9.664	0	0	2.000	1.375
14	5	35.262911	-82.614355	0	0	0	0	0	0	0
14	6	35.265325	-82.613749	0	0	0	0	0	0	0
14	7	35.265046	-82.611410	0	1.813	2.714	0	0	0	0.001
14	8	35.267884	-82.608728	0	48.83	1.255	0	0	0	0.075
14	9	35.270346	-82.609275	0	4.050	0.868	0	0	0	0
14	10	35.271274	-82.609270	0.500	0.075	6.526	0	0	0	0.975
14	11	35.272073	-82.606802	0.075	5.940	1.741	0	0	0	0
14	12	35.272803	-82.604780	0	0	7.040	0	0	0	0.075
14	13	35.276982	-82.609554	0	0	1.130	0	0	0	0
14	14	35.278366	-82.607521	0	0	0.833	0	0	0	0.775

WS	Plot	Latitude	Longitude	LOJA	MISI	MIVI	PATO	POCU	PUMO	ROMU
14	15	35.274450	-82.606759	0.663	0	1.901	0	0	0	0.275
14	16	35.275061	-82.601298	18.113	0	0.664	0	0	0	13.125
14	17	35.278398	-82.604410	0	0	5.664	0	0	0	0
14	18	35.276451	-82.601829	1.264	3.475	0.583	0	0	0	0
14	19	35.271322	-82.601330	0	15.97	0	0	0	0	0
14	20	35.269659	-82.596095	0	25.07	0.945	0	0	0	0.937
14	21	35.271580	-82.598149	0	7.738	3.063	0	0	0	0.700
14	22	35.273843	-82.597082	0	3.125	1.030	0	0	0	0
14	23	35.274562	-82.600402	0.315	1.638	6.539	0	0	0	13.263
14	24	35.278784	-82.600322	7.363	0	0.629	0	0	32.263	3.200
14	25	35.283178	-82.599823	0	0	14.550	0	0	0	0
14	26	35.289550	-82.599555	15.313	0	0	0	0	0	1.013
15	1	35.369974	-82.633774	0.188	0	2.125	0	0	0	28.938
15	2	35.371562	-82.629499	4.713	0	0.500	0	0	0	14.225
15	3	35.375934	-82.629697	0	0	5.105	0	0	0	0
15	4	35.375258	-82.626688	0.163	0	23.013	0	0	0	3.363
15	5	35.374646	-82.624451	4.651	0	0.038	0	0	0	11.151
15	6	35.375065	-82.623378	0	0	0.139	0	0	0	0
15	7	35.374673	-82.619521	1.038	0	0.418	0	0	0	0.012
15	8	35.372688	-82.623029	22.400	0	0.603	0	0	0	2.663
15	9	35.372849	-82.614226	2.175	0	0.076	0	0	0.775	1.638
15	10	35.375773	-82.614527	0.600	0	6.250	0	0	0	9.500
15	11	35.382156	-82.615219	1.463	0	0.451	0	0	0	0
15	12	35.382162	-82.615219	10.600	0	0.014	0	0	0	0
15	13	35.389516	-82.619639	2.938	0	0.305	0	0	0	6.475
15	14	35.383497	-82.632358	0	0	0	0	0	0	0
15	15	35.382468	-82.628190	0	0	0	0	0	0	0
15	16	35.382451	-82.624440	0	0	0.076	0	0	0	0
15	17	35.384071	-82.628034	0	0	0	0	0	0	0
15	18	35.386346	-82.629086	0	0	0	0	0	0	0
15	19	35.385252	-82.624263	0	5.763	0	0	0	0	0
15	20	35.385423	-82.617043	19.200	4.813	0.069	0	0	0	1.875
15	21	35.384656	-82.615289	1.425	0	0.201	0	0	0	6.013
15	22	35.386056	-82.610976	0.151	0	2.539	0	0	0	2.913
15	23	35.386877	-82.607022	1.978	0	20.289	0	0	0	4.675
15	24	35.387682	-82.599844	1.301	0	2.939	0	0	0	9.862
15	25	35.389436	-82.602205	13.025	0	0.039	0	0	0	5.638
15	26	35.389726	-82.597404	0.088	0	8.031	0	0	0	0
16	1	35.753481	-82.707245	6.576	0	3.440	0	0	0	1.638
16	2	35.757070	-82.708114	18.763	0	3.464	0	0	0	3.312
16	3	35.761163	-82.709144	12.413	0	0.313	0	0	0	1.587
16	4	35.763749	-82.711489	10.601	0	0.295	0	0	0	6.887
16	5	35.759752	-82.711811	0.513	0	1.414	0	0	0	0.188
16	6	35.766651	-82.713339	20.463	0	2.275	0	0	0	3.025
16	7	35.769639	-82.714192	11.313	0	0.163	0	0	0	0.375
16	8	35.772847	-82.716987	1.375	0	0.715	0	0	0	0
16	9	35.778034	-82.724771	5.250	0	4.463	0	0	0	0.288
16	10	35.776516	-82.721939	0	0	4.350	0	0	0	0
16	11	35.774150	-82.720555	0	0	9.400	0	0	0	0.075
16	12	35.775803	-82.718559	0.625	0	0.238	0	0	0	0
16	13	35.778206	-82.716424	22.125	0	0.003	0	0	0	0
16	14	35.781966	-82.715002	30.850	0	0.114	0	0	0	4.112
16	15	35.784600	-82.716617	29.500	0	0.478	0	0	0	2.000
16	16	35.784144	-82.708206	5.725	0	10.213	8.125	0	0	0.012
16	17	35.782803	-82.705427	10.888	0	3.575	0	0	0	6.875
16	18	35.781757	-82.704504	16.888	0	0.600	0	0	0	18.575
16	19	35.782793	-82.709461	28.263	0	0.200	0	0	0	0.513

WS	Plot	Latitude	Longitude	LOJA	MISI	MIVI	PATO	POCU	PUMO	ROMU
16	20	35.785008	-82.711183	1.638	0	0.376	0	0	0	0.813
16	21	35.787385	-82.714734	12.938	0	24.775	0	0	0	9.463
16	22	35.790072	-82.715871	7.000	0	3.625	0	0	0	0.012
16	23	35.792373	-82.716306	17.138	0	2.764	0	4.200	0	0
17	1	35.657405	-82.543582	0	0	8.438	0	0	0	3.375
17	2	35.658520	-82.542949	0	0	2.151	0	0	0	0
17	3	35.661412	-82.539339	0	0	7.013	0	0	0	1.650
17	4	35.664341	-82.537226	0.376	0	0.450	0	0	0	0
17	5	35.664067	-82.532376	0	0	0.003	0	0	0	0
17	6	35.664673	-82.533653	0	0	0	0	0	0	0
17	7	35.666304	-82.533996	2.200	0	0	0	0	0	0
17	8	35.667956	-82.529753	0.014	0	0.253	0	0	0	0.188
17	9	35.667543	-82.532414	15.238	0	5.551	0	0	0	1.600
17	10	35.668225	-82.535825	0.975	0	0.951	0	0	0	5.500
17	11	35.669104	-82.540750	11.725	0	0.450	0	0	0	19.388
17	12	35.673037	-82.540884	6.851	0	0.013	0	0	0	0.950
17	13	35.674565	-82.543325	1.801	0	0	0	0	0	2.888
17	14	35.676545	-82.545245	14.000	0	0	0	0	0	1.013
17	15	35.673975	-82.545642	4.351	0	5.625	0	0	0	5.376
17	16	35.673251	-82.549628	29.000	0	0	0	0	0	1.462
17	17	35.671862	-82.553340	3.388	0	0.378	0	0	0	0.438
17	18	35.674265	-82.553179	51.875	0	0.263	0	0	0	7.937
17	19	35.675241	-82.563270	0	0	0	0	0	0	1.400
17	20	35.675043	-82.558077	5.175	0.513	2.904	0	0	0	33.650
17	21	35.676357	-82.555776	5.275	0	0.100	0	0	0	2.125
17	22	35.679957	-82.557868	15.413	3.750	0.200	0	0	0	12.013
17	23	35.682414	-82.559359	4.825	0	0.278	0	0	0	9.725
18	1	35.526942	-82.483796	10.250	0.513	7.825	0	0	0	4.438
18	2	35.526867	-82.478721	0	0	10.266	0	0	0	4.850
18	3	35.524625	-82.480213	0	2.100	20.126	0	0	0	0
18	4	35.521143	-82.479360	0	0	4.244	0	0	0	1.500
18	5	35.524238	-82.474210	0	0	13.863	0	0	0	2.588
18	6	35.522323	-82.475326	0	0.188	18.113	0	0	0	1.525
18	7	35.520296	-82.472198	4.700	0	5.400	0	0	0	6.013
18	8	35.517656	-82.467676	0	0	1.200	7.500	0	0	0
18	9	35.516251	-82.471029	0.938	0	1.501	0.438	0	0	1.088
18	10	35.512447	-82.467236	4.063	0.438	10.800	0	2.638	0	6.513
18	11	35.512383	-82.460809	0	3.100	5.990	0	0	0	2.200
18	12	35.507872	-82.466544	11.038	0.588	2.179	0	0	0	3.025
18	13	35.501681	-82.468373	15.201	0	0.013	0	0	0	0
18	14	35.498741	-82.471560	26.763	0	0.325	0	0	0	0
18	15	35.499229	-82.477096	0	0	13.100	50.62	0	0	3.913
18	16	35.496778	-82.482369	0	0	16.625	13.06	0	0	1.713
18	17	35.498317	-82.479880	0	0	5.976	0	0	0	0.263
18	18	35.493532	-82.475653	3.613	0	6.604	0	0	0	11.625
18	19	35.489718	-82.476790	29.925	0	3.713	0	0	0	4.388
18	20	35.485883	-82.471581	1.525	0	19.178	0	0	0	0.513
18	21	35.489879	-82.486682	0.638	0	8.675	0	2.438	0	2.725
18	22	35.483721	-82.482787	12.388	0	17.575	0	0	0	2.000
18	23	35.481956	-82.475728	0	0	2.144	0	0	0	3.025
18	24	35.471560	-82.474124	0.925	0	3.593	0	0	0	12.663
18	25	35.465010	-82.471871	6.700	0	0.250	0	0	0	5.738
19	1	35.472751	-82.382559	0	0	0.891	0	0	0	11.488
19	2	35.474687	-82.383948	0	0	11.600	0	0	0	0.525
19	3	35.478372	-82.384688	8.100	0	6.803	0	0	0	2.800
19	4	35.480180	-82.384206	4.089	0	5.064	0	0	0	30.225
19	5	35.480588	-82.387998	0	0	0	0	0	0	0

WS	Plot	Latitude	Longitude	LOJA	MISI	MIVI	PATO	POCU	PUMO	ROMU
19	6	35.482873	-82.384152	0.138	0	2.013	0	0	0	24.088
19	7	35.479236	-82.389055	15.214	0	0.088	0	0	0	0.450
19	8	35.477461	-82.396871	0.114	0	3.514	0	0	0	1.638
19	9	35.479665	-82.395567	5.950	0	5.663	0	0	0	30.775
19	10	35.481285	-82.392408	3.238	0	2.716	0	0	0	0.075
19	11	35.482723	-82.396951	3.325	0	7.101	0	4.375	6.588	1.575
19	12	35.488817	-82.394929	0	0	0.405	0	0	0	0
19	13	35.490394	-82.398555	0.239	0	0.200	0	0	0	0.012
19	14	35.488157	-82.400014	17.638	0	0	0	0	0	10.963
19	15	35.485218	-82.402369	14.863	0	0.778	0	0	0	14.500
19	16	35.486172	-82.404848	16.938	0	0.101	0	0	0	22.563
19	17	35.491714	-82.406291	0	0	3.605	0	0	0	0.700
19	18	35.489032	-82.408168	0.926	0	4.169	0	0	0	1.650
19	19	35.489751	-82.409048	0.750	0	5.789	0	0	0	2.275
19	20	35.485234	-82.410320	4.788	0	0	0	0	0	6.738
19	21	35.494037	-82.408968	11.063	0.075	0.164	0	0	0	0
19	22	35.489096	-82.417154	5.403	0.513	0.989	0	0	0	3.738
19	23	35.490534	-82.413436	1.913	0	0.075	0	22.625	0	0
19	24	35.493361	-82.412605	8.000	0	0	0	0	0	12.213
19	25	35.494117	-82.416886	1.900	0	0.928	0	0	0	5.601
20	1	35.770556	-82.823616	0	0	4.925	0	0	0	0.375
20	2	35.765369	-82.825407	0	0	0.088	0	0	0	1.387
20	3	35.767729	-82.823787	0	0	1.276	0	0	0	3.163
20	4	35.772895	-82.822774	3.563	0	1.826	0	0	0	0.075
20	5	35.775239	-82.820934	8.650	0	0.014	0	0	0	0
20	6	35.778313	-82.818756	11.788	0	0	0	0	0	1.387
20	7	35.780540	-82.816449	6.066	0	0	0	0	0	0
20	8	35.783243	-82.815650	7.350	0	1.326	0	0	0	0
20	9	35.784692	-82.813364	4.788	0	0.003	0	0	0	0
20	10	35.759522	-82.816840	0	0	0.040	0	0	0	0
20	11	35.760825	-82.815317	0	0	0	0	0	0	0
20	12	35.763615	-82.813450	0	0	0	0	0	0	0
20	13	35.766383	-82.811519	2.438	0	0.001	0	0	0	0
20	14	35.767826	-82.810500	0.075	0	0.125	0	7.100	0	0
20	15	35.770138	-82.808295	0	0	1.529	0	0	0	0
20	16	35.772745	-82.807404	4.575	0	3.614	0	0	0	1.638
20	17	35.774521	-82.807737	12.638	0	1.051	0	0	0	0.075
20	18	35.776286	-82.807061	15.338	0	0.456	0	0	0	2.075
20	19	35.777788	-82.807297	4.150	0	0.088	0	0	0	0
20	20	35.780711	-82.808193	0	0	0.675	0	0	0	0.263
20	21	35.782192	-82.808890	7.450	0	0.001	0	0	0	6.250
20	22	35.784198	-82.809915	38.250	0	0	0	0	0	0
20	23	35.786365	-82.811868	13.313	0	4.063	0	0	0	0
21	1	35.435387	-82.730908	0	0	0	0	0	0	0
21	2	35.438719	-82.728204	0	0	0	0	0	0	0
21	3	35.442227	-82.726960	0	0	0.728	0	0	0	0
21	4	35.447533	-82.726750	0	0	0	0	0	0	0
21	5	35.445516	-82.724154	0	0	0.003	0	0	0	0
21	6	35.448949	-82.720817	0	0	0	0	0	0	0
21	7	35.450048	-82.719342	0	0	0.351	0	0	0	0
21	8	35.451234	-82.724095	0	0	1.253	0	0	0	0
21	9	35.454120	-82.727748	0	0	0	0	0	0	0
21	10	35.451969	-82.730366	0	0	1.251	0	0	0	0
21	11	35.451990	-82.734577	0	0	8.676	0	0	0	0
21	12	35.454147	-82.734127	0	0	1.721	0	0	0	0
21	13	35.458106	-82.728360	2.538	0	2.794	0	0	0	2.688
21	14	35.457301	-82.734143	0.688	0	2.565	0	0	0	0

WS	Plot	Latitude	Longitude	LOJA	MISI	MIVI	PATO	POCU	PUMO	ROMU
21	15	35.452575	-82.742956	0.088	0	0.054	0	0	0	2.500
21	16	35.453970	-82.741229	7.065	0	1.143	0	0	0	0.075
21	17	35.458712	-82.736862	7.550	0	7.430	0	0	0	0
21	18	35.462392	-82.735993	0.900	0	0.765	0	0	0	0.012
21	19	35.465906	-82.738016	2.151	0	4.113	0	0	0	1.450
21	20	35.469607	-82.740247	5.175	0	0.075	0	0	0	1.750
21	21	35.469693	-82.744485	0	0	2.341	0	0	0	0.150
21	22	35.472735	-82.740628	8.838	0	0.101	0	0	0	1.400
21	23	35.478056	-82.744598	8.813	0	0	0	0	0	2.513
21	24	35.481940	-82.740972	7.788	0	0.076	0	0	0	0
21	25	35.484359	-82.740623	20.875	0	0	0	0	0	0
22	1	35.660924	-82.859005	0	0	0	2.000	0	0	0
22	2	35.660350	-82.860196	0	0	10.651	0	0	0	0
22	3	35.655420	-82.864283	0	0	1.314	0	0	0	0
22	4	35.656745	-82.861161	0	0	0.153	0	0	0	0.538
22	5	35.658638	-82.860904	0	0	12.775	0	0	0	0
22	6	35.659153	-82.859488	0	0	6.013	0	0	0	0
22	7	35.658944	-82.855958	1.575	0	35.000	0	0	0	0.450
22	8	35.658016	-82.855293	0	0	14.339	0	0	0	9.875
22	9	35.655940	-82.850851	0	0	0	0	0	0	1.375
22	10	35.659588	-82.849140	0	0	0.614	0	0	0	1.025
22	11	35.662002	-82.847326	0	0	12.313	0	0	0	13.513
22	12	35.664942	-82.845368	0	0	4.504	0	0	0	0
22	13	35.667307	-82.842804	0	0	3.576	0	0	0	0
22	14	35.672184	-82.854408	1.438	0	2.714	0	0	0	31.050
22	15	35.669239	-82.855336	0.013	0	0.064	0	0	0	1.850
22	16	35.669255	-82.851457	0	0	1.576	0	0	0	1.962
22	17	35.669029	-82.848314	0	0	0.100	0	0	0	0.188
22	18	35.668654	-82.844489	2.500	0	1.025	0	0	0	8.450
22	19	35.682655	-82.854676	0	0	4.263	0	0	0	0
22	20	35.680069	-82.852374	0	0	2.428	0	0	0	2.038
22	21	35.678750	-82.851511	0	0	4.814	0	0	0	1.900
22	22	35.675724	-82.849161	0	0	3.101	0	0	0	1.525
22	23	35.673106	-82.846844	6.588	0	0.744	0	0	0	16.338
22	24	35.670295	-82.843663	32.600	0	0.388	0	0	0	0
22	25	35.669426	-82.840760	0	0	3.350	0	0	0	0.225
23	1	35.519346	-82.678310	26.938	0	0.703	1.563	0	0	8.437
23	2	35.516487	-82.673948	3.238	0	0	0	0	0	0.375
23	3	35.512710	-82.670789	17.625	0	0	0	8.688	0	0.075
23	4	35.515478	-82.669593	16.775	0	0.438	0	0	0	10.813
23	5	35.520145	-82.668423	13.863	0	1.276	0	0	0	5.063
23	6	35.521529	-82.672559	7.263	0	0	4.188	0	0	2.500
23	7	35.522940	-82.667388	25.063	0	0.075	0	0	0	1.000
23	8	35.525810	-82.662560	4.339	0	0.801	0	0	0	15.525
23	9	35.504771	-82.664057	0.550	0	0.675	0	0	0	0.513
23	10	35.512378	-82.662726	0.850	0	0	0	0	0	0
23	11	35.510430	-82.665124	0	0	0	0	0	0	0
23	12	35.508644	-82.662383	7.213	0	0	0	0	0	5.063
23	13	35.503097	-82.661133	0	0	5.050	0	0	0	0
23	14	35.506493	-82.660098	3.625	0	1.200	0	0	0	8.475
23	15	35.511589	-82.656863	3.663	0	7.340	0	0	0	16.613
23	16	35.508891	-82.654969	23.563	0	0.013	0	0	0	2.700
23	17	35.508134	-82.651745	0.075	0	4.464	0	0	0	6.412
23	18	35.514309	-82.658150	12.213	0	0	0	0	0	1.900
23	19	35.512340	-82.652614	4.039	0	0.728	0	0	0	1.150
23	20	35.513451	-82.648881	5.138	0	1.013	0	0	0	0
23	21	35.517077	-82.652148	4.038	0	0.494	0	0	0	0.950

WS	Plot	Latitude	Longitude	LOJA	MISI	MIVI	PATO	POCU	PUMO	ROMU
23	22	35.524453	-82.653059	2.764	0	11.665	0	0	0	0.300
23	23	35.523144	-82.657431	5.425	0	5.239	0	0	0	0
23	24	35.528149	-82.654620	8.063	0	1.476	0	0	0	0
23	25	35.532698	-82.652008	6.163	0	7.765	0	0	0	20.288
24	1	35.602489	-82.694585	5.076	0	0	0	0	0	0
24	2	35.605552	-82.691383	5.700	0	1.764	0.938	5.775	0	0
24	3	35.605053	-82.685922	23.963	0	0	0	0	0	0
24	4	35.600821	-82.690047	0	0	0	0	0	0	0
24	5	35.600896	-82.687687	0.088	0	4.854	0	0	0	0.001
24	6	35.597774	-82.693121	30.625	0	0.780	4.375	0	0	3.713
24	7	35.598546	-82.687204	2.263	0	8.341	0	0	0	2.725
24	8	35.601239	-82.684318	39.425	0	0.039	0	0	0	0
24	9	35.603836	-82.682237	0	0	0.278	0	0	0	6.750
24	10	35.609581	-82.677725	28.500	0	0	0	0	0	2.613
24	11	35.605997	-82.679367	10.150	0	9.126	0	0	0	0.513
24	12	35.596862	-82.676395	0.763	0	2.238	0	0	0	0
24	13	35.599329	-82.676303	0	0	0.756	0	0	0	0.200
24	14	35.602489	-82.675182	18.525	0	2.963	0	0	0	16.250
24	15	35.605761	-82.674211	0.625	0	3.463	0	0	0	0
24	16	35.603031	-82.664362	1.875	0	8.101	0	0	0	2.275
24	17	35.607902	-82.669979	0.078	0	0.813	0	0	0	1.600
24	18	35.611158	-82.669212	6.225	0	1.025	0	0	0	12.588
24	19	35.608873	-82.664690	2.988	0	7.713	0	0	0	2.550
24	20	35.607827	-82.662098	1.750	0	0.026	0	0	0	0
24	21	35.612821	-82.661879	19.688	0	0.013	0	0	0	2.900
24	22	35.615369	-82.669464	19.388	0	0	0	0	0	1.275
24	23	35.621892	-82.665532	8.165	0	34.588	0	0	0	1.375
24	24	35.620814	-82.658998	0	0	0.039	0	0	0	0
24	25	35.625374	-82.665033	35.413	0	0	0	0	0	0
25	1	35.701994	-82.390004	0	0	0	0	0	0	0
25	2	35.700771	-82.396157	0	0	0	0	0	0	0
25	3	35.700148	-82.399151	0	0	0	0	0	0	0
25	4	35.700722	-82.402359	0	0	0	0	0	0	0
25	5	35.704579	-82.402949	0	0	0	0	0	0	0
25	6	35.707707	-82.401002	0	0	0	0	0	0	0
25	7	35.704654	-82.400814	0	0	0	0	0	0	0
25	8	35.706865	-82.399365	0	0	0	0	0	0	0
25	9	35.708120	-82.395718	0	0	0	0	0	0	0
25	10	35.711462	-82.396420	0	0	0	0	0	0	0
25	11	35.714804	-82.395836	0	0	0	0	0	0	0
25	12	35.716075	-82.398266	0	0	0	0	0	0	0
25	13	35.720501	-82.401763	0	0	0	0	0	0	0
25	14	35.721257	-82.403501	0	0	0.216	0	0	0	0
25	15	35.724648	-82.405234	0	0	0.098	0	0	0	0
25	16	35.727099	-82.408453	0	0	0.530	0	0	0	0.075
25	17	35.730259	-82.409096	0	1.775	15.403	0	0	0	1.525
25	18	35.733059	-82.407884	0	3.525	0.604	0	0	0	0
25	19	35.736959	-82.408694	0	0	0	0	0	0	0
25	20	35.739695	-82.408898	0	0	0	8.750	0	0	0.075
25	21	35.740859	-82.412873	12.775	0	1.264	0	0	0	2.725
25	22	35.743434	-82.413737	0	0	6.264	0	0	0	3.825
25	23	35.747210	-82.412267	0	0	0	0	0	0	0.075
25	24	35.749662	-82.411151	0	0	0	0	0	0	1.638
25	25	35.751684	-82.409370	0	0	0	0	0	0	0

THESIS CONCLUSIONS

1. Land-use history strongly influences invasion by non-native plants in the southern Appalachians. As evidenced from the fine-scale (single-watershed) studies described in the first two chapters and by the broad-scale study described in Chapter 3, historic land use seems to have a profound impact on invasion throughout the forest-dominated study region. Land-use history is not always easily discernable, and its impact on forest ecosystems is therefore seldom considered. Nonetheless, it can have important and long-lasting effects on forests that should not be overlooked.

2. Forests on sites that were previously cultivated exhibit higher invasibility. Historic land-use might facilitate invasion by providing a disturbance that affords non-native plants an opportunity to become established around the time of abandonment and subsequently proliferate in those areas. However, results from the field experiment described in Chapter 2 indicate that formerly cultivated areas abandoned a century ago also had higher invasibility than adjacent areas that lacked an agricultural history, illustrating the long-lasting influence of land-use legacies.

3. Overstory dominance by tulip poplar (*Liriodendron tulipifera* L) in historically cultivated sites may explain their higher invasibility. High tulip polar dominance is often associated with areas that have experienced large-scale disturbances such as agriculture and subsequent abandonment in the region. Such areas had the highest occurrence and abundance of invasive plants, as evidenced from the field surveys detailed in Chapter 1. Results from the field

experiments (Chapter 2) suggest that forest floor conditions likely shaped by the overstory community, especially thin leaf litter layers and high soil moisture content, may be responsible for the higher invasibility of tulip poplar stands. Correspondingly, thick leaf litter layers typical of oak-dominated stands in areas that were not formerly cultivated may confer resistance to invasion.

4. Non-native plants in the forest understory are heterogeneously distributed and typically in low abundance away from roadsides. The heterogeneous distribution of invasive plants in the forest understory seems to result from the combined effects of spatial variation in site invasibility and propagule pressure from established populations. The low abundance may indicate that invasion of the forest interior is in its early stages. These latent invaders (already more common in areas with disturbance histories) are likely to respond favorably to subsequent disturbance events. Multiple disturbances may therefore be important for substantial expansion of non-native populations in forest interiors in the study region.

5. Roads facilitate invasion of forests by non-native plants. The concept that roads play a major role in determining spread of invasive plants is not novel, but results from Chapters 1 and 3 underscore the importance of roads for invasion of southern Appalachian forests. The profusion of forest invaders observed along roads throughout the study region demonstrates the importance of roads as conduits for rapid spread across the forest-dominated landscape. The work described in Chapter 1 also highlights the apparent role of roadside populations in providing sufficient propagule pressure to facilitate invasion of the adjacent forest understory. Where they were present along roads, non-native species commonly occurred beyond 50 m into

the forest and were considerably more common downslope from the roads, demonstrating the importance of propagule pressure combined with short-range dispersal mechanisms.

6. The factors affecting distributions of non-native invasive plants are scale dependent.

The invasive plant species considered in Chapter 3 were examined at local and regional scales, and the factors that explained their distributions varied between the two scales. At the regional scale, species were typically more common at lower elevations and closer to the region's city center, Asheville, NC. Common species also occurred more frequently in watersheds with lower forest cover. At the local scale, land-use history and surrounding forest cover were considerably more important factors, with most species showing higher abundance or likelihood of occurrence in plots where more of the surrounding area had regrown to forest since the 1940s and in plots with less surrounding forest cover. Elevation was still important for explaining presence/absence of the common focal species at the local scale, but less so for explaining their abundance.

7. Non-native plant species capable of spread in the forest-dominated southern Appalachians show idiosyncratic responses to factors influencing their distribution.

Although some species such as *Lonicera japonica*, *Ligustrum sinense*, and *Rosa multiflora* showed remarkably similar responses to the factors considered in the region-wide investigation (Chapter 3), other species such as *Microstegium vimineum* exhibited more singular responses. For example, *M. vimineum* was the only species that occurred more frequently and had higher abundance in areas with greater forest cover, suggesting that it may be a particularly formidable invader of intact forest in the region and highlighting the need to consider certain species individually.