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Invasibility of mature and 15-year-old deciduous forests by exotic plants

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Abstract

High species richness, resource availability and disturbance are community characteristics associated with forest invasibility. We categorized commonly measured community variables, including species composition, topography, and landscape features, within both mature and 15-year-old clearcuts in West Virginia, USA. We evaluated the importance of each variable for predicting the degree of forest invasion by early-establishing exotic invasive plants. Biotic variables, including overall richness (excluding exotic invasive species) and mutually exclusive native and exotic non-invasive species richness, were the strongest indicators of invasibility. Sites that were located on northeast-facing slopes, more mesic conditions, or in clearcuts were more likely to be invaded by exotic invasive plants. Invasion of clearcut sites was more dependent on available microsites (e.g., lower solar radiation, northeast-facing slopes, and lower elevations) within each site than on the condition of the surrounding landscape, whereas invasion into the mature forests was dependent more on the surrounding landscape (e.g., proximity to paved roads). Our results indicate that exotic invasive plant species in our study area respond similarly as other plant species to resource availability and that competitive interactions are relatively unimportant. Current invasion into this landscape is more likely to be a passive reaction to site conditions instead of a driver of change.

Introduction

Anthropogenic influences (e.g., fragmentation and urbanization), disturbance (e.g. harvesting and windthrows) (Lonsdale 1999; Buckley et al. 2002; Pyšek et al. 2002), and resource availability (Burke and Grime 1996; Davis et al. 2000) are characteristics associated with high community invasibility. While anthropogenic influences in the landscape may promote seed dispersal by increasing proximity to seed sources and dispersal corridors, disturbance may promote invasion by increasing resources or reducing potential competitors. The effect of plant community richness, whether it is functional-group or species richness, on community invasibility is likely scale-dependent. Several landscape or regional scale studies show a positive relationship between richness and invasibility (Planty-Tabacchi et al. 1996; Wiser et al. 1998; Higgins et al. 1999; Lonsdale 1999; Stohlgren et al. 1999; but see Robinson et al. 1995) while other smaller scale studies show a negative relationship (Tilman 1997; Symstad 2000; Kennedy et al. 2002). This relationship between richness and invasibility may also be a function of habitat type, i.e., some deserts, grasslands and savannahs exhibit the greatest resistance to invasion (Richardson et al. 1994; Lonsdale 1999; Pyšek et al. 2002). Invasibility defined by habitat type and species richness may in turn coincide with a soil fertility gradient (Howard et al. 2004).

Forest clearcuts temporarily elevate resource availability due to increased nitrogen mineralization caused by increased soil temperature, greater soil aeration, and extreme wetting and drying cycles (Boring et al. 1981). These changes stimulate regeneration of early-successional species, which quickly assimilate excess nitrogen and phosphorus resulting from the harvest and rapidly increase evapotranspiration, adjusting the mineralization rates to pre-harvest levels. Clearcut forests generally recover to pre-cut mineralization rates within 1–2 years (Whittaker et al. 1979; Boring et al. 1981; Phillips and Shure 1990; Attiwill and Adams 1993; Gilliam and Turrill 1993; Gilliam 2002). Forest clearcuts may also temporarily reduce abundance of dominant species that competitively exclude other species prior to the harvest, releasing niche space and increasing colonization rates of early-successional species and possibly exotics (Parendes and Jones 2000; Roberts and Zhu 2002). Species diversity and richness may recover within a relatively short time frame after a clearcut (2–20 years; Halpern and Spies 1995; Gilliam 2002; Roberts and Zhu 2002; but see Meier et al. 1995). However, species composition may not recover for 50 or more years (Leopold and Parker 1985; Mou et al. 1993; Scheller and Mladenoff 2002). This slow recovery is in spite of evident declines in early-successional species (Schuler and Gillepsie 2000; Yorks et al. 2000). Though acting initially as colonizing, early-successional species, some invasive exotic plants are retained in recovering stands through forest maturity (Luken 2003), possibly out-competing native early-successional species and re-colonizers in the process.

While several studies support similar indicators (anthropogenic influences, disturbance, resource availability, and species richness) of invasibility, these studies do not compare the relative importance of such indicators. We suggest organizing potential invasibility indicators into three categories that include relatively easy to measure variables: (1) biotic (e.g., vascular plant species composition, richness, and diversity), (2) non-anthropogenic (e.g. physiography, environmental conditions, such as available space and light), and (3) anthropogenic (e.g., man-made disturbance and landscape features, such as fragmentation and roads) factors. Distinguishing among these factors may facilitate the prioritization of management strategies when predicting forest invasions. Using variables (or potential indicators) that are relatively easy to obtain also makes them more accessible to land managers. Such a synthesis may in turn enable us to better understand the possible mechanisms behind each individual indicator. We address the following question: during early stages of exotic invasive species establishment, what are the most important biotic, non-anthropogenic and anthropogenic factors that define forest community invasibility?

Methods

Study area

We worked in the Cheat Ranger District of the Monongahela National Forest in Tucker County, West Virginia (approximately 39°03′ N and 79°41′ E; Figure 1). The Cheat Ranger District encompasses approximately 47,500 ha. This mixed mesophytic forest is part of the Allegheny Mountain Section of the Unglaciated Allegheny Plateau (Forest Service 1987; Muzika et al. 1999). Vegetation types range from more mesic sites dominated by sugar maple, basswood and beech to relatively xeric sites dominated by oak species (Braun 1950). Precipitation occurs primarily in the growing season averaging about 145 cm/year. Soils are typically well-drained, loamy sands (Forest Service 1987; Muzika et al. 1999).

Most, if not all, of the forests of the Cheat Ranger District were cut and possibly burned between 1879 and 1920 (Clarkson 1964). Grazing records since 1960 are available but imprecise. None of our sites were grazed after 1960, though some of our sample area is located within clearly delineated grazing allotments abandoned between 1951 and 1960, and a few sites are located in poorly delineated or unfenced allotments of the same time period and may have been grazed. Deer browsing has likely varied temporally, but historic differences among the sites are presumed to be small.

Site selection

Twenty-four sites were randomly selected from each of two forest ages: (1) 80-year-old or older

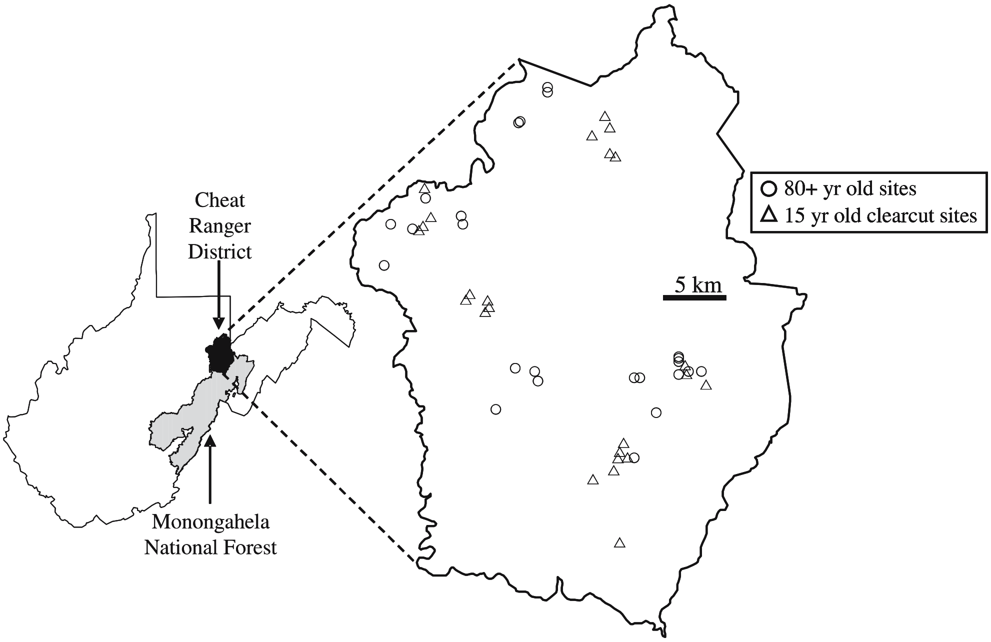

Figure 1. Map of the study site locations for the mature and the 15-year-old clearcuts within the Cheat Ranger District within the Monongahela National Forest, West Virginia, USA.

mature second-growth sites and (2) 15-year-old clearcuts (cut between 1985 and 1989), and stratified by three ecological land types (ELTs, 7–9 of each per forest age), which may also be considered forest types. More recent clearcuts of adequate sample size do not exist due to a decrease in logging in Monongahela National Forest since the mid-1980s. Ecological land types were defined according to Barnes et al. (1982) and Hurst (1994), using physiographic and vegetation information to define potential vegetation types. This finer scale classification (1:15,000) is most useful for defining forest management strategies and evaluating habitats (Host et al. 1996). The chosen ELTs are common in our region and reflect a fertility and moisture gradient. These include sites dominated by (1) *Acer saccharum* Marshall and *Tilia americana* L. and also containing *Laportea canadensis* (L.) Wedd. and/or *Caulophyllum thalictroides* (L.) Michx. in the understory, (ELT 220, more mesic and fertile), (2) *A. saccharum* and *Quercus rubra* L. and also containing *L. canadensis* and/or *C. thalictroides* in the understory, (ELT 230, intermediate), and (3) *Q. rubra* and also containing *Vaccinium* L. sp. and/or *Kalmia latifolia* L. in the understory, (ELT 300, less mesic and fertile). The total area sampled for the mature stands and clearcut stands was 112 and 126 ha, respectively. The closest sites, which varied in size between 2.9 and 9.2 ha, were at least 100 m apart. Some site clustering was evident (Figure 1) and spatial autocorrelation analysis was consequently conducted.

Sampling design

A systematic plot design was used with four 1 m^2 subplots per plot (400 m^2) and one plot every 0.4 ha for each site in June 2001 (mature forest sites) and June 2002 (15-year-old clearcuts). Within each 1 m^2 subplot, percent cover of all herb, shrub and vine species, and percent cover and density of all tree seedlings under 1 m in height were measured. Relative cover (cover of individual species divided by the total cover all species) was used to calculate importance values of the herbs, shrubs and vines, and relative density and relative cover were both used to calculate the importance values of the tree seedlings. These relative values were calculated both with and without the exotic invasive plants. Because we were interested in early-establishing species, we only gathered understory data as described. Data on saplings, small trees and canopy trees were gathered for other studies and confirmed that invasion had not yet occurred in these strata in these sites. In addition to sampling individual subplots, each site was walked for additional understory species that the subplots did not capture.

Surface data, which included percent cover of moss or lichen, rock, coarse woody debris, and bare ground, as well as litter depth (cm) were measured at each 1 m^2 subplot. Slope aspect (linearized using SIN (°−135) +1, where ° is the angular data (Huebner and Vankat 2003), such that larger values were more southwest facing and smaller values were more northeast facing), percent slope inclination, and elevation (m) were measured at each plot center. Instantaneous light measurements of photosynthetically active radiation (PAR in μmol m^{-2} s^{-1}) at each plot center, approximately 1 m above ground, were taken using a quantum meter (Spectrum Technologies, Inc., model BQM) between 0800 and 1700 under similar sky conditions. Each site had one or two plots from which light measurements were taken between 1200 and 1400 (highest expected solar radiation) while the remaining plot light measurements were taken in early morning or late afternoon. Surface data and light estimates were averaged per plot for each site.

Biotic variables

Vascular plant species found at each site were categorized into four mutually exclusive categories (1) invasive exotic plant species (our response variable), (2) exotic non-invasive plant species, (3) native weedy species, and (4) native non-weedy species. Total species counts of each category per site were determined using both plot and site walk-through data. Exotic species were defined using several flora (Fernald 1970; Strausbaugh and Core 1977; Gleason and Cronquist 1993; Rhoads and Block 2000). Determination of invasive exotic species was relatively conservative and was based on species included as a severe threat on multiple Mid-Atlantic state exotic invasive plant species lists (Harmon 1999; Pennsylvania Department of Conservation and Natural Resources 2000; McAvoy 2001; Virginia Department of Conservation and Recreation and Virginia Native Plant Society 2001; Invasive Plant Council of New York 2003; Native Plant Society of New Jersey 2003), a USDA Forest Service list (USDA Forest Service ER 1998), and floras (Strausbaugh and Core 1977; Gleason and Cronquist 1993; Rhoads and Block 2000). The native weeds category was based on several flora and general ecological literature (Fernald 1970; Strausbaugh and Core 1977; Gleason and Cronquist 1993; Rhoads and Block 2000). Species lists by categories are available upon request; nomenclature follows Gleason and Cronquist 1993. Species diversity and richness (excluding exotic invasive plant species) were averaged per plot for each site. Diversity values were calculated using the Shannon index (Shannon and Weaver 1949).

Non-anthropogenic variables

Our chosen non-anthropogenic variables included surface data (percent cover of moss/lichen, bare ground and rock, and litter depth), topography (elevation, slope aspect, and slope inclination, distance to the nearest river or creek (m)), and light (instantaneous PAR) variables. ELT for each site was also used as a categorical variable.

Anthropogenic variables

Two types of anthropogenic variables were measured for each site. The first type, the landscape variables, included distance (m) to nearest paved road, gravel road, open (non-forested) public land area, and open private land area. The second type, the disturbance categorical variables, included whether or not the site was clearcut 15 years ago (two levels) and whether or not the site was grazed or possibly grazed (located in the outer borders of poorly delineated grazing allotment areas; i.e., three levels).

Statistical analysis

The distribution of independent variables were verified for normality and transformed using the $\log_{10}(Z+1)$ transformation. Because spatially autocorrelated data can complicate tests of significance due to the violation of independence (Clifford et al. 1989), we measured the spatial autocorrelation function for each independent variable using a nonparametric approach (Bjørnstad and Falck 2001) in R (R Development Core Team 2004). This approach also incorporates a bootstrap method to generate a distribution of the spatial autocorrelation function (Efron and Tibshirani 1993; Bjørnstad and Falck 2001). Independent variables were considered to be spatially autocorrelated if the median and interquartile range of the function, based on 500 replications, were > 0 as the lag distance (distance between sampled values) approached 0. Independent variables that were spatially autocorrelated were then detrended (Sharov et al. 1996; Paradis et al. 2000) using a second-order polynomial model through stepwise regression (PROC REG, SAS Institute 2004) from which residuals were obtained. The detrended residuals for each spatially autocorrelated variable were used in all analyses.

Analysis of variance was performed on variables with equal variances, while nonparametric ANOVAs were run on three of the variables, which had unequal variances, to compare the 80-year-old sites with the 15-year-old clearcut sites and the three ELTs (PROC GLM, Kruskal–Wallis, PROC NPAR1WAY, SAS Institute 2004).

In order to predict invasibility, four different cumulative logistic regression models (Allison 1999; PROC LOGISTIC, SAS Institute 2004) were run with backwards selection. The response variable (abundance of exotic invasive plants) had four different levels using the ordinal category of zero as a reference value. The four logistic regression models included one containing only biotic variables, a second containing only non-anthropogenic variables, a third containing only anthropogenic variables, and a final combined model containing the most important variables ($p \leq 0.05$) from each of the three separate models. Combining the important variables not only allowed us to make direct comparisons of the different variable types, it also reduced the size (number of variables) of the combined models and the possibility of significant variables by chance alone. All four of these models were run with both the mature and harvested stands combined (48 sites) as well as separately (24 sites each). Due to multicollinearity, ELT could not be included in any models containing topographic variables and the richness and diversity variables could not be included in the same model with each other or with the other plant species categories. Since our sample size was less than 50, we calculated the confidence intervals using profile likelihood instead of Wald χ^2 (Allison 1999). Odds ratios should not be compared across variables or models, only within each variable in each model. We used the standardized estimates to compare the relative importance of each continuous variable within each combined regression model. Only the combined models using the important variables from the separately run biotic, non-anthropogenic, and anthropogenic variable types are presented.

Because sites varied in size, a subset of randomly chosen sites was used to calculate diversity and richness per plot for each site. The subset diversity and richness per plot values produced the same general results for all analyses as using all plots and, thus, are not presented. In addition size was included as a variable in all logistic regression models. In each case, site size was not a significant variable.

Results

There were a total of 252 species and an average plant cover of 11% in the mature sites, and 305 species, with an average plant cover of 5% in the 15-year-old clearcuts. The mature sites had significantly fewer exotic invasive weeds ($F = 18.4$, $p < 0.001$), exotic weeds ($\chi^2 = 21.1$, $p < 0.001$), native weeds ($F = 41.62$, $p < 0.001$), and native species ($F = 5.54$, $p = 0.023$) than the clearcut sites in an ANOVA (Table 1). There were a total of four and 10 different exotic invasive species in the mature and clearcut site, respectively, with *Berberis thunbergii* DC. and *Rosa multiflora* Thunb. as the most common species in both areas. The mature sites also had significantly lower richness per plot ($F = 5.17$, $p = 0.028$) and diversity per plot ($F = 22.5$, $p < 0.001$) than the clearcut sites. The mature sites differed in terms of non-anthropogenic variables by having significantly higher percent moss/lichen cover ($F = 35.1$, $p \leq 0.001$), lower PAR values ($F = 14.6$, $p < 0.001$), and shallower slopes ($F = 9.94$, $p = 0.003$) than the clearcut sites. None of the anthropogenic variables differed significantly between the mature and clearcut sites. The most mesic ELT was significantly richer, more diverse, had more native species, and was more northeast-facing than the least mesic ELT for all sites combined

Table 1. Biotic, non-anthropogenic, and anthropogenic variable means compared by age (mature forest or 15-year-old clearcut) as well as by ecological land type (mesic-*Tilia-Acer* or 220, *Acer-Quercus* or 230, and least-mesic-*Quercus* or 300) for the combined sites, within the 80+ sites and within the 15-year-old clearcut sites using ANOVA and nonparametric ANOVA (identified by *).

			Combined sites			80+ year			15-year Clearcut		
Variable	80+ (24)	CC (24)	220 (15)	230 (16)	300 (17)	220 (7)	230 (8)	300 (9)	220 (8)	230 (8)	300 (8)
Biotic											
Total EIW	0.04	0.15	ns	ns	ns	ns	ns	ns	ns	ns	ns
Total EW*	0.03	0.22	ns	ns	ns	ns	ns	ns	ns	ns	ns
Total NW	0.10	0.50	ns	ns	ns	ns	ns	ns	ns	ns	ns
Total N*	5.3	5.6	6.3^{A}	5.6^{AB}	4.7^{B}	5.7^{A}	5.8^{AB}	4.6^{B}	ns	ns	ns
Diversity	1.4	1.9	1.9^{A}	1.8^{A}	1.4^{B}	1.7^{A}	1.5^{AB}	1.2^{B}	ns	ns	ns
Richness	11	14	15^{A}	12^{AB}	9.5^{B}	15^{A}	10^{AB}	7.9^{B}	ns	ns	ns
Non-anthropogenic											
Bare rock	ns	ns	ns	ns	ns	ns	ns	ns	2.3^{A}	1.8^{AB}	0.74^{B}
Moss/lichen	3.0	1.2	ns	ns	ns	4.0^{A}	2.9^{AB}	2.3^{B}	ns	ns	ns
% Slope	26	35	ns	ns	ns	ns	ns	ns	38^{AB}	28^{B}	39^{A}
Light*	15.8	133	ns	ns	ns	ns	ns	ns	ns	ns	ns
Taspect	NA	NA	0.72^{A}	1.2^{AB}	1.3^{B}	0.74^{A}	1.4^{B}	1.3^{B}	ns	ns	ns
Anthropogenic											
Open private	NA	NA	1110^{A}	746^{B}	1036^{A}	ns	ns	ns	1377^{A}	662.2^{B}	483.5^{B}

Only significantly different variables are presented (p-value ≤ 0.05). Number of sites is in parentheses. Significant differences among the three ELTs were differentiated with letters. ns = not significant; total EIW = count of exotic invasive weeds, total EW = count of exotic weeds, total NW = count of native weeds, total N = count of native species, taspect = transformed aspect (larger numbers are more southwest), and open private = distance (m) to non-forested private land. Non-anthropogenic variables not listed include course woody debris (CWD, % cover), elevation (m), litter depth (cm), and distance (m) to the nearest river or creek. Anthropogenic variables not listed include grazed (three levels – not grazed, grazed, probably grazed), distance (m) to the nearest paved road, gravel road, and non-forested public land (open public).

($F = 5.01$, $p = 0.011$; $F = 4.44$, $p = 0.017$; $F = 3.52$, $p = 0.038$; $\chi^2 = 6.75$, $p = 0.034$, respectively) and just the mature sites ($F = 5.51$, $p = 0.019$; $F = 4.50$, $p = 0.024$; $F = 4.83$, $p = 0.019$; $\chi^2 = 4.65$, $p = 0.021$, respectively). The intermediate ELT was significantly closer to non-forested private land than the other ELTs ($F = 3.94$, $p = 0.027$) for the combined sites, while it was significantly less steep than the least mesic ELT for the clearcut sites ($F = 5.37$, $p = 0.013$). The most mesic ELT had more moss/lichen cover than the least mesic ELT in the mature sites ($F = 3.83$, $p = 0.038$), and more bare rock cover ($F = 3.40$, $p = 0.050$) in the clearcut sites (Table 1). These differences in ELTs may help support the use of this single variable as a surrogate of multiple variables defining forest composition and physiography.

Logistic regression models identified variables significantly ($p \leq 0.05$) related to invasion. Sites were more vulnerable to invasion in terms of biotic variables if they were relatively rich (all, mature, and clearcut sites), diverse (all, mature, and clearcut sites), had high counts of native species (all and mature sites) as well as exotic (all, mature, and clearcut sites) and native weeds (clearcut sites). In terms of the non-anthropogenic variables, sites that were northeast-facing (clearcut-sites), had more (mature sites) or less (all and clearcut sites) moss/lichen cover, had less bare rock (mature sites), less light (clearcut sites), were at lower elevations (clearcut sites) and were the most mesic ELT instead of the least mesic ELT (all sites) were more likely to be invaded. Significant anthropogenic variables showed sites that were cut (all sites) or closer to paved roads (mature sites) were more likely to be invaded.

The combined biotic, non-anthropogenic and anthropogenic logistic regression, using only the significant variables from the separate regressions and all sites, revealed the importance of the biotic variables (Table 2). Clearcut sites with high richness were the most likely to have significantly more exotic invasive plants. For every 0.1 unit increase in richness, an 128% increase in the odds of invasion was predicted. Moreover, if a site was clearcut, there was an 829% increase in the likeli-

Table 2. Cumulative logistic regression results using all sites ($N = 48$) and a combined model of all significant variables defined in the separate biotic, non-anthropogenic and anthropogenic models.

Models (six different ones)	Adj. R^2	Significant variable(s)	Estimate (SE)	Unit	Odds ratio (CI)
Richness + Taspect + Moss/Lichen + Cut	0.55	Richness	8.22 (2.23)	0.1	2.28 (1.50–3.69)
		$\chi^2 = 13.6$ ($p < 0.001$)	0.831		128%
		Cut vs. Uncut	2.23 (0.678)	1	9.29 (2.60–37.6)
		$\chi^2 = 10.8$ ($p = 0.001$)	–		829%
Diversity + Taspect + Moss/Lichen + Cut	0.52	Diversity	4.35 (0.956)	0.1	1.55 (1.30–1.90)
		$\chi^2 = 20.7$ ($p < 0.001$)	1.07		55%
Total EW + Total N + Taspect + Moss/Lichen + Cut	0.77	Total EW	1.47 (0.350)	0.1	1.16 (1.09–1.25)
		$\chi^2 = 17.8$ ($p < 0.001$)	1.76		16%
		Total N	0.068 (0.021)	0.1	1.01 (1.00–1.01)
		$\chi^2 = 10.5$ ($p = 0.001$)	0.804		0.9%
Richness + ELT + Cut	0.55	Richness	8.22 (2.23)	0.1	2.28 (1.50–3.69)
		$\chi^2 = 13.6$ ($p < 0.001$)	0.831		128%
		Cut	2.23 (0.678)	1	9.29 (2.60–37.6)
		$\chi^2 = 10.8$ ($p = 0.001$)	–		829%
Diversity + ELT + Cut	0.52	Diversity	4.35 (0.956)	0.1	1.55 (1.30–1.90)
		$\chi^2 = 20.7$ ($p < 0.001$)	1.07		55%
Total EW + Total N + ELT + Cut	0.77	Total EW	1.47 (0.350)	0.1	1.16 (1.09–1.25)
		$\chi^2 = 17.8$ ($p < 0.001$)	1.76		16%
		Total N	0.069 (0.021)		1.01 (1.00–1.01)
		$\chi^2 = 10.5$ ($p = 0.001$)	0.804		0.7%

Variables shown are significant at a p-value of 0.05. SE = standard error, CI = confidence interval, χ^2 = Wald Chi-square. Standardized estimates are below the estimates (except for the categorical variable, Cut), and percent change in exotic invasive species invasion per unit change of each variable are shown below the odds ratio.

hood of invasion. After replacing richness with diversity in this combined model, only diversity was significant with a 55% increase in the odds of invasion for every 0.1 increase in diversity. Similarly, counts of exotic weeds and native species were both more important than any non-anthropogenic or anthropogenic variable in terms of their positive relationship with higher counts of exotic invasive plants. A 0.1 unit increase in exotic weeds corresponded to a 16% increase in the odds of greater invasion, while the same increase in native species resulted in only a 0.9% increase in the odds of invasion. The standardized estimates of these two variables showed that exotic weeds were more important than native weeds in terms of defining invasibility (Table 2). Only the cut vs. not cut categorical variable was significant when the biotic variables, but not slope aspect and moss/lichen cover, were removed, with cut sites 1143% more likely to have higher numbers of exotic invasive plants. The individual ELT model (no other variables) was relatively weak ($R^2 = 0.13$) and when included in a regression model with any of the biotic variables, ELT was not significant. However, when run with just the cut vs. not cut variable, ELT and the cut vs. not cut variables were both significantly important, with the mesic ELT 13% and cut sites 1353% more likely to have more exotic invasive weeds than the least mesic ELT and uncut sites, respectively.

A combined model with all the significant variables of the three variable types using only the mature sites showed a similar pattern of biotic variable importance (Table 3). Sites with higher values of richness and that were closer to the nearest paved road were more likely to have higher levels of invasion, with richness being the most important (based on the standardized estimates). For every 0.1 unit increase in richness there was a 382% increase in the odds of invasion. Likewise, for every 100 m further from a paved road, there was a 21% decrease in the odds of a higher level of invasion. Diversity and total native species were the only significant variables when run separately with the significant non-anthropogenic and anthropogenic variables, and they showed a 98 and 1.5% increase in the odds of invasion for every 0.1 unit increase in diversity and number of native species, respectively. Removing the biotic variables showed that no remaining variables were significant.

A comparison of combined significant variables with the clearcut sites showed that richness and

Table 3. Cumulative logistic regression results using the 80 years of age or older sites ($N = 24$) and a combined model of all significant variables defined in the separate biotic, non-anthropogenic and anthropogenic models.

Models (three different ones)	Adj. R^2	Significant variable(s)	Estimate (SE)	Unit	Odds ratio (CI)
Richness + Moss/lichen + Bare rock	0.70	Richness	15.7 (5.70)	0.1	4.82 (1.96–19.4)
+ Paved road		$\chi^2 = 7.61$ ($p = 0.006$)	1.64		382%
		Paved road	−0.002 (0.001)	100	0.787 (0.619–0.932)
		$\chi^2 = 5.38$ ($p = 0.020$)	−1.41		21%
Diversity + Moss/lichen + Bare rock	0.61	Diversity	6.81 (2.23)	0.1	1.98 (1.37–3.36)
+ Paved road		$\chi^2 = 9.31$ ($p = 0.002$)	1.45		98%
Total N + Moss/lichen + Bare rock	0.68	Total N	0.144 (0.047)	0.1	1.02 (1.01–1.03)
+ Paved road		$\chi^2 = 9.29$ ($p = 0.002$)	1.79		1.5%

Variables shown are significant at a *p*-value of 0.05. SE = standard error, CI = confidence interval, χ^2 = Wald Chi-square. Standardized estimates are below the estimates and percent change in exotic invasive species invasion per unit change of each variable are shown below the odds ratio.

Table 4. Cumulative logistic regression results using the 15-year-old clearcut sites ($N = 24$) and a combined model of all significant variables defined in the separate biotic, non-anthropogenic and anthropogenic models.

Models (three different ones)	Adj. R^2	Significant variable(s)	Estimate (SE)	Unit	Odds ratio (CI)
Richness + Moss/lichen	0.62	Moss/Lichen	−21.5 (8.26)	0.1	0.116 (0.016–0.483)
+ Light + Taspect + Elevation		$\chi^2 = 6.79$ ($p = 0.009$)	−1.49		88%
		Light	−0.017 (0.007)	10	0.843 (0.717–0.945)
		$\chi^2 = 6.53$ ($p = 0.011$)	−1.42		16%
		Taspect	−4.96 (1.73)	0.1	0.609 (0.404–0.819)
		$\chi^2 = 8.25$ ($p = 0.004$)	−1.50		39%
		Elevation	−0.014 (0.005)	10	0.873 (0.781–0.943)
		$\chi^2 = 8.68$ ($p = 0.003$)	−1.43		13%
Diversity + Moss/Lichen	0.62	Moss/Lichen	−21.5 (8.26)	0.1	0.116 (0.016–0.483)
+ Light + Taspect + Elevation		$\chi^2 = 6.79$ ($p = 0.009$)	−1.49		88%
		Light	−0.017 (0.007)	10	0.843 (0.717–0.945)
		$\chi^2 = 6.53$ ($p = 0.011$)	−1.42		16%
		Taspect	−4.96 (1.73)	0.1	0.609 (0.404–0.819)
		$\chi^2 = 8.25$ ($p = 0.004$)	−1.50		39%
		Elevation	−0.014 (0.005)	10	0.873 (0.781–0.943)
		$\chi^2 = 8.68$ ($p = 0.003$)	−1.43		13%
Total EW + Total NW	0.79	Total EW	1.80 (0.603)	0.1	1.20 (1.09–1.39)
+ Moss/Lichen + Light		$\chi^2 = 8.90$ ($p = 0.003$)	2.37		20%
+ Taspect + Elevation		Moss/Lichen	−18.7 (8.45)	0.1	0.154 (0.021–0.714)
		$\chi^2 = 4.92$ ($p = 0.027$)	−1.29		85%
		Taspect	−4.84 (2.03)	0.1	0.616 (0.378–0.868)
		$\chi^2 = 5.67$ ($p = 0.017$)	−1.47		38%
		Elevation	−0.007 (0.004)	10	0.930 (0.851–0.992)
		$\chi^2 = 3.86$ ($p = 0.050$)	−0.771		7%

Variables shown are significant at a *p*-value of 0.05. SE = standard error, CI = confidence interval, χ^2 = Wald Chi-square. Standardized estimates are below the estimates and percent change in exotic invasive species invasion per unit change of each variable are shown below the odds ratio.

diversity were no longer important, leaving moss/lichen cover, light, slope aspect, and elevation as significant variables, with very little difference in their relative importance (Table 4). No anthropogenic variables were significant in the individual model. In the model containing exotic weeds and native weeds, exotic weed richness was the most important variable showing that with every 0.1 unit increase in exotic weeds there was an expected 20% increase in exotic invasive plants. Thus, clearcut sites with relatively low moss/lichen cover, on northeast-facing slopes, at lower elevations, and with relatively low light levels were more likely to be invaded. Also, the more exotic weeds a clearcut site had the more likely it was to be invaded by exotic invasive plants. Compared to mature sites, many of the biotic variables and all the anthropogenic variables were poor predictors of invasion on clearcut sites.

Discussion

The positive relationship between richness and site invasibility by exotic invasive weeds, corroborated by several other landscape level studies (Planty-Tabacchi et al. 1996; Wiser et al. 1998; Higgins et al. 1999; Lonsdale 1999; Stohlgren et al 1999), suggests that community saturation had not occurred, resources or propagules were abundant, and this system's degree of invasibility was driven by immigration processes rather than competitive interactions among native and exotic invasive species (Brown and Peet 2003). Though this relationship with diversity and richness includes all species categories (except our response variable – invasive exotic plants), richness and diversity appears to be driven by native species (exclusive of the other weedy categories) in the mature sites and exotic (primarily) and native weeds in the clearcut sites. This suggests the mature sites may be closer to community saturation, and possibly influenced less by immigration processes, than the 15-year-old clearcuts. However, despite possible community saturation, non-anthropogenic variables were very poor predictors of invasion of mature forests relative to biotic and anthropogenic variables. Conversely, despite the apparent importance of biotic variables (immigration processes) in the clearcut sites, diversity and richness were no longer important when combined with non-anthropogenic variables. Nonetheless, exotic non-invasive weeds were still better predictors of invasion than the non-anthropogenic variables in clearcuts.

There was a general trend of more exotic species in what appeared to be less stressed clearcut sites, in which there was a positive association between exotic invasive species and lower elevations, lower PAR values, and north-east facing slopes. Bastle et al. (1997) found a similar trend when comparing very young clearcuts (more severe environmental conditions) to older clearcuts, where relatively high topsoil moisture was the main factor controlling seedling survivorship. However, higher light conditions in conjunction with high soil moisture as found on road verges and skid roads, are conditions that are characteristically susceptible to invasion (Parendes and Jones 2000; Buckley et al. 2002; Gelbard and Belnap 2003), suggesting that soil moisture may be the driving force of invasion in the clearcut sites but that both soil moisture (not directly measured in our study) and relatively high light levels (as found with the clearcut sites compared with the mature sites) are important when considering all sites. The negative relationship between moss/lichen cover and invasibility may indicate that within these less stressed clearcut patches, weedy plants more rapidly colonized these areas than any moss or lichen species. We did attempt to look at soil fertility using soil type (of which there were nine different types, cf. Tucker County Soil Survey 1967), but none were correlated with exotic invasive plant species and their inclusion in the logistic regression models made convergence unstable. Measuring fertility directly may have shown a relationship between high fertility and exotic invasive plant species (Howard et al. 2004), but such measures may be considered unrealistic for most land managers. It is important to point out that the 15-year-old clearcuts likely had similar fertility, in terms of total N and P, as the mature sites (Whittaker et al. 1979; Boring et al. 1981; Attiwill and Adams 1993), but also had significantly higher numbers of exotic species, indicating that other factors, such as soil moisture and relative PAR, were more important than soil fertility. A subset of soil from six of our 48 sites (three paired mature and clearcut sites) was analyzed and, indeed, there was no significant difference in percent total N or P (mg/kg) between the two site types, though the clearcuts may have a more heterogeneous distribution of nutrient levels that such tests would not detect.

In terms of disturbance and landscape features, cut sites were the most likely to be invaded. When evaluating clearcut sites separately, no anthropogenic variable was important, suggesting that the condition of the surrounding landscape is less important than the environmental conditions within severely disturbed sites. In contrast, the mature sites were susceptible to the effects of the surrounding landscape in terms of distance to paved roads. This suggests that the effect of outside anthropogenic forces depends on the severity of anthropogenic forces within the site. However, these results may not translate to more fragmented or urbanized landscapes.

We observed that early invasion in mature and clearcut sites was driven by immigration processes and was more a passenger of environmental change rather than the driver of change (MacDougall and Turkington 2005). The biotic variables were so strongly related to the degree of invasion, in part because they too were responding similarly to available resources or changes in resources in response to a disturbance (e.g., harvesting), that they may be considered passengers of change themselves. Our results also indicated that within this relatively non-urbanized landscape, non-anthropogenic factors were more important than anthropogenic factors. However, proximity to paved roads, which may serve as conduits of exotic invasive species dispersal, was somewhat important in predicting invasion into mature forests. This information may help in prioritizing areas for conservation. Given that the majority of protected areas in the United States are located in less fertile soils and extreme climates at higher elevations, the evident vulnerability of less stressed areas to invasion is increasingly important (Scott et al. 2001; Lawler et al. 2003).

Propagule pressure is a very important aspect of immigration, and we did not attempt to measure dispersal potential of exotic invasive species into our sites. However, we do know that large populations of exotic invasive plants did not exist near any of our sites. Distribution of such species was sporadic within private land inholdings, or intermittent in low-abundance along roads. Our more common invaders in the sites, *R. multiflora*, *B. thunbergii*, and *Celastrus orbiculatus* Thunb., are bird-dispersed species. Clearly, without a seed source and the necessary dispersal mechanism, the most receptive environmental conditions will not result in an invasion (Halpern et al. 1997; Zobel et al. 2000). Nonetheless, even with ample seed, a lack of suitable microsites will prevent successful establishment, which is why simple reaction-diffusion models have been found to be inadequate for predicting spread of invasive plants species (Higgins et al. 1996). The spatial pattern of microsites within a given area will also define the success of establishment (Halpern et al. 1997) and the rate of spread (Bergleson et al. 1993). We argue that the establishment stage of invasion is an ongoing process as long as resource or microsite availability is most important and propagule pressure is relatively low. Once propagule pressure increases and microsite availability remains high, the invasive species may convert to a spread stage. At the spread stage, it may become difficult to distinguish the environmental variables associated with a microsite vulnerable to invasion, because larger populations make adjacent marginal sites more accessible (especially if the invader is also a transformer; Richardson et al. 2000). We would also predict that at the spread stage, the strong positive relationship with other weedy and native species that we observed may decrease if the seed load of such species has not similarly increased. Inter- and intra-specific competitive interactions may also become more important during spread when the invaders are acting as drivers of system degradation rather than passive responders. Such heavily infested sites (unless the infestation promotes a new disturbance, such as fire) may actually be less receptive to any kind of species colonization. We hope to test these hypotheses in future studies.

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