

Agricultural land-use history increases non-native plant invasion in a southern Appalachian forest a century after abandonment

Timothy R. Kuhman, Scott M. Pearson, and Monica G. Turner

Abstract: Land-use history can play a significant role in shaping forest communities. We considered the effects of agricultural land-use legacies on the distribution of non-native invasive plants a century after abandonment in a watershed in western North Carolina, USA. Forest sites that were previously in cultivation and abandoned ca. 1905 were compared with nearby reference sites that were never cultivated. The most common invasive plants were *Celastrus orbiculatus* Thunb., *Microstegium vimineum* Trin., and *Lonicera japonica* Thunb. Formerly cultivated sites and plots positioned downslope from roads had the most invasives. Soil cation concentration and pH were positively correlated with invasive presence and abundance. Historic agricultural plots where the successional tree *Liriodendron tulipifera* L. was dominant had the highest soil cation concentrations and soil pH and the greatest abundance of invasive plants. Disentangling the cause-effect relationships between land-use history, 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 plants in forest ecosystems. Our results suggest that land-use history at Bent Creek may be facilitating plant invasion indirectly by causing a shift in overstory community composition that in turn creates more suitable understory conditions for shade-tolerant invasive plants.

Résumé : L'utilisation passée des terres peut jouer un rôle important dans la formation des communautés forestières. Nous avons examiné les effets de l'utilisation passée des terres à des fins agricoles sur la distribution des plantes exotiques invasives, un siècle après l'abandon de l'agriculture dans un bassin versant le l'ouest de la Caroline du Nord, aux États-Unis. Les stations forestières précédemment cultivées et abandonnées autour de 1905 ont été comparées à des stations témoins situées à proximité et qui n'ont jamais été cultivées. Les plantes invasives les plus fréquentes étaient *Celastrus orbiculatus* Thunb., *Microstegium vimineum* Trin. et *Lonicera japonica* Thunb. Les stations précédemment cultivées et les parcelles situées en aval d'un chemin avaient la plus grande quantité de plantes invasives. La concentration des cations et le pH du sol étaient positivement corrélés avec la présence de plantes invasives et leur abondance. Les parcelles jadis occupées par l'agriculture, où dominait l'espèce successioneuse *Liriodendron tulipifera* L., avaient les plus fortes concentrations de cations dans le sol, le pH du sol le plus élevé et la plus grande abondance de plantes invasives. C'est un défi de démêler les relations de cause à effet entre l'utilisation passée des terres, la communauté biotique et la plate-forme abiotique mais la compréhension du rôle de l'héritage laissé par l'utilisation des terres peut fournir de précieuses indications concernant les mécanismes sous-jacents à l'établissement et à la propagation des plantes invasives dans les écosystèmes forestiers. Nos résultats indiquent que l'utilisation passée des terres à Bent Creek pourrait indirectement faciliter l'invasion des plantes en provoquant un changement dans la composition de la communauté de l'étage dominant qui à son tour crée des conditions plus favorables en sous-bois pour les plantes invasives tolérantes à l'ombre.

[Traduit par la Rédaction]

Introduction

Non-native invasive plants represent a significant driver of change in natural ecosystems by displacing native species, disrupting succession, and altering ecosystem structure and function (Vitousek et al. 1996). A number of invasive plant species are currently posing such threats to forests of eastern North America, including shade-tolerant species that may be-

come established in closed-canopy forests but proliferate slowly compared with their shade-intolerant counterparts in more open habitats (Martin et al. 2009). To understand and predict the spread of these species, one must consider not only how they are responding to the contemporary landscape but also how they respond to less conspicuous factors related to land-use history. In this study, we elucidate factors influencing the establishment and spread of non-native plants in

Received 29 July 2010. Accepted 8 February 2011. Published at www.nrcresearchpress.com/cjfr on 19 April 2011.

T.R. Kuhman.* Department of Zoology, University of Wisconsin-Madison, 430 Lincoln Drive, Madison, WI 53706, USA; Department of Biological Sciences, Edgewood College, 1000 Edgewood College Drive, Madison, WI 53711, USA.

S.M. Pearson. Department of Natural Sciences, Mars Hill College, Mars Hill, NC 28754, USA.

M.G. Turner. Department of Zoology, University of Wisconsin-Madison, 430 Lincoln Drive, Madison, WI 53706, USA.

Corresponding author: T.R. Kuhman (e-mail: tkuhman@edgewood.edu).

*Current affiliation: Department of Biological Sciences, Edgewood College, 1000 Edgewood College Dr., Madison, WI 53711, USA.

the forest understory of a southern Appalachian watershed and propose possible mechanisms related to historic land use that facilitate invasion a century after agricultural abandonment.

A number of studies have addressed the impacts of land-use legacies and demonstrated their longlasting effects on ecosystems (Compton and Boone 2000; Dupouey et al. 2002; Foster et al. 2003). Other studies have specifically implicated land-use history in the establishment and spread of non-native invasive plants (Lundgren et al. 2004; Von Holle and Motzkin 2007; Brown and Boutin 2009). However, little is known about the actual mechanisms related to historic land use that might facilitate invasion by non-native plants, especially in closed-canopy forest (Martin et al. 2009). Although there is evidence that land-use history may be the *ultimate* driver of invasion in certain cases, the *proximate* causes are often poorly understood. In some cases, land use may create a disturbance that provides an ephemeral 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). In this case, once the species becomes established, it may then persist throughout the successional stages at that site even if its abundance remains low. In other cases, land-use change may facilitate invasion by causing fluctuations in levels of resources (e.g., soil nutrients) that persist for some period of time (Davis et al. 2000), as in the case of soil amendments added to agricultural fields. We suggest that another possibility is that land-use history may facilitate invasion of the forest understory by shade-tolerant non-native species *indirectly* through its influence on succession. During early- to midsuccessional stages, the overstory community assemblage may differ substantially from that which was present prior to forest clearing and may in turn alter site conditions in a manner that facilitates invasion in much the same way that successional forests facilitate colonization by shade-tolerant native species (Bazzaz 1975; Clebsch and Busing 1989).

In this study, we address two overarching questions: (i) to what extent does historic agricultural land use affect the presence and abundance (percent cover) of invasive plants in the understory of a southern Appalachian mixed-hardwood forest and (ii) what specific factors (e.g., land use, biotic, topographic, and edaphic variables) 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. The southern Appalachians are densely forested, and we were especially interested in shade-tolerant non-native species whose abundance could potentially increase in the understory of closed-canopy forests. To our knowledge, no previous studies have employed a paired sampling design to evaluate the effect of historic agricultural land use on non-native understory species while controlling for differences in topography and bedrock geology between historically cultivated and reference sites. Given that such factors might be correlated with land-use history, they could confound interpretations of land-use history's role in invasions. By comparing paired post-agricultural and reference areas, this study provides an opportunity to address the factors related to his-

toric land use that might contribute to greater invasion by non-native plants.

Methods

Study area

The study was conducted at the Bent Creek Experimental Forest (BCEF) 15 km southwest of Asheville, North Carolina, USA, in the Pisgah National Forest (35°28'N, 82°39'W). The 2500 ha BCEF is situated within the French Broad River Basin in the Southern Blue Ridge Province. BCEF lies at between 700 and 1100 m elevation and is covered primarily by mixed-oak and mixed-mesophytic forest. Granites, gneisses, and schists dominate the bedrock geology of the Bent Creek basin, and soils are predominantly Ultisols and Inceptisols. Common overstory species include *Quercus coccinea* Muenchh., *Quercus velutina* Lam., *Quercus prinus* L., *Quercus alba* L., *Oxydendrum arboreum* (L.) DC., *Pinus rigida* Mill., and *Pinus echinata* P. Mill. on xeric sites. On mesic lower slopes and coves, dominant species include *Liriodendron tulipifera* L. and *Quercus rubra* L., with *Tsuga canadensis* (L.) Carr., *Fagus grandifolia* Ehrh., and *Cornus florida* L. also relatively common. *Acer rubrum* L., *Carya* spp., and *Pinus strobus* L. are common throughout the basin. Common non-native invasive plants at BCEF include the woody climber Asiatic bittersweet (*Celastrus orbiculatus* Thunb.), the annual grass Japanese stiltgrass (*Microstegium vimineum* Trin.), and the trailing or climbing perennial vine Japanese honeysuckle (*Lonicera japonica* Thunb.). These species exhibit high plasticity with respect to light conditions (Baars and Kelly 1996; Horton and Neufeld 1998; Ellsworth et al. 2004) and achieve their highest abundance along roads at BCEF. However, as shade-tolerant species, they also occur in the forest understory away from roads. While they occur in relatively low abundance in most understory areas at BCEF, this may indicate early stages of invasion rather than invasion resistance.

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 1941). 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, and nearly all cultivated lands were abandoned. Subsequent forest regrowth ensued, with periodic timber harvesting throughout the basin. The basin has been managed by the US Forest Service since the establishment of BCEF in 1925.

Data collection

The study was conducted between June and August 2006. Twenty sites were selected based on a land-use history report and corresponding map produced for BCEF (Nesbitt 1941) that indicated which areas had been in cultivation, when they were first cultivated, and when they were abandoned. Four 20 m × 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 30–100 years prior to abandonment between 1900 and 1910. Reference plots were paired with the respective HA plots based on their similarity in slope, aspect, elevation, terrain shape, bedrock geology, and proximity to paired plots (see supplementary Table S1).¹ Although reference plots tended to be on slightly steeper slopes (3% greater on average) and at slightly higher elevations (11 m higher on average), these are unlikely to represent ecologically significant differences. Farmers who selected sites for cultivation in the 1800s undoubtedly chose the gentlest slopes at lower elevations; therefore, paired reference plots, although selected to match the topography of HA sites as closely as possible, were often on slightly steeper and higher slopes. There was a moderate difference in aspect between the paired plots, with the reference plots actually on slightly more northeasterly aspects. There were minor differences between HA and reference plots with respect to terrain shape and total basal area (Table S1).¹

Slope was determined for each plot using a clinometer. Aspect was converted from degrees azimuth (θ) to an index of insolation (A') adapted from Beers et al. (1966): $A' = \cos(22.5^\circ - \theta) + 1$. North-northeast (22.5°) is considered here to represent the most mesic aspect and takes on a value of 2. Correspondingly, the most xeric aspect (south-southwest) takes on a value of 0 and the index increases symmetrically from 0 to 2 as the compass direction changes in either direction from south-southwest to north-northeast. 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 subcardinal 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 at the University of Wisconsin-Madison Soil and Plant Analysis Laboratory to determine pH, organic matter, total N (organic-N, NH_4 , NO_3 , and NO_2), P, K^+ , Ca^{2+} , and Mg^{2+} (macronutrients that are commonly associated with plant performance and may vary with historic land use). We also performed soil particle size analysis using the hydrometer method (Gee and Bauder 1986) to determine percent clay, silt, and sand.

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 at breast height (DBH) of all trees >10 cm DBH within the 20 m \times 20 m plots. Understory vegetation sampling was conducted in twenty-five 1 m² quadrats arranged in a 5 \times 5 grid spaced every 5 m within the 20 m \times 20 m

plot. In each quadrat, non-native plant species were identified and their covers were estimated based on the following cover classes: <0.1%, 0.1%–1%, 2%–5%, 6%–10%, 11%–25%, 26%–50%, 51%–75%, and 76%–100%. Total cover of ground layer (within 0.5 m of the ground), native vegetation and shrub layer (0.5–2.5 m above the ground) native vegetation were likewise measured. Quadrat-level native species richness was determined by tallying all native vascular plant species within each quadrat. Litter depth was measured in each quadrat using a wire probe inserted through the leaf litter to the surface of the soil. Measurements were averaged across all quadrats in the respective plots. For vegetation cover, the cover classes were converted to percent cover using the midpoint of each class before averaging across the 25 quadrats to determine percent cover for the plot.

Data analysis

A two-way χ^2 analysis was used to test for differences in the frequency of invasive presence and absence in plots that differed in land-use history (HA versus reference) and proximity to roads (adjacent versus 50 m away). Tests of partial independence 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 with a logit link; the function employs the Laplace approximation for parameter estimation (Bates and Sarkar 2006). Linear mixed-effects models were similarly used to explain the abundance (percent 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 method of parameter estimation. In both cases, “site” was treated as a random effect. In the case of the linear mixed-effects models, invasive cover was log transformed to improve 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 nonmetric multidimensional scaling (NMDS). Similarly, NMDS was used to explore how overstory composition was related to

¹Supplementary data are available with the article through the journal Web site (<http://www.nrcresearchpress.com/cjfr>).

Table 1. Explanatory variables used in model selection for both the generalized linear mixed-effects models in which invasive presence–absence was the response variable and the linear mixed-effects models in which invasive abundance (percent cover) was 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	Insolation index (northeasterliness): $A' = \cos(22.5^\circ - \theta) + 1$
TSI	Local terrain shape index (convex < 0 < concave)
Biotic community	
BA	Total basal area for all trees >10 cm DBH
Canopy	Overstory canopy cover (average % cover)
Shrub	Average shrub cover (0.5–2.5 m above ground)
Native cover	Average 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)
Litter	Average litter depth

Table 2. Number of plots in which non-native invasive plants were either present or absent.

	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
Ref. plots ($N = 40$)	7	13	3	17

Note: Presence–absence of invasives was dependent on land-use history ($\chi^2 = 16.9$, $P < 0.001$) but was independent of proximity to roads ($\chi^2 = 2.6$, $P = 0.456$). HA, historic agriculture plots that were cultivated and abandoned ca. 1905; Ref., reference plots that were not previously cultivated.

the presence–absence and abundance of invasive exotic plants. Total basal area (of trees >10 cm DBH) for each species was square root transformed and used in the ordination of sampling units (plots). NMDS was performed in R 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. Sørensen (Bray–Curtis) distance was used to generate the dissimilarity matrix. The relationship between the overstory species and the NMDS solution was examined 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 *C. orbiculatus* (in 44% of plots), *M. vimineum* (in 18% of plots), and *L. japonica* (in 13% of plots). Less common invasive species included *Rosa multiflora* Thunb., *Elaeagnus umbellata* Thunb., and *Albizia julibrissin* Durazz (see supplementary Table S2).¹ The invasive species frequently co-occurred in the forest understory, and initial analyses indicated that they responded similarly to ex-

planatory variables. Subsequent analyses therefore grouped all non-native invasive plant species together.

Based on the two-way contingency table (Table 2), a χ^2 analysis of partial independence showed that the presence–absence of invasives was dependent on land-use history ($\chi^2 = 16.9$, $P < 0.001$), with invasives more likely to occur in the HA plots than in the reference plots. However, their presence–absence was independent of road proximity ($\chi^2 = 2.6$, $P = 0.456$). Abundance (percent cover) of invasives also varied with land-use history. For those plots ($N = 38$) in which invasive species were present, cover was higher in the HA plots ($t = 2.61$, $P = 0.013$); 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, $N = 10$). Although mean cover of invasives was nearly sevenfold greater in the HA plots than in the reference plots, mean cover of invasives was relatively low and they seldom dominated the plots (Table S2).¹

PCA results for the soils data revealed two axes to be used in the regression models (Table 3). Axis 1 primarily represents a gradient of exchangeable cations (Ca^{2+} , K^+ , and Mg^{2+}) and pH (all positively correlated), explaining 35.2% of the variation. Axis 2 explains 25.2% of the variation and represents a gradient in soil texture and organic matter. Higher axis 2 values are associated with sandier soils and lower organic matter.

Results from the logistic GLMMs revealed several important variables for explaining the presence–absence of non-na-

Table 3. Mean values for soils variables and their structure correlations with the first two principal component axes based on the principal components analysis (PCA).

Soils variable	Mean (SE)	PCA axis 1 (<i>r</i>)	PCA axis 2 (<i>r</i>)
Total N (mg·L ⁻¹)	0.12 (0.005)	0.554	-0.598
Organic matter (%)	6.1 (0.2)	0.244	-0.764
P (ppm)	3.2 (0.1)	-0.183	-0.120
pH	4.6 (0.04)	0.703	0.054
K (ppm)	59.9 (2.8)	0.859	-0.080
Ca (ppm)	118.3 (23.5)	0.836	0.353
Mg (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

Note: Mean and SE values are across all plots (*N* = 80). Pearson's correlation coefficients with $|r| > 0.6$ are shown in bold.

Table 4. Summary of the best generalized linear mixed-effects model for presence-absence of non-native invasive plants.

Predictor variable	Estimate	SE	<i>z</i>	<i>P</i>
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 and pH)	1.185	0.332	3.57	0.0004

Note: Model parameters were calculated based on the Laplace approximation. Backward stepwise selection was used to determine the best model using $|z| \geq 2$ as the criterion for inclusion in the model; "site" was treated as a random effect.

Table 5. Summary of the best linear mixed-effects model for abundance (log-transformed cover) of non-native invasive plants for plots in which they were present (*N* = 38).

Predictor variable	Estimate	SE	df	<i>t</i>	<i>P</i>
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 and pH)	0.562	0.117	16	4.82	0.0002

Note: Model parameters were estimated using restricted maximum likelihood. Backward stepwise selection was used to determine the best model using $|t| \geq 2$ as the criterion for inclusion in the model; "site" was treated as a random effect.

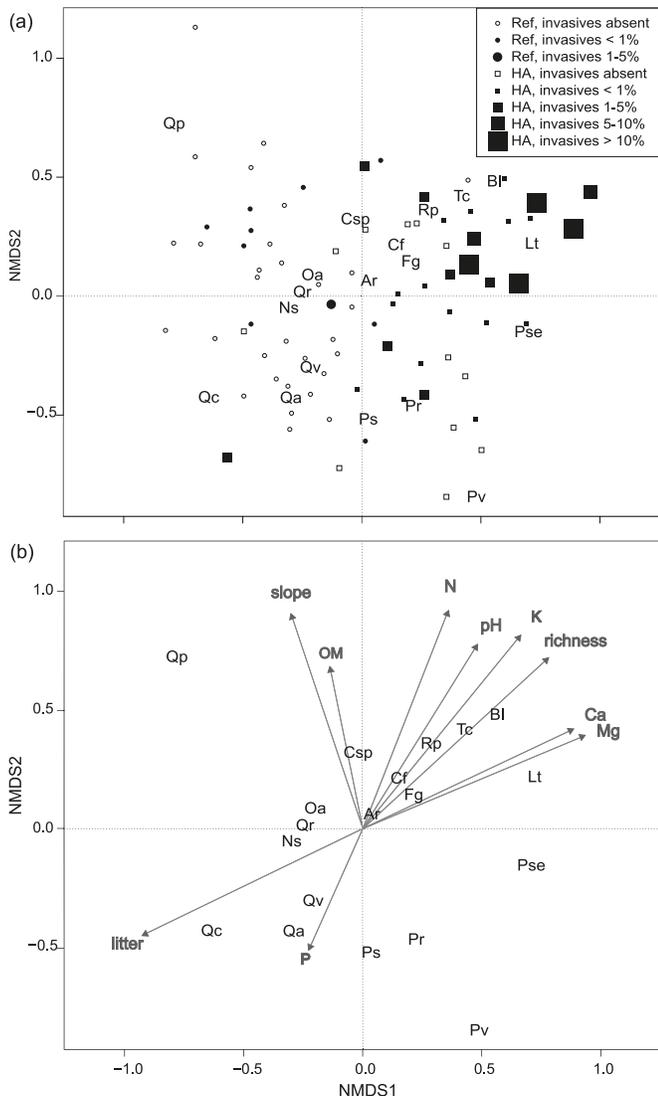
tive invasive plants (Table 4). The best model included land-use history (invasives more likely present in HA sites), topographic position with respect to roads (more likely downslope from roads), and soils PCA axis 1 (more likely in plots with soil having higher exchangeable cation concentrations and pH).

Results from the linear mixed model selection (with invasive cover as the response variable) were similar to those for the presence-absence model described above (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. 1). HA plots, many of which had invasive plants present, fell primarily along the upper end of the first NMDS axis, and the abundance (percent cover) of invasive species was also much higher in plots represented along the upper end of the first axis (Fig. 1a). Successional tree species such as *L. tulipifera*, *Betula lenta* L., and *Prunus serotina* Ehrh. were more common in plots positioned along the upper end of the first NMDS axis and the oak species *Q. coccinea*, *Q. alba*, *Q. velutina*, and *Q. prinus* were more common along the lower end of axis 1 (also see Table 6 for average basal areas of overstory species in HA and reference plots). *Quercus prinus* was more dominant in plots along the upper end of the second NMDS axis and the three pine species *P. strobus*, *P. rigida*, and *Pinus virginiana* P. Mill. were more common in plots along the lower end of axis 2, perhaps revealing a gradient in topographic position among the more xeric sites. (*Quercus prinus* typically occurs on middle to upper, steeper slopes and ridges whereas the pine species typically occur on lower, gentler slopes at BCEF.)

Fig. 1. Nonmetric multidimensional scaling (NMDS) based on the overstory species composition (basal area of trees >10 cm DBH). (a) Sampling units (plots) are coded based on their land-use history, with reference (Ref) plots indicated by circles and historic agriculture (HA) plots represented by squares. Open symbols indicate plots in which invasives were absent and solid symbols are sized to represent invasive abundance (percent cover) in the respective plots. Two-letter codes represent overstory species centroids: Ar, *Acer rubrum*; Bl, *Betula lenta*; Csp, *Carya* spp.; Cf, *Cornus florida*; Fg, *Fagus grandifolia*; Lt, *Liriodendron tulipifera*; Ns, *Nyssa sylvatica*; Oa, *Oxydendrum arboreum*; Pr, *Pinus rigida*; Ps, *Pinus strobus*; Pv, *Pinus virginiana*; Pse, *Prunus serotina*; Qa, *Quercus alba*; Qc, *Quercus coccinea*; Qp, *Quercus prinus*; Qr, *Quercus rubra*; Qv, *Quercus velutina*; Rp, *Robinia pseudoacacia*; Tc, *Tsuga canadensis*. (b) Fitted environment vectors that were significantly correlated with the NMDS ordination. Significance is defined for vectors as having $P < 0.05$ based on permutation tests (see Table 7 for R and P values). Environmental variable: P, soil phosphorus; litter, average litter depth; slope, slope steepness measured at plot center; 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.



Correlations between environmental vectors and the NMDS solution (Fig. 1b; Table 7) revealed several notable relationships. The concentrations of exchangeable cations (Ca^{2+} , Mg^{2+} , and K^+), pH, and total N were all significantly correlated with the NMDS solution and higher along the upper end of the first axis, corresponding to plots dominated by *Liriodendron* and other successional tree species. Average quadrat-level native understory species richness was also greater in plots along the upper end of the first axis and litter depth was lower. The most notable relationships between the second axis and the environmental variables were steeper slopes, higher levels of soil organic matter, and lower soil P levels along the upper end of the axis. Soil N, K^+ , and pH were also higher along the upper end of axis 2.

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 in the forest understory at BCEF. Although native species were dominant in all plots, the likelihood of presence and the abundance of invasive understory 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 HA plots than in the reference plots. That the absolute abundance of invasive species was low is not surprising because rates of invasion in closed-canopy forest are slow (Martin et al. 2009). However, the nearly threefold increase in likelihood of presence and sevenfold increase in abundance of invasives suggest that the landscape patterns of historic agriculture could facilitate expansion of invasives in southern Appalachian forests.

Landscape position with respect to roads was also important for explaining invasion. Invasive plant abundance was higher adjacent to roads than in plots 50 m away, but presence-absence was not dependent on road proximity. This indicates that invasives were often established in the forest understory beyond 50 m from the road corridor, albeit at lower abundance than in areas adjacent to roads. The importance of roads as conduits for invasive plants is well known, particularly for shade-intolerant, “weedy” species (Gelbard and Belnap 2003; Christen and Matlack 2006). Less is known about the role of roads in facilitating invasion of intact forests, but their importance for invasion of the understory by shade-tolerant species has been noted (Parendes and Jones 2000; Watkins et al. 2003). The shade-tolerant invasive plants 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., *C. orbiculatus* (Ellsworth et al. 2004), *M. vimineum* (Horton

Can. J. For. Res. Downloaded from www.nrcresearchpress.com by Depository Services Program on 07/26/11 For personal use only.

Table 6. Overstory tree species and their average dominance (basal area) in historic agriculture and reference plots, respectively.

Overstory tree species	Basal area in historic agriculture plots (m ² ·ha ⁻¹)		Basal area in reference plots (m ² ·ha ⁻¹)	
	Mean	SE	Mean	SE
<i>Acer rubrum</i>	3.85	0.56	3.26	0.44
<i>Betula lenta</i>	0.51	0.17	0.43	0.25
<i>Carya</i> spp.	0.56	0.22	0.94	0.40
<i>Cornus florida</i>	0.31	0.09	0.20	0.06
<i>Fagus grandifolia</i>	0.23	0.22	0.09	0.07
<i>Liriodendron tulipifera</i>	11.72	1.80	0.92	0.27
<i>Nyssa sylvatica</i>	0.27	0.14	0.29	0.08
<i>Oxydendrum arboreum</i>	2.10	0.33	3.25	0.35
<i>Pinus rigida</i>	1.02	0.31	0.31	0.14
<i>Pinus strobus</i>	2.70	0.91	1.96	0.75
<i>Pinus virginiana</i>	1.96	0.71	0.36	0.20
<i>Prunus serotina</i>	0.71	0.27	0.03	0.03
<i>Quercus alba</i>	1.88	0.63	4.13	0.85
<i>Quercus coccinea</i>	0.34	0.13	2.97	0.72
<i>Quercus prinus</i>	0.71	0.53	6.25	1.25
<i>Quercus rubra</i>	0.81	0.38	1.61	0.53
<i>Quercus velutina</i>	0.86	0.29	1.00	0.33
<i>Robinia pseudoacacia</i>	0.24	0.12	0.17	0.08
<i>Tsuga canadensis</i>	0.87	0.36	0.24	0.12

Table 7. Axis scores, correlation coefficients (*R*), and probability of significance (*P*) for environmental vectors fitted on the overstory community nonmetric multidimensional scaling (NMDS) ordination shown in Fig. 1.

Environmental variable	NMDS1	NMDS2	<i>R</i>	<i>P</i>
Total N (soil)	0.37	0.93	0.55	<0.001
Organic matter (soil)	-0.20	0.98	0.39	0.001
P (soil)	-0.41	-0.91	0.31	0.014
pH (soil)	0.53	0.85	0.51	<0.001
K ⁺ (soil)	0.63	0.77	0.58	<0.001
Mg ²⁺ (soil)	0.92	0.39	0.56	<0.001
Ca ²⁺ (soil)	0.90	0.43	0.54	<0.001
Clay content	-0.42	-0.91	0.14	0.442
Sand content	0.20	-0.98	0.07	0.827
Litter depth	-0.90	-0.44	0.57	<0.001
Slope	-0.32	0.95	0.53	<0.001
Local terrain shape (TSI)	0.99	0.15	0.26	0.072
Quadrat-level native species richness	0.74	0.68	0.59	<0.001

Note: Correlation coefficients (*R*) reflect correlations between the environmental vectors and the final ordination solution. *P* values represent probabilities of significant correlation based on permutation tests with 1000 permutations; variables with *P* < 0.05 are shown in bold and are included as significant environmental vectors in Fig. 1b.

and Neufeld 1998), and *L. 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. Although they are less abundant away from the 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 of plots with respect to roads (i.e., upslope or downslope of the road) was important in explain-

ing both the presence and the abundance of invasive plants at BCEF. Invasives were more likely 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 found for *Phytophthora lateralis* Tucker & Milbrath 1942, a root pathogen of Port Orford cedar in the US Pacific Northwest where infection was more common in host trees positioned downslope from roads (Jules et al. 2002).

Areas at BCEF where invasive plants were present and in higher abundance were associated with high soil cation concentrations and pH. These areas were typically in formerly cultivated sites. Land-use history can have longlasting effects on soil chemistry (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. First, 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 selected to match the slope, aspect, terrain shape, and bedrock geology of the respective HA sites as closely as possible; 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. Another possibility is that 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 1941), it is unlikely that any soil amendments were applied. While some farmers in the region applied commercial manures to cash crops such as tobacco and cotton during the early 1900s, these fertilizers were too expensive for most subsistence farmers and rarely used on crops such as corn (Otto 1983). It is also noteworthy that the most striking differences in soil chemistry are related to the labile exchangeable cations and associated pH rather than altered levels of N and P in which land-use history is more frequently implicated (see review by McLaughlan 2006). Other studies have actually demonstrated substantial *decreases* in soil pH and exchangeable cations within only a few decades of oak-hickory and pine forest aggradation following agricultural abandonment (Johnson et al. 1988; Richter et al. 1994), suggesting that the elevated soil pH and cation concentrations in many of the HA plots (in which oak and pine dominance was typically lower) in our study are unlikely explained by the direct effects of agricultural land use a century ago. A third possible explanation for the observed differences in soil chemistry between HA and reference sites is that ecosystem-level processes that were set in motion at the time of agricultural abandonment could have produced and perpetuated the differences in soil chemistry observed in the HA areas today. Forest succession has resulted in a community composition following abandonment in many areas that likely differs considerably from that prior to cultivation, as demonstrated by differences in adjacent uncultivated areas. The observed differences in soil chemistry may be a product of these differences in community composition.

Many of the HA sites at BCEF were dominated by early-successional tree species, particularly *L. tulipifera*. *Liriodendron tulipifera* is a long-lived tree species capable of persisting in the canopy for over 200 years (Beck 1990). In the southern Appalachians, it is well suited to both cove-hardwood and midslope mixed hardwood forests and achieves its

highest dominance in even-aged stands following larger-scale disturbances such as agricultural abandonment or clearcutting (Elliott et al. 2002). In our study, high *L. tulipifera* dominance was only observed in HA plots, with the highest dominance on lower- to midslope positions. The paired reference plots located in analogous lower- to midslope positions were most often dominated by oak species, and *L. tulipifera* abundance was low. Those areas dominated by *L. tulipifera* had high soil exchangeable cation concentrations, elevated pH, and thinner leaf litter layers. Other authors have noted that soils in *L. tulipifera* dominated stands in the southern Appalachians have higher concentrations (Kalisz 1986) and less spatial heterogeneity (Fraterrigo et al. 2005) of Ca in particular. Tree species such as *Acer saccharum* Marsh. and *Cornus florida* L. are known to regulate the cycling of Ca and other base cations in forest ecosystems (Thomas 1969; Dijkstra and Smits 2002). Like these species, *L. tulipifera* leaves contain high cation concentrations (Boettcher and Kalisz 1990) and decompose rapidly due to their relatively low lignin and C:N ratio (Kominoski et al. 2007). Thus, *L. tulipifera* might be redistributing cations from deeper horizons to the soil surface via litterfall. Furthermore, rapid decomposition of their leaves likely contributes to swift turnover of nutrients and a more shallow litter layer in *L. tulipifera* stands in contrast with the deeper litter observed in the reference areas where oaks dominated the overstory.

Exchangeable cations are important for supporting growth in forest ecosystems (Finzi et al. 1998). However, relatively little is known about their role in the spread of non-native invasive plants. One study in southeastern New York noted that plant invasion in forests was positively correlated with soil Ca²⁺ and Mg²⁺ concentrations (Howard et al. 2004). Soil pH was also found to be positively correlated with invasion rates of *M. vimineum* (Cole and Weltzin 2004) and *C. orbiculatus* (Silveri et al. 2001; Pande et al. 2007). However, further study is needed to determine whether elevated soil cation concentrations and pH promote invasion by non-native plants or whether other correlated variables are actually responsible. A field seeding experiment initiated by the authors at BCEF suggests that differences in soil chemistry between *L. tulipifera* dominated and oak-dominated stands had little effect on seed germination and first-year seedling survival of *C. orbiculatus*; rather, lower leaf litter mass and greater soil moisture better explained the higher invasibility of *L. tulipifera* stands (Kuhman 2009). Correspondingly, the greater leaf litter mass common in reference stands dominated by oaks may confer resistance to invasion by providing a physical barrier and (or) creating drier soil surface conditions.

Certain invasive plants seem to have an affinity for successional forests, irrespective of the type of disturbance that initiates the succession. For example, high abundance of *C. orbiculatus* has also been observed in areas that were previously clearcut for timber harvest or experienced large-scale windthrow events at BCEF (McNab and Loftis 2002; T.R. Kuhman, personal observations). As in the case of historic agriculture, such disturbances have resulted in successional overstory communities. Invasive abundance in the HA areas may thus be due to conditions arising from large-scale disturbance history (and (or) subsequent succession) in general rather than the agricultural land-use history per se.

One possible explanation for the higher invasive abun-

dance in the historic agriculture sites is that the species could have become established immediately following abandonment, resulting in longer residence time than in adjacent reference stands. However, in the case of at least one invasive species that we observed, *M. vimineum*, it could not have been present at BCEF at the time of abandonment because it was first introduced into the United States in 1919 (Fairbrothers and Gray 1972). Furthermore, higher germination and survival of experimentally seeded *C. orbiculatus* in HA areas dominated by *L. tulipifera* than in nearby oak-dominated reference stands (Kuhman 2009) indicated that invasibility is indeed greater in the HA areas. Although we cannot fully elucidate the relationship between land-use history and increased invasibility without knowing the pre-agricultural site conditions and subsequent changes that may have ensued, our results suggest that overstory succession and associated changes in forest floor conditions play a major role.

It is noteworthy that the areas with higher abundance of non-native invasive plants (i.e., areas with *L. tulipifera* dominance, higher soil cation concentrations, and higher pH) also had greater native species richness. This suggests that conditions in such areas may be more favorable for plant performance in general, enhancing overall species richness in the understory. The similarity in 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 establishment and spread of non-native plants depends on many factors related to characteristics of the invaded range. Mounting evidence suggests that land-use history contributes substantially to invasibility of forested landscapes (Lundgren et al. 2004; Von Holle and Motzkin 2007; Brown and Boutin 2009), but disentangling the factors related to historic land use and elucidating the specific mechanisms underlying the invasion process presents a considerable challenge. Our results from Bent Creek suggest that the land-use legacy that is influencing current patterns of invasion by non-native plants in closed-canopy forests may not be the *direct* result of the historic land use itself but rather the *indirect* result of changes to understory and soil conditions that accompanied shifts in tree community composition following agricultural abandonment. This study also underscores the importance of considering both land-use history and the contemporary landscape to understand the patterns of invasion by non-native plants in the forest understory and to predict their subsequent spread.

Acknowledgements

This study was funded by the Long-term Ecological Research (LTER) Program of the National Science Foundation (DEB-0218001 and DEB-0823293, Coweeta LTER). We are grateful to Henry McNab, Cathryn Greenberg, and David Loftis at BCEF for assistance with logistics, permits, and general support in this project. Diana Flores, Jared Nix, Chris Brunton, Ellen Fidler, Stephanie McFarlane, Andrea Van Gunst, and Thomas Albright provided field and laboratory assistance. Claudio Gratton, Phil Townsend, and Cecil Ané offered statistical advice. We thank Jennifer Fraterrigo, Anthony Ives, Donald Waller, and Robert Peet for valuable comments on the manuscript.

References

- Baars, R., and Kelly, D. 1996. Survival and growth responses of native and introduced vines in New Zealand to light availability. *N. Z. J. Bot.* **34**(3): 389–400.
- Bates, D., and Sarkar, D. 2006. lme4: linear mixed-effects models using S4 classes. R package version 0.99875-8. Available from <http://cran.r-project.org/>.
- Bazzaz, F.A. 1975. Plant species diversity in old-field successional ecosystems in southern Illinois. *Ecology*, **56**(2): 485–488. doi:10.2307/1934981.
- Beck, D.E. 1990. *Liriodendron tulipifera* L. yellow-poplar. In *Silvics of North America*. Edited by R.M. Burns and B.H. Honkala. U.S. Dep. Agric. Agric. Handb. 654. pp. 406–416.
- Beers, T.W., Dress, P.E., and Wensel, L.C. 1966. Aspect transformation in site productivity research. *J. For.* **64**(10): 691–692.
- Boettcher, S.E., and Kalisz, P.J. 1990. Single-tree influence on soil properties in the mountains of eastern Kentucky. *Ecology*, **71**(4): 1365–1372. doi:10.2307/1938273.
- Brown, C.D., and Boutin, C. 2009. Linking past land use, recent disturbance, and dispersal mechanism to forest composition. *Biol. Conserv.* **142**(8): 1647–1656. doi:10.1016/j.biocon.2009.02.035.
- Christen, D., and Matlack, G. 2006. The role of roadsides in plant invasions: a demographic approach. *Conserv. Biol.* **20**(2): 385–391. doi:10.1111/j.1523-1739.2006.00315.x. PMID:16903099.
- Clebsch, E.E.C., and Busing, R.T. 1989. Secondary succession, gap dynamics, and community structure in a southern appalachian cove forest. *Ecology*, **70**(3): 728–735. doi:10.2307/1940223.
- Cole, P.G., and Weltzin, J.F. 2004. Environmental correlates of the distribution and abundance of *Microstegium vimineum*, in east Tennessee. *Southeast. Nat.* **3**(3): 545–562. doi:10.1656/1528-7092(2004)003[0545:ECOTDA]2.0.CO;2.
- Compton, J.E., and Boone, R.D. 2000. Long-term impacts of agriculture on soil carbon and nitrogen in New England forests. *Ecology*, **81**(8): 2314–2330. doi:10.1890/0012-9658(2000)081[2314:LTIOAO]2.0.CO;2.
- Davis, M.A., Grime, J.P., and Thompson, K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.* **88**(3): 528–534. doi:10.1046/j.1365-2745.2000.00473.x.
- Dijkstra, F.A., and Smits, M.M. 2002. Tree species effects on calcium cycling: the role of calcium uptake in deep soils. *Ecosystems* (N. Y.), **5**(4): 385–398. doi:10.1007/s10021-001-0082-4.
- Dupouey, J.L., Dambrine, E., Laffite, J.D., and Moares, C. 2002. Irreversible impact of past land use on forest soils and biodiversity. *Ecology*, **83**(11): 2978–2984. doi:10.1890/0012-9658(2002)083[2978:IIOPLU]2.0.CO;2.
- Elliott, K.J., Boring, L.R., and Swank, W.T. 2002. Aboveground biomass and nutrient accumulation 20 years after clear-cutting a southern Appalachian watershed. *Can. J. For. Res.* **32**(4): 667–683. doi:10.1139/x02-009.
- Ellsworth, J.W., Harrington, R.A., and Fownes, J.H. 2004. Survival, growth and gas exchange of *Celastrus orbiculatus* seedlings in sun and shade. *Am. Midl. Nat.* **151**(2): 233–240. doi:10.1674/0003-0031(2004)151[0233:SGAGEO]2.0.CO;2.
- Fairbrothers, D.E., and Gray, J.R. 1972. *Microstegium vimineum* (Trin.) A. Camus (Gramineae) in the United States. *Bull. Torrey Bot. Club*, **99**(2): 97–100. doi:10.2307/2484205.
- Finzi, A.C., Breemen, N.V., and Canham, C.D. 1998. Canopy tree – soil interactions within temperate forests: species effects on soil carbon and nitrogen. *Ecol. Appl.* **8**(2): 440–446.
- Foster, D., Swanson, F., Aber, J., Burke, I., Brokaw, N., Tilman, D., and Knapp, A. 2003. The importance of land-use legacies to ecology and conservation. *Bioscience*, **53**(1): 77–88. doi:10.1641/0006-3568(2003)053[0077:TIOULU]2.0.CO;2.
- Fraterrigo, J.M., Turner, M.G., Pearson, S.M., and Dixon, P. 2005.

- Effects of past land use on spatial heterogeneity of soil nutrients in southern Appalachian forests. *Ecol. Monogr.* **75**(2): 215–230. doi:10.1890/03-0475.
- Gee, G.W., and Bauder, J.W. 1986. Particle-size analysis. *In* Methods of soil analysis: Part 1 — Physical and mineralogical methods. Edited by A. Klute. American Society of Agronomy, Inc. and Soil Science Society of America, Inc., Madison, Wis. pp. 383–411.
- Gelbard, J.L., and Belnap, J. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. *Conserv. Biol.* **17**(2): 420–432. doi:10.1046/j.1523-1739.2003.01408.x.
- Hobbs, R.J., and Huenneke, L.F. 1992. Disturbance, diversity, and invasion: implications for conservation. *Conserv. Biol.* **6**(3): 324–337. doi:10.1046/j.1523-1739.1992.06030324.x.
- Horton, J.L., and Neufeld, H.S. 1998. Photosynthetic responses of *Microstegium vimineum* (Trin.) A. Camus, a shade-tolerant, C-4 grass, to variable light environments. *Oecologia (Berl.)*, **114**(1): 11–19. doi:10.1007/s004420050414.
- Howard, T.G., Gurevitch, J., Hyatt, L., Carreiro, M., and Ler dau, M. 2004. Forest invasibility in communities in southeastern New York. *Biol. Invasions*, **6**(4): 393–410. doi:10.1023/B:BINV.0000041559.67560.7e.
- Johnson, D.W., Henderson, G.S., and Todd, D.E. 1988. Changes in nutrient distribution in forests and soils of Walker Branch Watershed, Tennessee, over an eleven-year period. *Biogeochemistry*, **5**(3): 275–293. doi:10.1007/BF02180068.
- Jules, E.S., Kauffman, M.J., Ritts, W.D., and Carroll, A.L. 2002. Spread of an invasive pathogen over a variable landscape: a nonnative root rot on Port Orford cedar. *Ecology*, **83**(11): 3167–3181. doi:10.1890/0012-9658(2002)083[3167:SOAIP0]2.0.CO;2.
- Kalisz, P.J. 1986. Soil properties of steep Appalachian old fields. *Ecology*, **67**(4): 1011–1023. doi:10.2307/1939824.
- Kominoski, J.S., Pringle, C.M., Ball, B.A., Bradford, M.A., Coleman, D.C., Hall, D.B., and Hunter, M.D. 2007. Nonadditive effects of leaf litter species diversity on breakdown dynamics in a detritus-based stream. *Ecology*, **88**(5): 1167–1176. doi:10.1890/06-0674. PMID:17536403.
- Kuhman, T.R. 2009. The influence of past and present land use on non-native plant invasion in the southern Appalachians. Ph.D. dissertation, University of Wisconsin-Madison, Madison, Wis.
- Levine, J.M., and D'Antonio, C.M. 1999. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos*, **87**(1): 15–26. doi:10.2307/3546992.
- Lundgren, M.R., Small, C.J., and Dreyer, G.D. 2004. Influence of land use and site characteristics on invasive plant abundance in the Quinebaug Highlands of southern New England. *Northeast. Nat.* **11**(3): 313–332. doi:10.1656/1092-6194(2004)011[0313: IOLUAS]2.0.CO;2.
- Martin, P.H., Canham, C.D., and Marks, P.L. 2009. Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. *Front. Ecol. Environ.* **7**(3): 142–149. doi:10.1890/070096.
- McCune, B., and Mefford, M.J. 1999. PC-ORD: Multivariate analysis of ecological data. MJM Software Design, Glenden Beach, Ore.
- McLauchlan, K. 2006. The nature and longevity of agricultural impacts on soil carbon and nutrients: a review. *Ecosystems (N.Y.)*, **9**(8): 1364–1382. doi:10.1007/s10021-005-0135-1.
- McNab, W.H. 1993. A topographic index to quantify the effects of mesoscale landform on site productivity. *Can. J. For. Res.* **23**(6): 1100–1107. doi:10.1139/x93-140.
- McNab, W.H., and Loftis, D.L. 2002. Probability of occurrence and habitat features for Oriental bittersweet in an oak forest in the southern Appalachian mountains, USA. *For. Ecol. Manag.* **155**(1–3): 45–54. doi:10.1016/S0378-1127(01)00546-1.
- Nesbitt, W.A. 1941. History of early settlement and land use on the Bent Creek Experimental Forest, Buncombe County, N.C. U.S. Dep. Agric. For. Serv. Rep. Southern Research Station, Bent Creek Experimental Forest, Asheville, NC.
- Oksanen, J., Kindt, R., and O'Hara, R.B. 2005. Vegan: Community Ecology Package version 1.6-10. Available from <http://cc.oulu.fi/~jarioksa>.
- Otto, J.S. 1983. The decline of forest farming in southern Appalachia. *J. For. Hist.* **27**(1): 18–27.
- Pande, A., Williams, C.L., Lant, C.L., and Gibson, D.J. 2007. Using map algebra to determine the mesoscale distribution of invasive plants: the case of *Celastrus orbiculatus* in Southern Illinois, USA. *Biol. Invasions*, **9**(4): 419–431. doi:10.1007/s10530-006-9049-x.
- Parentes, L.A., and Jones, J.A. 2000. Role of light availability and dispersal in exotic plant invasion along roads and streams in the H. J. Andrews Experimental Forest, Oregon. *Conserv. Biol.* **14**(1): 64–75. doi:10.1046/j.1523-1739.2000.99089.x.
- Pinheiro, J.C., and Bates, D.M. 2000. Mixed-effects models in S and S-Plus. Springer, New York.
- Richter, D.D., Markewitz, D., Wells, C.G., Allen, H.L., April, R., Heine, P.R., and Urrego, B. 1994. Soil chemical change during three decades in an old-field loblolly pine (*Pinus taeda* L.) ecosystem. *Ecology*, **75**(5): 1463–1473. doi:10.2307/1937469.
- Silveri, A., Dunwiddie, P.W., and Michaels, H.J. 2001. Logging and edaphic factors in the invasion of an Asian woody vine in a mesic North American forest. *Biol. Invasions*, **3**(4): 379–389. doi:10.1023/A:1015898818452.
- Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Schell, L. D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M., and Son, Y. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecol. Monogr.* **69**(1): 25–46. doi:10.1890/0012-9615(1999)069[0025:EPSIHS]2.0.CO;2.
- Thomas, W.A. 1969. Accumulation and cycling of calcium by dogwood trees. *Ecol. Monogr.* **39**(2): 101–120. doi:10.2307/1950739.
- Vitousek, P.M., D'Antonio, C.M., Loope, L.L., and Westbrooks, R. 1996. Biological invasions as global environmental change. *Am. Sci.* **84**(5): 468–478.
- Von Holle, B., and Motzkin, G. 2007. Historical land use and environmental determinants of nonnative plant distribution in coastal southern New England. *Biol. Conserv.* **136**(1): 33–43. doi:10.1016/j.biocon.2006.10.044.
- Watkins, R.Z., Chen, J.Q., Pickens, J., and Brososke, K.D. 2003. Effects of forest roads on understory plants in a managed hardwood landscape. *Conserv. Biol.* **17**(2): 411–419. doi:10.1046/j.1523-1739.2003.01285.x.