

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

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Abstract Determining what factors explain the distribution of non-native invasive plants that can spread in forest-dominated landscapes could advance understanding of the invasion process and identify forest areas most susceptible to invasion. We conducted roadside surveys to determine the presence and abundance of 15 non-native plant species known to invade forests in western North Carolina, USA. Generalized linear models were used to examine how contemporary and historic land use, landscape context, and topography influenced presence and abundance of the species at local and regional scales. The most commonly encountered species were *Microstegium vimineum*, *Rosa multiflora*, *Lonicera japonica*, *Celastrus orbiculatus*, *Ligustrum sinense*, and *Dioscorea oppositifolia*. 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 focal species were also more common in watersheds at lower elevation and with less forest cover. At the local scale, elevation was important for explaining the species' presence, but forest cover and land-use history were more important for explaining their abundance. In general, species were more common in plots with less forest cover and more area reforested since the 1940s. Our results underscore the importance of considering both the contemporary landscape and historic land use to understand plant invasion in forest-dominated landscapes.

Keywords Exotic species · Blue Ridge · Roads · City center · *Microstegium vimineum* · *Rosa multiflora* · *Lonicera japonica* · *Celastrus orbiculatus* · *Ligustrum sinense* · *Dioscorea oppositifolia*

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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). Numerous factors have been implicated, but there is no simple or universal answer. Life history traits of non-native species can play a major role in determining their

invasion success (Rejmánek and Richardson 1996; Kolar and Lodge 2001). Moreover, the biotic community (e.g., predators, competitors, and mutualists) and abiotic characteristics of ecosystems in the introduced range influence invasibility (Richardson et al. 2000; Shea and Chesson 2002). The factors that determine invasion success therefore may vary among functional groups or taxa (Rejmánek and Richardson 1996; Tilman 1997), geographic regions (Lonsdale 1999; Pysek and Richardson 2006), or scales of analysis (Stohlgren et al. 2002; Knight and Reich 2005; Brown et al. 2008).

Invasive plants 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; Gelbard and Belnap 2003) and residential development (Alston and Richardson 2006; Kowarik 2008) can provide suitable habitat for invasive plants. Recent research has also highlighted the influence of historic land use on plant invasions, with invasive plants more often present in historically altered forests than those without a human disturbance history (Lundgren et al. 2004; 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 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 likely pose the greatest threat to native biota in forest-dominated landscapes. Among the vast pool of species introduced for horticulture, 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; Sanford et al. 2003), often resulting in comparatively low population densities in forests that has led some to regard forests as resistant to non-native plant invasion (Crawley 1987; Rejmánek 1989). 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 many latent invaders (Webb et al. 2000; 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; Christen and Matlack 2006). Roadside populations may provide the propagule pressure necessary for invasion of adjacent forest. Most plant species experience low germination and seedling survival in the forest understory (Valladares and Niinemets 2008) and therefore require substantial propagule pressure for successful establishment (Lonsdale 1999). 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.

We determined the distribution and abundance of a suite of forest-adapted non-native invasive plants along roadsides in western North Carolina. We used generalized linear models to address the following 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? We conducted analyses at both local and regional scales. At the local scale, we expected invasive plants to respond more strongly to local land use/cover, land-use history, and landform. At the regional scale we expected invasive plants to respond more strongly to landscape context (e.g., distance from the regional city center and regional forest cover) and elevation. Different factors may affect invasion at different scales, resulting in complex patterns of invasibility that give rise to heterogeneous distributions of invasive plants. Multi-scale analyses may therefore be necessary to understand current patterns of plant invasion in forested landscapes and predict future spread.

Methods

Study area

The study was conducted in the French Broad River Basin in Madison, Buncombe, Henderson, and

Transylvania Counties of western North Carolina, USA (Fig. S1 in Supplementary material). Situated in the Blue Ridge Physiographic Province, the region is characterized by steep terrain, expansive forest, and high biological diversity. Elevation is from 350 to 1900 m. Dominant 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 coves (SAMAB 1996). Bedrock geology is late Precambrian in origin and predominantly metamorphic. Gneisses and schists are common throughout the basin, with interspersed granitic intrusions (Carpenter 1970).

Widespread European settlement in the region began in the late 1700s, resulting in forest clearing for agriculture primarily along rivers and livestock grazing 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. World War II marked the beginning of an out-migration period, resulting in widespread agricultural abandonment and the regeneration of large tracts of forest that characterize the region today. Forest cover has continued to increase despite recent exurban development (Wear and Bolstad 1998) and associated expansions of road networks. 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 identified 15 non-native invasive plant species (Table 1) that were of concern in the study region. Sampling for these focal species was conducted between June and August 2007. We selected 25 second- and third-order watersheds to represent a range of forest cover (63–99%) and development intensity representative of the study region (Fig. S1 in Supplementary material). Watersheds varied from 700 to 1500 ha; 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. Invasive plant cover was measured in 1-m² quadrats placed every 3 m on both sides of the transects (40 quadrats per plot).

GIS-derived data

Watershed-level variables

The same set of GIS-derived explanatory variables was used in all watershed-level models. Minimum elevation and mean aspect were derived from digital elevation models (DEMs). Minimum elevation was taken as the elevation at the lowest point in a watershed and was chosen to minimize correlation with other explanatory variables (Table 2a). Mean aspect was derived from 30-m 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): $I = \cos(22.5^\circ - \theta) + 1$, where 22.5° is considered to have the lowest insolation. Index values were averaged across all raster cells in a watershed to describe the watershed's predominant aspect. The proportion of each watershed in forest cover was calculated from the 2001 National Land Cover Dataset (NLCD). Forest regrowth was included as a land-use history variable and was calculated by extracting the non-forest areas from 1940s USGS 7.5-min quadrangle maps and overlaying the 2001 NLCD to determine proportions of watersheds that have regrown to forest since the 1940s. Distance to city center was measured as the distance from the centroid of each watershed to Asheville, NC. Edge density, road density, and building density were excluded due to high (negative) correlations with forest cover (Table 2a).

Plot-level variables

Plot-level models were also fitted using a set of GIS-derived explanatory variables. Plot elevation was extracted from 30-m DEMs. Distance to stream was meant to describe landform position, with plots closer to streams occupying 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.

Table 1 Focal non-native invasive plant species

Species name (common name)	Growth form	Escaped cultivar? (Y/N)	Non-human dispersal mechanisms	% Plots with species	% Water-sheds with species	Mean cover (%)	Max. % plot cover
<i>Ailanthus altissima</i> (tree of heaven)	Deciduous tree	Y	Wind, water	6.5	52	0.37	25.0
<i>Albizia julibrissin</i> (silktree/mimosa)	Deciduous tree	Y	Mammals, water	5.1	64	0.04	9.8
<i>Alliaria petiolata</i> (garlic mustard)	Biennial forb	?	Gravity, water	2.9	24	0.02	7.2
<i>Berberis thunbergii</i> (Japanese barberry)	Shrub	Y	Birds, mammals	3.1	36	0.004	1.0
<i>Celastrus orbiculatus</i> (Oriental bittersweet)	Woody vine	Y	Birds	52.5	100	2.54	40.9
<i>Dioscorea oppositifolia</i> (Chinese yam)	Vine	Y	Water	16.6	100	0.32	20.9
<i>Elaeagnus umbellata</i> (autumn olive)	Shrub	Y	Birds, mammals	5.1	32	0.25	43.9
<i>Ligustrum sinense</i> (Chinese privet)	Shrub	Y	Birds, mammals	31.2	96	0.71	32.0
<i>Lonicera japonica</i> (Japanese honeysuckle)	Woody vine	Y	Birds, mammals	58.1	96	4.77	51.9
<i>Microstegium vimineum</i> (Japanese stiltgrass)	Annual grass	N	Gravity, water	84.0	100	2.75	35.0
<i>Miscanthus sinensis</i> (Chinese silvergrass)	Perennial grass	Y	Wind	14.2	56	0.38	48.8
<i>Paulownia tomentosa</i> (princesstree)	Deciduous tree	Y	Wind, water	6.0	72	0.23	50.6
<i>Polygonum cuspidatum</i> (Japanese knotweed)	Perennial forb	Y	Wind, water	6.2	48	0.34	32.8
<i>Pueraria montana</i> (kudzu)	Woody vine	Y	Wind, water, mammals	2.0	32	0.22	32.3
<i>Rosa multiflora</i> (multiflora rose)	Shrub	Y	Birds, mammals	68.5	100	2.88	57.0
All focal species	–	–	–	–	–	15.82	91.5

The percent of plots ($N = 613$) and watersheds ($N = 25$) in which the species were present are given as estimates of their regional abundance. Mean percent cover is the average cover for the species across all plots. The mean percent cover for all focal species is the average aggregate cover across all plots. Max. % plot cover is the maximum cover for a species (or all focal species together) observed in any single plot

The “?” indicates that it is uncertain whether or not garlic mustard was introduced as an escaped cultivar

Streams were defined as having a flow accumulation >100 pixels.

We included three local landscape context variables in the plot-level models (forest cover, forest regrowth, and number of developed parcels), which 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 minimizing overlap with adjacent plots. Forest cover and regrowth proportions were calculated for the 5-ha area as described for the watershed-

level analysis. The number of developed parcels (i.e., having at least one maintained building based on county property records) around each plot was used as a proxy for building density. For each plot, we tallied the number of developed parcels contained within or intersected by the 126-m radius.

Data analysis

Analyses were performed at the regional (watershed-level) and local (plot-level) scales using generalized

Table 2 Correlation tables for watershed-level (a) and plot-level (b) explanatory variables

	Edge density	Road density	Forest regrow ^a	Ashe. dist. ^a	Min. elev. ^a	Max. elev.	Mean elev.	Mean aspect ^a	Building density
(a) Watershed-level									
Forest cover ^a	-0.79***	-0.69***	ns	ns	0.49*	0.74***	0.77***	ns	-0.68***
Edge density		0.45*	ns	ns	-0.56*	-0.72***	-0.77***	ns	ns
Road density			ns	-0.41*	ns	-0.43*	-0.48*	ns	0.88***
Forest regrow ^a				ns	ns	ns	ns	ns	ns
Ashe. dist. ^a					ns	ns	ns	ns	-0.53**
Min. elev. ^a						0.66***	0.82***	ns	ns
Max. elev.							0.93***	ns	-0.39*
Mean elev.								ns	-0.47*
Mean aspect ^a									ns
		Distance to stream ^a		Developed parcels ^a		Forest cover ^a		Forest regrow ^a	
(b) Plot-level									
Elevation ^a		0.266***		-0.318***		0.406***		-0.189***	
Distance to stream ^a				ns		0.150***		-0.307***	
Developed parcels ^a						-0.411***		-0.092*	
Forest cover ^a								0.175***	

All variables were derived from GIS-based data. For the watershed-level variables, “forest regrow” refers to the proportion of a watershed that has regrown to forest since the 1940s and “Ashe. dist.” refers to the distance from a watershed’s centroid to the regional city center, Asheville, NC. For the plot-level variables, developed parcels, forest cover, and forest regrowth are measured within a 5-ha area surrounding each plot. Pearson’s correlation values significant at $P < 0.05$ are shown ($N = 25$ watersheds and $N = 613$ plots, respectively)

ns non-significant

* $P < 0.5$, ** $P < 0.01$, *** $P < 0.001$

^a Explanatory variables included in the model selection process

linear models 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 second order Akaike information criterion (AIC_c) for model selection (Burnham and Anderson 1998). All possible models (32 per model set) were considered as candidate models. Akaike weights (w_i) were calculated for all candidate models. We calculated the relative variable importance of each explanatory variable in a given model set by summing the Akaike weights of all candidate models in which that variable was included (Burnham and Anderson 1998). Given the number of model sets we wished to compare, we considered the “best” model in each set to be the one with the lowest AIC_c ($\Delta_i = 0$). For reference, we’ve included all comparable “good” models ($\Delta_i < 2$) from watershed-level model selection (Table S1) and plot-

level model selection (Table S2) as Supplementary materials.

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 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 (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 species. The linear mixed models were fitted using the *lme* function (Pinheiro and Bates 2000) with maximum likelihood parameter estimation. We also used generalized linear mixed effects models (GLMMs) to analyze presence/absence for each of the six most common focal species. These 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 models only included plots in which the species were present ($88 < N < 502$). 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 common focal invasive species each occurred in >95% of watersheds and >16% of plots (see Table 1). *Microstegium vimineum* was the most common, occurring in all watersheds and in 84% of plots. *Rosa multiflora*, *Lonicera japonica*, and *Celastrus orbiculatus* were the next most common species, occurring in 69, 58, and 53% of plots, respectively. *Lonicera* also had the greatest overall cover (4.8%). *Ligustrum sinense* was present in 31% of plots. Although only in 17% of plots, *Dioscorea oppositifolia* occurred in every watershed. The mean aggregate cover for all focal species was 15.8%.

Watershed-level model selection results

At the regional scale, focal species total cover was greater in watersheds at lower elevation and closer to Asheville, NC. The best model for focal species

richness included only distance to Asheville, with more of the species encountered in watersheds closer to Asheville (Table 3). The other explanatory variables had considerably lower importance for total cover and focal species richness models (Fig. 1a).

Among the plot frequency models, minimum elevation, distance to city center, and forest cover had the highest relative variable importance (Fig. 1b). *Ligustrum*, *Lonicera*, and *Microstegium* were more frequently encountered in watersheds at lower elevation (Table 3). *Celastrus*, *Ligustrum*, *Lonicera*, and *Rosa* were encountered more frequently in watersheds closer to Asheville. *Celastrus*, *Ligustrum*, *Lonicera*, and *Rosa* were encountered more frequently in watersheds with less forest cover. Mean aspect was included in the best model for *M. vimineum*, with higher plot frequency in watersheds with more southwesterly aspects (higher insolation). *Rosa* was encountered more frequently in watersheds with more forest regrowth.

Among the watershed-level presence/absence models, distance to city center was the most important explanatory variable (Fig. 1c). *Ailanthus altissima*, *Berberis thunbergii*, *Elaeagnus umbellata*, and *Paulownia tomentosa* were more likely present in watersheds closer to Asheville (Table 3). *Alliaria petiolata*, was more likely present in watersheds further from Asheville. Elevation was included in the best model for *Elaeagnus*, with greater likelihood of presence in watersheds at lower elevation. *Albizia julibrissin* was more likely present in watersheds with less forest cover. Forest regrowth was included in the model for *Elaeagnus*, 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. The best models for *Miscanthus sinensis*, *Polygonum cuspidatum*, and *Pueraria montana* included only the intercept term (Table 3).

Plot-level model selection results

Focal species total cover and richness were greater at lower elevations and in plots with more developed parcels, less forest cover, and more forest regrowth in the surrounding 5-ha area (Table 4). Distance to stream had a low variable importance for total cover and focal species richness models (Fig. 2a).

Among the plot-level presence/absence models, elevation was one of the most important variables (Fig. 2b). All six of the most common species were

Table 3 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)

Model set (response variables)	Intercept and model coefficients for explanatory variables in the best model for each model set						K	w _i
	Intercept	Elev	Aspect	Ashdist	Forest	Regrow		
Focal spp. total cover	0.55	−0.0004	–	−0.01	–	–	4	0.307
Focal spp. richness	13.24	–	–	−0.13	–	–	3	0.319
Plot frequency models								
<i>Celastrus orbiculatus</i>	2.91	–	–	−0.04	−1.03	–	4	0.495
<i>Dioscorea oppositifolia</i>	0.40	–	–	–	–	–	2	0.183
<i>Ligustrum sinense</i>	2.65	−0.002	–	−0.01	−0.68	–	5	0.255
<i>Lonicera japonica</i>	3.37	−0.002	–	−0.01	−0.67	–	5	0.401
<i>Microstegium vimineum</i>	2.49	−0.001	−0.53	–	–	–	4	0.214
<i>Rosa multiflora</i>	2.30	–	–	−0.01	−1.14	0.54	5	0.233
Presence/absence models								
<i>Ailanthus altissima</i>	3.35	–	–	−0.13	–	–	3	0.355
<i>Albizia julibrissin</i>	16.23	–	–	–	−13.50	–	3	0.370
<i>Alliaria petiolata</i>	−4.79	–	–	0.13	–	–	3	0.157
<i>Berberis thunbergii</i>	2.37	–	–	−0.13	–	–	3	0.162
<i>Elaeagnus umbellata</i>	50.03	−0.05	–	−0.40	–	−33.41	5	0.304
<i>Miscanthus sinense</i>	0.24	–	–	–	–	–	2	0.181
<i>Paulownia tomentosa</i>	5.50	–	–	−0.17	–	–	3	0.299
<i>Polygonum cuspidatum</i>	−0.08	–	–	–	–	–	2	0.198
<i>Pueraria montana</i>	−0.75	–	–	–	–	–	2	0.255

The model with the lowest AIC_c value in each model set is shown. 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

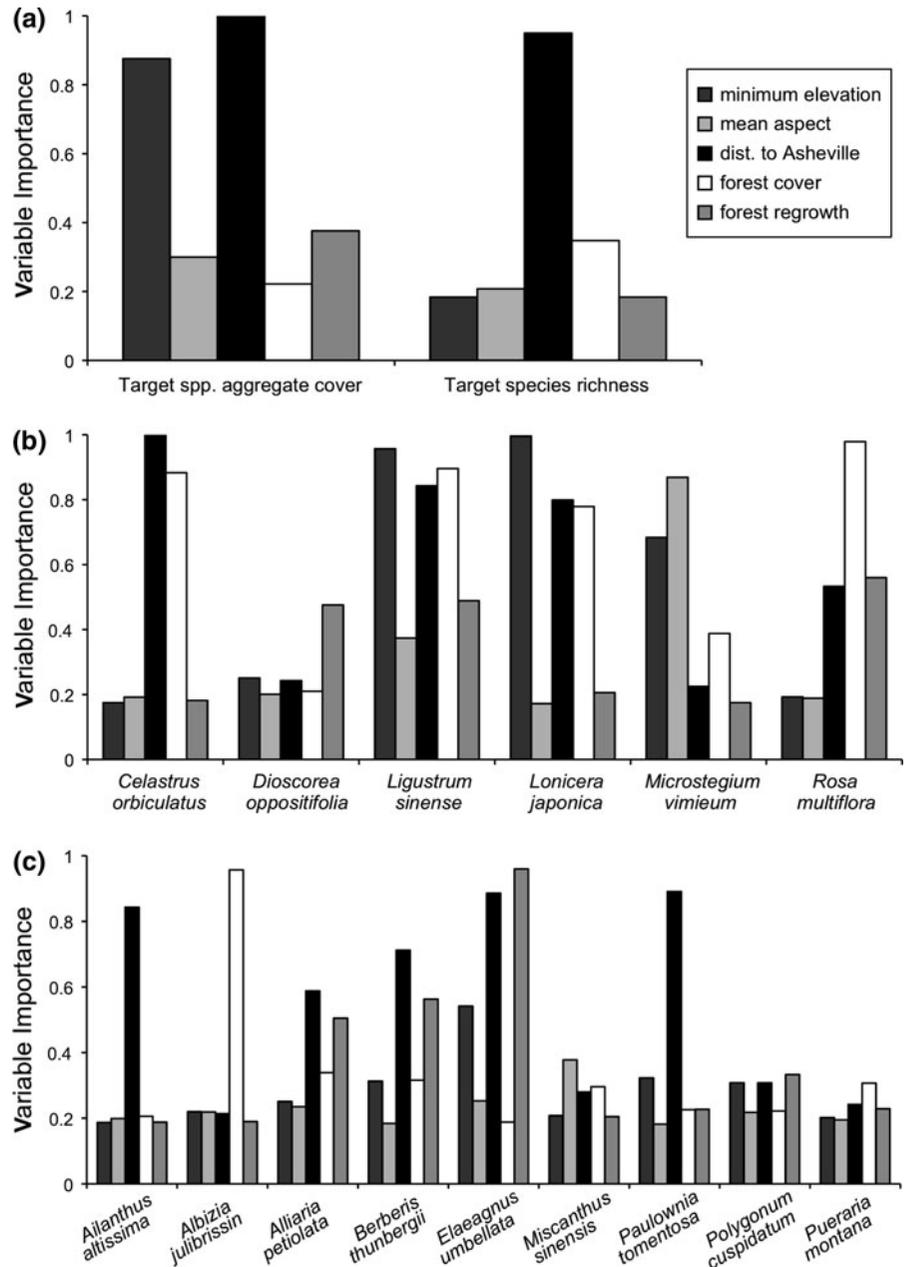
elev minimum elevation of watersheds, *aspect* mean aspect, or northeasterliness of watershed orientation, *ashdist* distance from watershed centroid to city center, Asheville, NC, *forest* proportion of watershed in forest cover, *regrow* proportion of watershed regrown to forest since the 1940s

more likely present at lower elevations (Table 4). Forest cover was also important (Fig. 2b). Presence of *Celastrus*, *Ligustrum*, *Lonicera*, and *Rosa* were negatively correlated with forest cover, but *Microstegium* presence was positively correlated. Forest regrowth was included in the best models for *Ligustrum*, *Lonicera*, *Microstegium*, and *Rosa*, with higher likelihood of presence in plots with greater forest regrowth in their vicinity. Distance to stream was included as an important explanatory variable in three of the best models (Table 4). For *Celastrus*, there was a positive relationship between distance to stream and likelihood of presence. For *Dioscorea* and *Microstegium*, there was a negative relationship, with plots closer to streams having a greater likelihood of presence. In four of the best models (*Celastrus*,

Dioscorea, *Ligustrum*, and *Rosa*), likelihood of presence was greater with more developed parcels in the plot vicinity.

Among the plot-level abundance (percent cover) models, forest cover and forest regrowth were the most important variables (Fig. 2c). Forest cover was included in four of the best models (Table 4). *Ligustrum*, *Lonicera*, and *Rosa* had lower abundance in plots with greater proportion of forest around them, while *Microstegium* abundance was positively related to forest cover. Forest regrowth was included in the best models for *Celastrus*, *Ligustrum*, *Lonicera*, and *Rosa*; abundance was greater in plots with more forest regrowth in the surrounding 5-ha area. The abundance of *Celastrus* and *Microstegium* was greater in plots with more developed parcels around

Fig. 1 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



them; however, in the best abundance model for *Lonicera*, cover was higher in plots with fewer developed parcels. Elevation was included only in the *Lonicera* best model, with greater cover in plots at lower elevation. Distance to stream was included in the best models for *Lonicera* and *Microstegium* (greater cover further from streams), however the variable had low relative importance (Fig. 2c).

Discussion

The distribution of the focal non-native plant species was influenced by contemporary land use, landscape context, historic land use, and topography. The relative importance of factors varied with the scale of analysis. We considered three explanatory variables at local and regional scales: elevation, forest

Table 4 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

Model set (response variables)	Intercept and model coefficients for explanatory variables in the best model for each model set						N	K	w_i
	Intercept	Elev	Strdist	Dparc	Forest	Regrow			
Focal spp. total cover:	3.54	-0.48	-	0.02	-0.12	0.17	613	7	0.299
Focal spp. richness:	34.20	-4.62	-	0.19	-0.85	1.21	613	7	0.441
<i>Celastrus orbiculatus</i>									
Pres/Abs	14.73	-2.23	0.23	0.31	-1.15	-	613	7	0.183
Cover	0.07	-	-	0.02	-	0.12	265	5	0.204
<i>Dioscorea oppositifolia</i>									
Pres/Abs	11.15	-1.81	-0.38	0.22	-	-	613	6	0.177
Cover	0.11	-	-	-	-	-	88	3	0.190
<i>Ligustrum sinense</i>									
Pres/Abs	34.90	-5.37	-	0.32	-2.36	2.20	613	7	0.422
Cover	0.17	-	-	-	-0.12	0.12	127	5	0.194
<i>Lonicera japonica</i>									
Pres/Abs	90.27	-13.25	-	-	-2.85	1.68	613	6	0.551
Cover	2.22	-0.29	0.01	-0.02	-0.19	0.17	338	8	0.298
<i>Microstegium vimineum</i>									
Pres/Abs	42.21	-6.09	-0.44	-	1.98	0.90	613	7	0.366
Cover	-0.01	-	0.01	0.03	0.08	-	502	6	0.269
<i>Rosa multiflora</i>									
Pres/Abs	38.13	-5.60	-	0.26	-1.20	1.89	613	7	0.396
Cover	0.20	-	-	-	-0.07	0.10	341	5	0.193

The species cover models only include plots in which the respective species were present ($88 < N < 502$). The model with the lowest AIC_c value in each model set is shown. 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

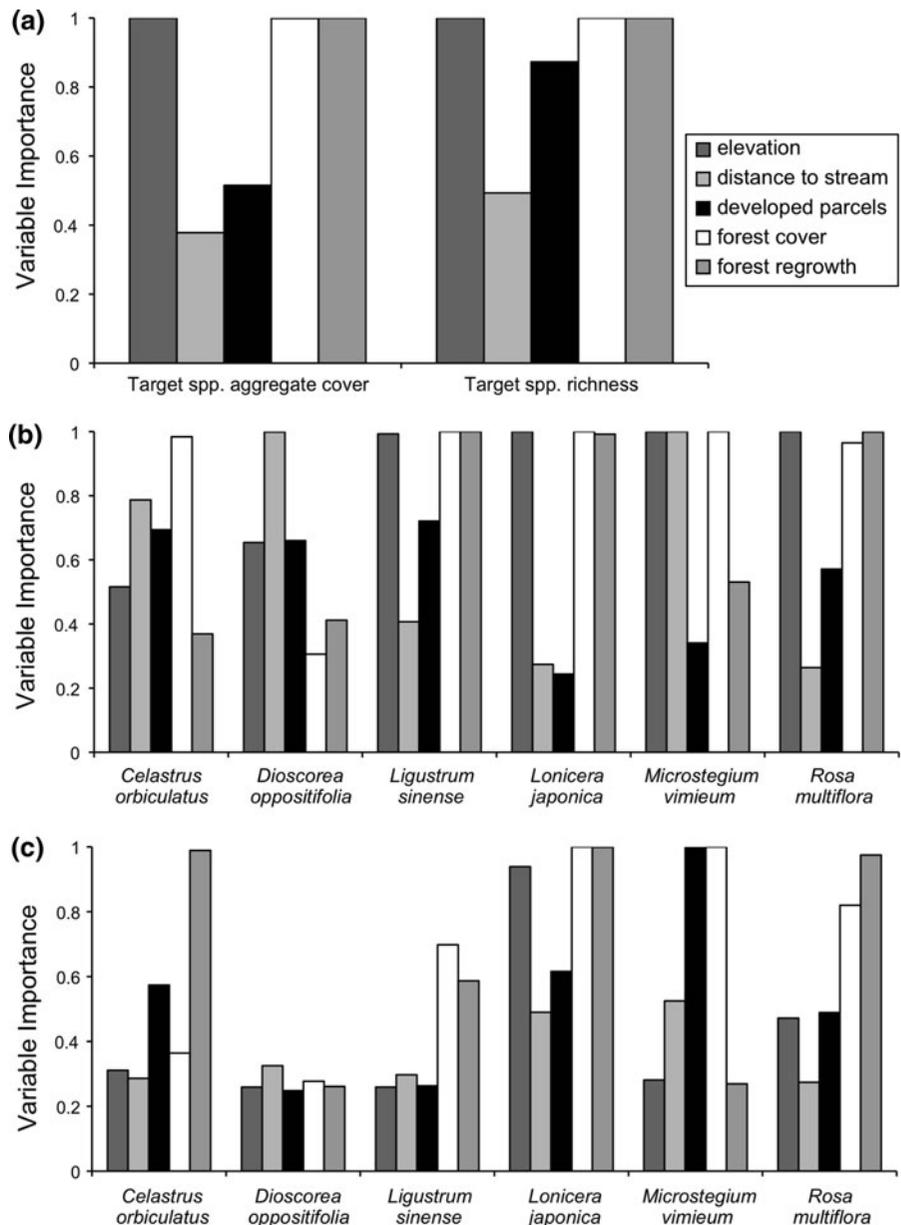
elev elevation of plot, *strdist* distance from plot center to nearest stream, *dparc* number of developed parcels within 126 m of plot, *forest* proportion of 5-ha area around plot in forest cover, *regrow* proportion of 5-ha area around plot regrown to forest since the 1940s

cover, and forest regrowth. At the regional 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. However, at the local scale elevation was more important for explaining presence of focal species than their abundance, suggesting that while elevation may play a role in determining broad-scale distributions of invasive plants, other factors may determine their abundance at finer scales. Forest cover was particularly important in the plot-level models, suggesting that the focal species responded more strongly to land cover patterns at finer scales. Land-use history was also more important in explaining patterns of invasion at the local scale than at the

watershed scale, suggesting that focal species responded to local site conditions influenced by land-use legacies rather than broader-scale patterns produced by historic land use.

Distance to city center (Asheville, NC) was considered only at the regional scale but was the most important variable at that scale. With the exception of *Alliaria* (whose distribution is primarily north of the study area), 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; Albright et al. 2009). The city center may act as the regional site of introduction for many escaped horticultural species (Reichard and White 2001). Local invasive abundance may be related to its residence time

Fig. 2 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



(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. Alternatively, factors associated with proximity to the city such as road density, development, and fragmentation 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 high traffic volume might also facilitate more

rapid spread of propagules closer to the city center (Forman and Alexander 1998; von der Lippe and Kowarik 2007).

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 shown that land-use

history can increase non-native plant invasion in forested regions (Lundgren et al. 2004; DeGasperis and Motzkin 2007; Von Holle and Motzkin 2007), but the mechanisms underlying its influence on invasion are poorly understood. Species might have become established around the time of abandonment and persisted in the regrown areas. Alternatively, the species might be responding to changes in site conditions caused by the former land use or those generated by the ensuing 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. Our plot-level model results offer insight into such differences by comparing the effects of factors on both presence/absence (establishment) and percent cover (abundance) of the six most common focal species. For example, elevation was important for explaining presence/absence of all six species, whereas it was included in the best abundance model only for *Lonicera*. Invasives were more common at lower elevations, a pattern that is commonly observed in mountainous regions (Wilson et al. 1992; Stohlgren et al. 2002). In some cases, elevation may influence invasibility due to differences in temperature and length of growing season that preclude establishment of certain species. However, the relatively modest elevations (<2000 m) in the region are unlikely to play a large role in limiting the distribution of many of these invasive plants that also occur at higher latitudes in North America. Likely source populations in the region tend to be at lower elevations for many species, perhaps related to the higher land-use intensity. Regardless of the reasons for elevation's influence on establishment, other factors seem to play a larger role in determining the abundance of species once they have become established. For example, the abundance of *Celastrus* was strongly influenced by land-use history (forest regrowth). While other factors were more important for determining where *Celastrus* 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 more time to proliferate.

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, *Lonicera*, *Ligustrum*, and *Rosa* had remarkably similar responses to the explanatory variables, suggesting that these three species could be grouped for management purposes. However, *Microstegium* behaved quite differently from the other species. It was the only species that showed a positive correlation with forest cover at the plot level. Due to its high shade tolerance (Horton and Neufeld 1998) this annual C4 grass may warrant special attention as a threat to forest understory communities in the eastern US (Leicht et al. 2005). It is also noteworthy that *Microstegium* 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 in forested areas with minimal clearing of the overstory (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 *Microstegium*) may seem counterintuitive. However, while the focal species are capable of spread in forested landscapes, they respond favorably to disturbance and forest edge conditions. In the forest-dominated study region, areas with comparatively low 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).

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

invasion. 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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References

- Albright TP, Anderson DP, Keuler NS, Pearson SM, Turner MG (2009) The spatial legacy of introduction: *Celastrus orbiculatus* in the southern Appalachians, USA. *J Appl Ecol* 46:1229–1238
- Alston KP, Richardson DM (2006) The roles of habitat features, disturbance, and distance from putative source populations in structuring alien plant invasions at the urban/wildland interface on the Cape Peninsula, South Africa. *Biol Conserv* 132:183–198
- Bates D, Sarkar D (2006) lme4: Linear mixed-effects models using Eigen and Eigen. R package version 0.995-2
- Beers TW, Dress PE, Wensel LC (1966) Aspect transformation in site productivity research. *J For* 64:691–692
- Brothers TS, Spingarn A (1992) Forest fragmentation and alien plant invasion of central Indiana old-growth forests. *Conserv Biol* 6:91–100
- Brown KA, Spector S, Wu W (2008) Multi-scale analysis of species introductions: combining landscape and demographic models to improve management decisions about non-native species. *J Appl Ecol* 45:1639–1648
- Buckley YM, Anderson S, Catterall CP, Corlett RT, Engel T, Gosper CR, Nathan R, Richardson DM, Setter M, Spiegel O, Vivian-Smith G, Voight FA, Weir JES, Westcott DA (2006) Management of plant invasions mediated by frugivore interactions. *J Appl Ecol* 43:848–857
- Burnham KP, Anderson DR (1998) Model selection and inference: a practical information-theoretic approach. Springer, New York
- Carpenter RH (1970) Metamorphic history of the Blue Ridge province of Tennessee and North Carolina. *Geol Soc Am Bull* 81:749–761
- Christen D, Matlack G (2006) The role of roadsides in plant invasions: a demographic approach. *Conserv Biol* 20:385–391
- Crawley MJ (1987) What makes a community invulnerable? In: Gray AJ, Crawley MJ, Edwards PJ (eds) Colonization, succession, and stability. Blackwell Scientific, Oxford, pp 429–453
- Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. *J Ecol* 88:528–534
- DeGasperis BG, Motzkin G (2007) Windows of opportunity: historical and ecological controls on *Berberis thunbergii* invasions. *Ecology* 88:3115–3125
- Elton CS (1958) The ecology of invasions by animals and plants. University of Chicago Press, Chicago
- ESRI (2006) ArcGIS, vol. 9.1. Environmental Systems Research Institute, Redlands, CA
- Forman RTT, Alexander LE (1998) Roads and their major ecological effects. *Annu Rev Ecol Syst* 29:207–231
- Gelbard JL, Belnap J (2003) Roads as conduits for exotic plant invasions in a semiarid landscape. *Conserv Biol* 17:420–432
- Gragson TL, Bolstad PV (2006) Land use legacies and the future of southern Appalachia. *Soc Nat Resour* 19:175–190
- Hobbs RJ, Huenneke LF (1992) Disturbance, diversity, and invasion: implications for conservation. *Conserv Biol* 6:324–337
- Horton JL, Neufeld HS (1998) Photosynthetic responses of *Microstegium vimineum* (Trin.) A. Camus, a shade-tolerant, C-4 grass, to variable light environments. *Oecologia* 114:11–19
- Kitajima K (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* 98:419–428
- Knight KS, Reich PB (2005) Opposite relationships between invasibility and native species richness at patch versus landscape scales. *Oikos* 109:81–88
- Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. *Trends Ecol Evol* 16:199–204
- Kowarik I (2008) On the role of alien species in urban flora and vegetation. In: Marzluff JM, Shulenberger E, Endlicher W, Alberti M, Bradley G, Ryan C, ZumBrunnen C, Simon U (eds) Urban ecology: an international perspective on the interaction between humans and nature. Springer, New York, pp 321–338
- Leicht SA, Silander JA, Greenwood K (2005) Assessing the competitive ability of Japanese stilt grass, *Microstegium vimineum* (Trin.) A. Camus. *J Torrey Bot Soc* 132:573–580
- Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology* 80:1522–1536
- Lundgren MR, Small CJ, Dreyer GD (2004) Influence of land use and site characteristics on invasive plant abundance in the Quinebaug Highlands of southern New England. *North East Nat* 11:313–332
- Martin PH, Canham CD, Marks PL (2009) Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. *Front Ecol Environ* 7:142–149
- Parendes LA, Jones JA (2000) Role of light availability and dispersal in exotic plant invasion along roads and streams in the H. J. Andrews Experimental Forest, Oregon. *Conserv Biol* 14:64–75
- Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-Plus. Springer, New York
- Pysek P, Richardson D (2006) The biogeography of naturalization in alien plants. *J Biogeogr* 33:2040–2050
- R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Reichard SH, White P (2001) Horticulture as a pathway of invasive plant introductions in the United States. *Bioscience* 51:103–113

- Rejmánek M (1989) Invasibility of plant communities. In: Drake JA, diCasti F, Groves R (eds) *Biological invasions: a global perspective*. Wiley and Sons, Chichester, pp 369–388
- Rejmánek M, Richardson DM (1996) What attributes make some plant species more invasive? *Ecology* 77:1655–1661
- Richardson DM, Allsopp N, D’Antonio CM, Milton SJ, Rejmánek M (2000) Plant invasions—the role of mutualisms. *Biol Rev* 75:65–93
- SAMAB (1996) The Southern Appalachian assessment summary report. U.S. Department of Agriculture Forest Service, Southern Region, Atlanta
- Sanford NL, Harrington RA, Fownes JH (2003) Survival and growth of native and alien woody seedlings in open and understory environments. *For Ecol Manage* 183:377–385
- Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. *Trends Ecol Evol* 17:170–176
- Stohlgren TJ, Chong GW, Schell LD, Rimar KA, Otsuki Y, Lee M, Kalkhan MA, Villa CA (2002) Assessing vulnerability to invasion by nonnative plant species at multiple spatial scales. *Environ Manage* 29:566–577
- Tikka PM, Hogmander H, Koski PS (2001) Road and railway verges serve as dispersal corridors for grassland plants. *Landscape Ecol* 16:659–666
- Tilman D (1997) Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78:81–92
- Turner MG, Pearson SM, Bolstad P, Wear DN (2003) Effects of land-cover change on spatial pattern of forest communities in the Southern Appalachian Mountains (USA). *Landscape Ecol* 18:449–464
- Valladares F, Niinemets U (2008) Shade tolerance, a key plant feature of complex nature and consequences. *Annu Rev Ecol Evol Syst* 39:237–257
- von der Lippe M, Kowarik I (2007) Long-distance dispersal of plants by vehicles as a driver of plant invasions. *Conserv Biol* 21:986–996
- Von Holle B, Motzkin G (2007) Historical land use and environmental determinants of nonnative plant distribution in coastal southern New England. *Biol Conserv* 136:33–43
- Wear DN, Bolstad P (1998) Land-use changes in Southern Appalachian landscapes: spatial analysis and forecast evaluation. *Ecosystems* 1:575–594
- Webb S, Dwyer M, Kaunzinger C, Wyckoff P (2000) The myth of the resilient forest: case study of the invasive Norway maple (*Acer platanoides*). *Rhodora* 102:332–354
- Wilson JB, Rapson GL, Sykes MT, Watkins AJ, Williams PA (1992) Distribution and climatic correlations of some exotic species along roadsides in South Island, New Zealand. *J Biogeogr* 19:183–193
- Wilson JR, Richardson DM, Rouget M, Proches S, Amis MA, Henderson L, Thuiller W (2007) Residence time and potential range: crucial considerations in modelling plant invasions. *Divers Distrib* 13:11–22
- With KA (2002) The landscape ecology of invasive spread. *Conserv Biol* 16:1192–1203