Patterns of exotic plant invasions in Pennsylvania's Allegheny National Forest using intensive Forest Inventory and Analysis plots

Cynthia D. Huebner [a],*, Randall S. Morin [b], Ann Zurbriggen [c], Robert L. White [c], April Moore [c], Daniel Twardus [d]

[a] Northern Research Station, USDA Forest Service, Morgantown, WV 26505, United States
[b] Northern Research Station, FIA, USDA Forest Service, Newtown Square, PA 19073, United States
[c] Allegheny National Forest, Warren, PA 16365, United States
[d] Forest Health, State and Private Forestry, Northern Area, Morgantown, WV 26505, United States

ABSTRACT

Intensive Forest Inventory and Analysis (FIA) plot data collected in the Allegheny National Forest (ANF), Pennsylvania, between 1999 and 2006 were evaluated for their ability to predict ANF's vulnerability to invasion by exotic plants. A total of 26 variables classified by biotic, abiotic, or disturbance characteristics were examined. Likelihood of colonization by invasive exotic and non-invasive exotic plants was analyzed using a logistic regression model. Approximately, 11% of the 449 species documented in these plots were exotic, which is higher than has been found in other northeastern forested plots. Only 1% of the ANF flora was invasive exotic plants and these were at low abundance, confirming that most invasions are still at an early stage of establishment. Sites richer in native or non-invasive exotic plants and with more alkaline soils were more likely to be invaded. Younger forests, forests with non-forest patches present, and forests rich in native species were more likely to be colonized by exotic (invasive or non-invasive) plants. *Frangula alnus*, which is starting to spread locally, differed from the other invasive exotic species in terms of its association with high sapling density to tree density ratios, high soil nitrogen levels, and the presence of fire. Variables representing mortality due to beech bark disease and distance to the nearest exotic planting manifested counterintuitive results. In both cases, the combined occurrence of mortality due to beech bark disease or a close (less than 500 m away) known propagule source and the presence of an invasive or non-invasive exotic plant was rare. We encourage increased use of intensive sampling for FIA in the U.S.A. and similar monitoring programs in other countries, but suggest adding a step to the plot selection phase that would allow forest-wide or regional stratified sampling of typically coarse-scale variables, such as historic or predicted defoliation or fire events, and forest or land type. A more accurate picture of the importance of disturbance variables in defining forest vulnerability to plant invasion may be achieved.

Published by Elsevier B.V.

1. Introduction

Forest vulnerability to invasion by exotic plants has been measured using a combination of biotic, abiotic, and disturbance variables. While disturbance may not be required for invasion, it has been characterized as one of the most reliable indicators of vulnerability to plant invasion (Lonsdale, 1999; Buckley et al., 2002; Pyšek et al., 2002). The association between invasion and disturbance has been attributed to changes in resource availability resulting from the disturbance (Burke and Grime, 1996; Davis et al., 2000). Environmental conditions not associated with

disturbance also play an important role in determining a site's vulnerability to invasion. Sites with ample water and nutrients are often the first to be invaded (Thompson et al., 2001; Huebner and Tobin, 2006). In fact, invasion of severely disturbed sites has been better defined by environmental conditions, such as topography (with relatively more mesic sites being more vulnerable to invasion) than surrounding anthropogenic landscape features, such as distance to the nearest road or waterway (Huebner and Tobin, 2006). Several studies support a positive relationship between native plant richness and invasibility by exotic invasive species (Higgins et al., 1999; Stohlgren et al., 1999; Huebner and Tobin, 2006; Belote et al., 2008). Such a relationship suggests that species saturation does not exist but that resources and propagules are abundant causing invasion to be driven by immigration processes rather than competitive interactions among the native

and non-native plants (Brown and Peet, 2003). Species-rich sites tend to be resource-rich sites and disturbed sites often show an increase in or a re-distribution of site resources; thus, variables associated with each of these three categories (biotic, abiotic, and disturbance) need to be addressed when attempting to predict vulnerability to invasion.

Most of the research on predicting forest invasion by exotic plants has understandably been designed to predict such invasions into management areas, which are often between 1 and 100 ha in size, or at the forest stand level, and these data are often collected at a single point in time. In contrast, the USDA Forest Service's Forest Inventory and Analysis (FIA) system, first started in 1930, has a goal to periodically assess the extent, condition, and trends of the Nation's forests. To do so requires coarser-scale inventories and longer time frames than most research studies. Historically, FIA inventories (mainly tree species) occurred once every 5–15 years, varying by state. Since 2000, FIA plots in Pennsylvania have been sampled in a 5-year cycle, with inventories occurring annually and 20% of all plots being sampled each year. Currently, all FIA plots are located approximately every 2400 ha. The FIA plots within the Allegheny National Forest (ANF) are sampled under the same temporal scale (starting in 1999) but are set up using a more intensive sampling approach that includes twice as many plots per area and additional measurements. These plots are located

approximately one per every 1200 ha (Morin et al., 2006), which is still a coarser scale than most research studies focused on managed forests. The additional measurements in the ANF FIA plots (also called Phase 3 or P3 plots) include understory vascular plants, soil variables, topography, coarse woody debris, and canopy conditions (Reams et al., 2005; Morin et al., 2006). Other P3 plots that measure these additional data exist nationwide but at a very coarse scale with one plot every 38,400 ha (Reams et al., 2005).

The capacity of chosen variables to predict invasion is scale-dependent, and independent variables measured at different scales from the response variables are less likely to be as informative as those measured at the same scale. For instance, many disturbances, such as fire and insect defoliation are typically measured at or interpolated over coarser scales, while biotic and abiotic variables, such as species richness, light, and total soil N are measured at finer scales. Not all disturbances need to be coarsely measured and these include such variables as distance to the nearest road and forest age. Moreover, forest type, a biotic variable, may be considered a coarse-scale variable, because more detailed community descriptions often result in statistically unmanageable levels for a categorical variable. Research focused on predicting vulnerability to invasion has dealt with this scale issue by stratifying samples within these coarse-scale variables, such as disturbance type or forest type. FIA does not currently employ such stratification
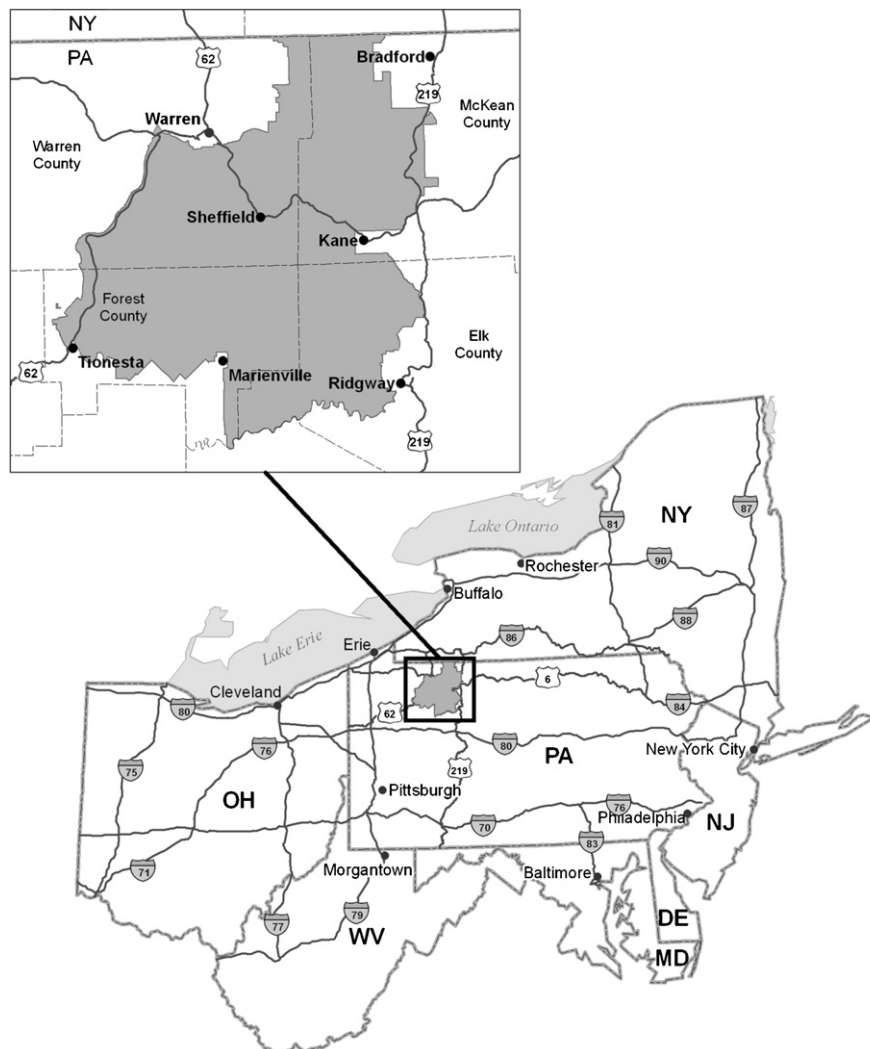

Fig. 1. Allegheny National Forest location in northwestern Pennsylvania (adapted from USDA FS 2006a.).

beyond Phase 1, which uses satellite imagery (Landsat Thematic Mapper with a 30 m resolution) to classify land as forest or non-forest (Frayer and Furnival, 1999; Reams et al., 2005).

The goal of this paper is to evaluate the ability of the coarse-scale FIA understory data to predict ANF's vulnerability to invasion by exotic plant species. Based on the literature using fine-scale methods, we predict that plant species richness, relatively mesic and fertile site conditions, disturbance, and anthropogenic landscape features are likely to be indicators of invasion. We also predict that some of the coarse-scale disturbance and landscape variables, and possibly forest type, will be underrated when evaluated together with the other biotic and abiotic variables.

2. Methods and materials

2.1. Study area

The ANF (41°45′N, 79°00′W) is located in northwestern Pennsylvania within the unglaciated portion of the Allegheny Plateau, encompassing Elk, Forest, McKean, and Warren Counties (Fig. 1). The legal proclamation boundary of the ANF contains approximately 300,560 ha, of which 202,590 ha are public land (USDA Forest Service, 2007). Average temperatures range between 20 °C in the summer and −1 °C in the winter with mean annual precipitation close to 104 cm (Cerutti, 1985; Abrams and Ruffner, 1995) and an average 100–139 days growing season (Whitney, 1990). The unglaciated plateau with elevations ranging between 300 and 720 m is a highly dissected landscape (Cerutti, 1985; Whitney, 1990) with soils derived from a variety of parent material including shale, sandstone, limestone, and chert (Abrams and Ruffner, 1995).

Braun (1950) placed this region in the hemlock-white-pine-northern hardwood type and Küchler (1964) placed it in the hemlock-northern-hardwood forest type with the potential for oak forests. Before about 1600, the ANF consisted of beech/maple/hemlock forests on the ridges and slopes with white pine and oak growing in the stream valleys (USDA Forest Service, 2006b). Between 1800 and 1890, harvesting in the region was sporadic and patchy, affecting primarily larger trees of select species, especially white pine. Clearcutting was the primary harvesting method between 1890 and 1920 and most of any remaining forest was removed because more species and tree size classes became marketable. Extensive fires followed in some areas of the ANF. Stands that experienced frequent, intensive burns were more likely to be composed of Populus L. sp. (aspen) and Prunus pensylvanica L.f. (pin cherry; Lutz, 1930; Hough and Forbes, 1943; Marquis, 1975). Heavy cutting and fires favored certain hardwoods such that the once dominant Tsuga canadensis (L.) Carriere. (Eastern hemlock), Pinus strobus L. (white pine), and Fagus grandifolia Ehrh. (American beech) stands gave way to forests dominated by Prunus serotina Ehrh. (black cherry), Acer saccharum Marshall (sugar maple), Acer rubrum L. (red maple), and Fraxinus americana L. (white ash; Marquis, 1975). Fire records kept by the ANF show that several large fires were documented during 1923–1928. The size and location were approximated on old maps and since digitized. Fire records were not kept from that point until 1980 (W. Wallace, ANF, 2006, personal communication).

More recent disturbances include harvesting, primarily thinning (approximately 1000 ha per year) and shelterwood (approximately 570 ha per year), and small-scale fires since 1980, with 91% 4 ha or less in size and 83% 2 ha or less in size (USDA Forest Service, 2007). An annual average of 106,672 m^3 (45.2 MMBF) was harvested between 1986 and 2005 (USDA Forest Service, 2006a). These harvests include skid trails and landings which are not mapped. There are 1081 km of mapped trails, and 7195 km of road

of which 25% are open to public access all year, 9% are restricted to occasional public access, and 66% are closed to the public (USDA Forest Service, 2003). Approximately, 255 oil and gas wells have been drilled per year between 1986 and 2005; 93% of the subsurface rights to minerals, oil, or natural gas on the ANF are privately owned (USDA Forest Service, 2007). While elm span-worm (Ennomos subsignaria Hubner) and cherry scallopshell moth (Hydria prunivorata Ferguson), both native defoliators, did much of their damage in the ANF between 1991 and 1996 (defoliating 244,400 ha), the European gypsy moth (Lymantria dispar Linnaeus, 1758) defoliated 126,800 ha on the ANF between 1985 and 1996 (Morin et al., 2004). Moreover, significant declines in A. saccharum between 1990 and 1995 in ANF were at a rate three to four times faster than in other northeastern forest plots. A. saccharum dieback, especially on the east side of the forest, has increased since 1995, reducing this species' relative importance (McWilliams et al., 1996). This dieback has been attributed to pear thrips, drought conditions, and poor base-cation status of soils (Horsley et al., 2000). The killing front of beech bark disease (a complex of both a European scale insect and Nectria fungi) has been moving at a rate of about 4.0 km per year in a southwesterly direction (ANF Forest Monitoring and Evaluation Report, 2001) since 1988 (ANF Forest Monitoring and Evaluation Report, 1989) and covers approximately 42% of the ANF (Morin et al., 2006). While the scale insect has colonized ANF relatively rapidly, the fungus has moved more slowly compared to other invaded forests in the northeast (ANF Forest Monitoring and Evaluation Report, 2001). Mortality due to beech bark disease was not mapped until 2000.

Intentional introductions of exotic (both those described as invasive and those as non-invasive) species were planted in wildlife openings to provide additional soft mast, deter deer, or serve as living fences. The Forest Service records are incomplete, but it appears that most of these plantings occurred between 1970 and 2003 (A. Moore, personal communication). The introductions could have included several invasive exotics including Coronilla varia L. (crown vetch), Berberis thunbergii DC. (Japanese barberry), Elaeagnus umbellata Thunb. (autumn olive), Lespedeza cuneata (Dum. Cours.), G. Don. (Chinese lespedeza), Lonicera L. sp. (non-native bush honeysuckles), Rosa multiflora Thunb. (multiflora rose), and Celastrus orbiculatus Thunb. (oriental bittersweet). However, most of these plantings occurred in open areas, which may not have met the FIA criteria of 10% stocking by forest trees of any size or historic stocking with current regeneration back to forest (USDA Forest Service, 2002a). None of the known planting locations corresponded with any FIA plot locations, but they could serve as a propagule source. Seed mixtures used up until the early 1990s on skid trails and landings after harvests contained several exotic grasses and forbs, including Dactylis glomerata L. (orchard grass), Lolium arundinaceum (Schreb.), S.J. Darbyshire (tall fescue), and Lotus corniculatus L. (birdsfoot trefoil) (R. White, personal communication).

2.2. Sampling design

We used the FIA data collected between 1999 and 2006 in which 182, 0.067-ha plots were sampled, with 173 of these sampled twice (determined by FIA sampling schedules). Plots were composed of four fixed-area 168 m^2 subplots (Fig. 2). Between 1999 and 2003, cover was estimated for all understory species (all herbs, vines, and shrubs, and trees less than 1.83 m tall) within three square 1 m × 1 m quadrats located in the subplots (USDA Forest Service, 2002b; Fig. 2). Sampling of the understory was conducted primarily by three botanists but as many as seven different botanists collected the data over this time period. Understory plots were sampled between mid-June and mid-
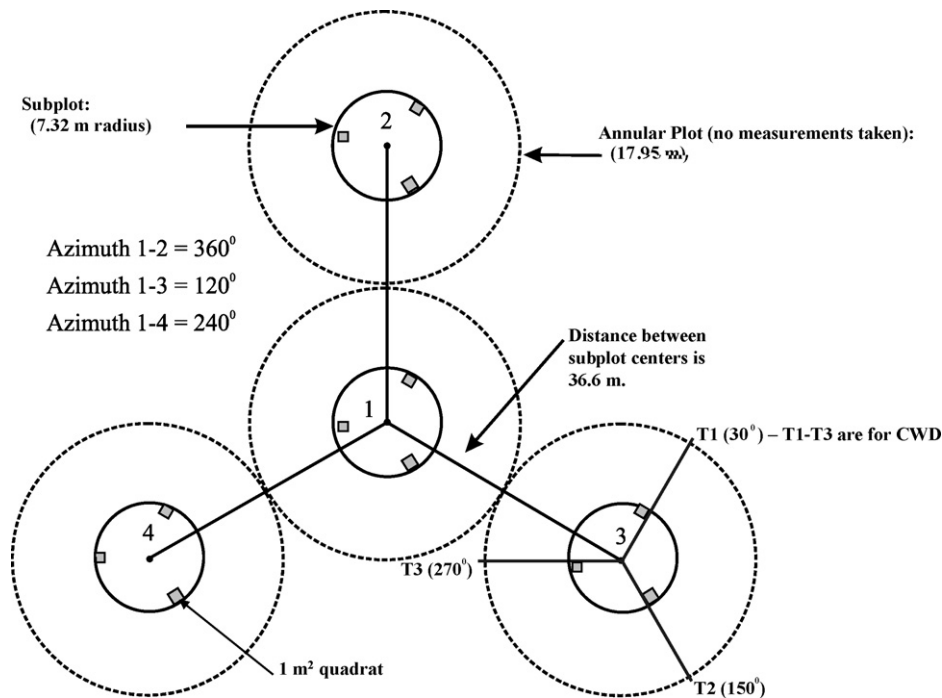
Fig. 2. Sampling design (adapted from Morin et al., 2006).

September. After 2003, cover was not estimated in the quadrats but instead was estimated for the larger subplots (from which presence/absence data are easily derived). Cover estimates of such large areas results in little differentiation among species except the most dominant. Because of this change in protocol and the fact most exotics were detected in low abundance, we evaluated the understory species of 1999–2006 using presence/absence data of the 168 m^2 subplots for all years. Plots sampled twice were sampled at different times of the year (e.g., June vs. September) and over different time periods (1–5 years). Any new species found in the second tally were added to the species list for the first tally. Missing species in the second tally were not removed from the first tally unless these were identification corrections. Trees (dbh ≥ 12.7 cm) and saplings (dbh ≥ 2.5 cm and <12.7 cm) within each subplot were tallied and measured for their dbh. Standing dead trees (≥12.7 cm dbh) were tallied in each subplot (USDA Forest Service, 2002a) and coarse woody debris was measured by tallying all debris ≥1 m in length and ≥8 cm in diameter at the point of intersection along three 7.5 m transects within each subplot (FIA, 2002; Fig. 2). Volumes were then estimated using this tally and the minimum 8-cm width and 1-m length. Subplot data were averaged for each plot.

2.3. Variables

Initial exploratory analyses were organized around three variable types: (1) biotic, (2) abiotic, and (3) disturbance or landscape features related to disturbance. There were seven biotic variables, including: (a) presence of invasive exotics (IE), (b) presence of all exotics (AE), (c) presence and richness of exotics that are not invasive (E), (d) presence and richness of native species (N), (e) sapling density to tree density ratio (S/T_D), (f) sapling basal area to tree basal area ratio (S/T_BA), and (g) forest type (four-level categorical variable) as defined by both USDA Forest Service Region 9 and FIA (results did not differ). Sapling basal area to tree relative density (a measure of tree crowding), as described by Stout and Nyland (1986), was also used but the results did not

change and will not be presented. Invasive exotics were defined conservatively such that they each existed on multiple MidAtlantic state lists as noxious or invasive (Harmon, 1999; Pennsylvania Department of Conservation and Natural Resources, 2000; Virginia Department of Conservation and Recreation and Virginia Native Plant Society, 2001). Exotic species were defined by non-native status as given in at least one taxonomic key (Gleason and Cronquist, 1993; Rhoades and Block, 2000).

The 10 abiotic variables included: (a) crown density (%), (b) foliar transparency (%), (c) aspect (five-level categorical variable of the four cardinal directions and no aspect, (d) slope (%), (e) coarse woody debris (m^3), and soil (f) pH in water suspension, (g) total C (%) using a combustible analyzer, (h) total N (%) using a combustible analyzer, (i) exchangeable aluminum (mg/kg), and (j) exchangeable calcium (mg/kg). Soils were sampled in subplots 2, 3 and 4 by depths of 0–10 and 10–20 cm (Morin et al., 2006; Amacher et al., 2003). Our analyses use the 0–10 cm depth because, aside from total N and total C, the soil variables at each depth were highly correlated.

The nine disturbance variables included: (a) distance to the nearest paved road (m), (b) distance to the nearest dirt or gravel road (m), (c) stand age (years), (d) standing dead tree density, (e) presence of non-forest area in the plot (two-level categorical variable), (f) fire (three-level categorical variable, with one category for fire directly on the plot and another with fire nearby, possibly including the plot), (g) defoliation by gypsy moth, cherry scallopshell moth, or elm spanworm (three-level categorical variable with the level representing 1, 2, or 3 years of defoliation), (h) mortality due to beech bark disease (two-level categorical variable), and (i) distance to documented planting of an exotic plant species (m). Road locations and type, fire locations, and locations of exotic plantings were provided by the USDA Forest Service Region 9 ANF. Forest defoliation and mortality due to beech bark disease data were determined by USDA Forest Service Forest Health Monitoring aerial surveys and sketch maps (McConnell et al., 2000). All other disturbance variables were collected as a part of the FIA protocol (FIA, 2002, 2007). Non-forest land is defined as

any area that is less than 10% stocked by trees of any size. Stand age was determined by coring two to three representative dominant or co-dominant overstory trees in each plot and weighting each tree by estimating the percentage of the total overstory it represented, making the overall plot age a weighted average (FIA, 2007).

2.4. Data analyses

A generalized linear model (Proc GENMOD, SAS v. 9.01) was used to determine significant differences between individual continuous variables in plots with and without invasive exotic and all exotic plants. A negative binomial distribution with a log link function was used for native and exotic species richness, number of standing dead trees, while a gamma distribution with a log link function was used for stand age, crown density, sapling to tree basal area ratio, pH, exchangeable Ca and Al, distance to dirt road, coarse woody debris, and slope inclination. All other variables used a normal distribution with an identity link function. These results along with evaluations of invasive exotics and exotics within each of the categorical variables, including forest type, defoliations by gypsy moth, elm spanworm, and cherry scallopshell moth, mortality due to beech bark disease, and presence or absence of non-forest area will be used to confirm the exploratory selection of important variables in the separate biotic, abiotic, and disturbance-logistic regression models described below.

The importance of all variable types as they related to the presence or absence of invasive exotic species and all exotic species (i.e., a binomial response variable) was evaluated using logistic regression analysis with backwards selection (Proc Logistics, SAS, v. 9.01). In both procedures, abiotic, biotic, and disturbance variables were evaluated in separate exploratory models and variables that had a final p-value of 0.1 or lower were included in a combined model of the most important variables of the three types. This p-value is an arbitrary, but conservative choice. The resulting important variables were also found to be significant as individual variables in the generalized linear models. Multicollinearity (using a Pearson correlation cut-off of $r > 0.5$; Proc

Corr, SAS, v. 9.01) was avoided by not including crown density and foliar transparency in the same models. This was also true for total soil N and C as well as all the defoliator variables. The final logistic regression models that combined all important variables for the two response variables also used backwards selection but a p-value of <0.05 was used to define the significant variables.

3. Results

3.1. Compositional patterns

A total of 449 vascular, understory species were found over the 1999–2006 time period (Appendix 1). These species were composed of 73 different plant families, the most common of which were Poaceae (56 different species), Cyperaceae (50 different species), Asteraceae (41 different species), and Rosaceae (28 different species). Of the 449 total species, 49 or 11% were exotic with five (or a total of 1% of the flora) of these being classified as invasive. *Frangula alnus* P. Mill. (European alder) was found in 12 of the 182 plots, followed by *R. multiflora* Thunb. (multiflora rose) in 11 plots, *B. thunbergii* DC. (Japanese barberry) in 8 plots, *Polygonum caespitosum* Blume. (Asian smartweed) in 4 plots, and *C. varia* L. (crown vetch) in 3 plots. *Rumex acetosella* L. (sheep sorrel), which occurred in 12 of the plots, is considered invasive in more open habitats and thus has been subjectively classified as just an exotic species here. *Veronica officinalis* L. (common speedweel; in 26 plots) and *Anthoxanthum odoratum* L. (sweet vernal grass; in 23 plots) were the top two most common exotic species found in the ANF. Taking into account the 68/100 ratio of oak-hickory to beech/maple/cherry sites, *F. alnus* was 7.47 times more likely to found in a beech/maple/cherry forest, while *B. thunbergii* and *R. multiflora* were 4.41 and 3.31 times more likely to found in the oak-hickory forest type, respectively. *C. varia* and *P. caespitosum* did not show a preference for a forest type. *R. acetosella* was 6.62 times more likely to be found in oak-hickory forests than beech/maple/cherry forests, while *A. odoratum* and *V. officinalis* were 1.35 and 1.02 times more likely to be found in beech/maple/cherry forests of the

Table 1
Means and standard deviations of continuous variables on sites where invasive exotic plant species (IE) were present compared with sites where they were not present

Variable	IE present			IE not present		
	N	Mean	S.D.	N	Mean	S.D.
Biotic (six continuous, including IE, and one categorical)						
Native species richness* (#; N)	37	61.84	21.84	145	48.95	16.79
Exotic (not invasive) species richness* (#, E)	37	2.43	3.51	145	1.09	2.46
All exotic species richness* (#; AE)	37	3.57	3.61	145	1.09	2.46
Sapling to tree density ratio (S/T_Den)	36	1.04	3.16	140	0.48	1.30
Sapling to tree basal area ratio (S/T_BA)	36	0.06	0.06	140	0.05	0.05
Abiotic (eight continuous and one categorical)						
Crown density (%; CrDen)	34	54.13	6.97	140	53.75	6.38
Foliar transparency (%: FolTr)	36	19.12	3.94	140	18.85	4.64
Soil pH* (pH)	30	4.19	0.47	125	4.00	0.39
Soil Ca (mg/kg; Ca)	30	121.85	218.28	125	87.45	239.38
Soil Al (mg/kg; Al)	27	456.67	195.74	115	453.88	236.02
Total soil N (%; TN)	30	0.25	0.23	125	0.20	0.12
Total soil C (%; TC)	30	4.32	5.12	125	3.25	1.70
Coarse woody debris (m³; CWD)	34	17.71	16.04	138	16.26	15.77
Slope (%)	34	12.39	11.12	138	12.01	11.26
Disturbance (five continuous and five categorical)						
Stand age (years; StAge)	36	61.58	30.52	144	71.79	26.31
Standing dead trees* (#; StDead)	36	2.76	2.62	137	4.03	3.55
Distance to nearest paved road (m; Dpaved)	37	1338.77	897.46	145	1350.30	874.37
Distance to nearest dirt road (m; Ddirt)	37	264.67	234.49	145	297.77	324.95
Distance to nearest exotic plant species planting* (m; Dplant)	34	3277.09	1973.79	139	2146.98	1845.85

In parentheses following each variable's full name is the units, where applicable, and any short name used in other tables or the text. Variables marked with asterisk (*) were significantly different at $p \leq 0.05$. There were 1.14 IE species per plot on average with a standard deviation (S.D.) of 0.35.

Table 2
Means and standard deviations of continuous variables on sites where any exotic plant species (E) were present compared with sites where they were not present

Variable	E present			E not present		
	N	Mean	S.D.	N	Mean	S.D.
Biotic (six continuous, including exotic species, and one categorical)						
Native species richness[*] (#; N)	91	60.81	19.95	91	42.33	11.18
Invasive exotic species richness[*] (#; IE)	91	0.46	0.60	91	0	0
All exotic species richness[*] (#; AE)	91	3.19	3.43	91	0	0
Sapling to tree density ratio (S/T_Den)	87	0.81	2.46	89	0.38	0.86
Sapling to tree basal area ratio (S/T_BA)	87	0.05	0.06	89	0.05	0.05
Abiotic (eight continuous and one categorical)						
Crown density (%; Crden)	87	53.20	6.98	89	54.45	5.93
Foliar transparency (%; Foltr)	87	19.40	5.26	89	18.41	3.56
Soil pH (pH)	79	4.05	0.41	76	4.03	0.42
Soil Ca (mg/kg; Ca)	79	110.72	217.97	76	76.85	252.07
Soil Al (mg/kg; Al)	69	444.53	257.11	73	463.74	198.55
Total soil N (%; TN)	79	0.22	0.16	76	0.20	0.13
Total soil C (%; TC)	79	3.68	3.56	76	3.24	1.41
Coarse woody debris (m^3; CWD)	86	16.79	17.11	86	16.32	14.44
Slope (%)	86	14.36	12.51	86	9.81	9.25
Disturbance (five continuous and five categorical)						
Stand age[*] (years; StAge)	90	63.16	29.19	90	76.34	23.93
Standing dead trees (#; StDead)	86	3.34	3.12	87	4.19	3.64
Distance to nearest paved road (m; Dpaved)	91	1292.66	856.39	91	1403.26	897.70
Distance to nearest dirt road (m; Ddirt)	91	267.12	232.47	91	314.96	368.92
Distance to nearest exotic plant species planting (m; Dplant)	87	2512.15	1900.50	86	2224.35	1938.57

In parentheses following each variable's full name is the units, where applicable, and any short name used in other tables or the text. Variables with an asterisk (*) were significantly different at $p \leq 0.05$. There were 2.73 exotic species per plot on average with a standard deviation (S.D.) of 3.339.

ANF. The other two forest types (10 hemlock/pine plots and 4 mixed forest plots), which were relatively uncommon, did not reveal any species preferences.

F. alnus was the only invasive exotic species that had cover values above 5% per subplot and in one plot just above 20%. This suggests that this may be the one invasive plant in the ANF that is now beyond the establishment stage and is spreading. Between 1999 and 2006, *F. alnus* spread to three new plots that it did not already occupy based on the 173 plots that were sampled twice within this time period. The new plots with *F. alnus* were all spatially autocorrelated with existing plots containing *F. alnus*.

Means for each of the continuous variables organized by plots with invasive exotic plants and those without them (Table 1) as well as plots with any exotic (including invasive) species and those without exotic species (Table 2) were examined for significant patterns using generalized linear models. Approximately, 20% of the plots had invasive exotic species present for each continuous variable measured, whereas, approximately half the plots had at least one exotic species present. Native species richness was significantly greater on average for plots with invasive exotic species and for plots that had any exotic plant species. Stands with invasive exotic species had significantly more alkaline soil, fewer standing dead trees, and were further from known invasive exotic planting locations than stands without invasive exotics. Stands with any exotic species were significantly younger than stands without these species.

Mapping the five invasive exotic species by plot revealed a spatial grouping of *F. alnus* in the southeast of the forest (Fig. 3). This is the approximate location of *A. saccharum* dieback (McWilliams et al., 1996) and historic (1923–1928) severe burns. Such patterns were not found with the defoliation, beech bark disease mortality, or the exotic species plantings maps (Figs. 4–6).

3.2. Presence/absence patterns

In the separate biotic, abiotic, and disturbance models, native species richness ($\chi^2 = 12.7$; $p = 0.0004$) was the only important biotic variable for presence of invasive exotic plant species as a response variable. Presence of invasive exotic plants was more likely with high native species richness. Exotic (non-invasive) species richness ($\chi^2 = 5.18$; $p = 0.023$) was significant if native species richness was removed from the model, showing that sites with high non-invasive exotic species richness were more likely to be invaded. Soil pH ($\chi^2 = 2.49$; $p = 0.114$) was the only marginally important abiotic variable associated with the presence of invasive exotic plants species, with alkaline sites being more susceptible to invasion. In terms of the disturbance variables, stand age ($\chi^2 = 4.27$; $p = 0.040$) and distance to the nearest exotic species planting ($\chi^2 = 11.68$; $p = 0.0006$) were significantly associated with the presence of invasive exotic plant species. The latter was true when including the elm spanworm defoliator; inclusion of either gypsy moth or cherry scallopshell moth resulted in unstable models (i.e., a quasi-complete separation of data points was detected). Younger sites further from exotic species plantings were more likely to be invaded. The relationship between invasive exotic species richness (found in 38 of the 182 plots) and known plantings was unexpected. It is important to point out that the combined occurrence of nearby exotic species planting and invasive exotic or exotic species was rare (as is seen in Fig. 6). Only 20 plots were closer than 500 m to a known exotic planting and invasive exotic species were present in none of these; 66% of the plots were over 1 km away from such plantings and only three of these had invasive exotic species present. Removing distance to the nearest exotic species planting resulted in only stand age ($\chi^2 = 3.41$; $p = 0.070$) being important; younger sites were more likely to be invaded.

Combining the variables that met the p-value ≤ 0.1 criterion with exotic invasive species as the response variable shows that native species richness ($\chi^2 = 12.3$; $p < 0.0001$) and distance to the nearest planting ($\chi^2 = 8.96$; $p = 0.003$) were significant (Table 3). Removing distance to the nearest planting showed that only native species richness ($\chi^2 = 13.3$; $p = 0.0003$) remained significant. When using exotic species richness instead of native species richness, only distance to the nearest planting ($\chi^2 = 9.82$; $p = 0.002$) remained
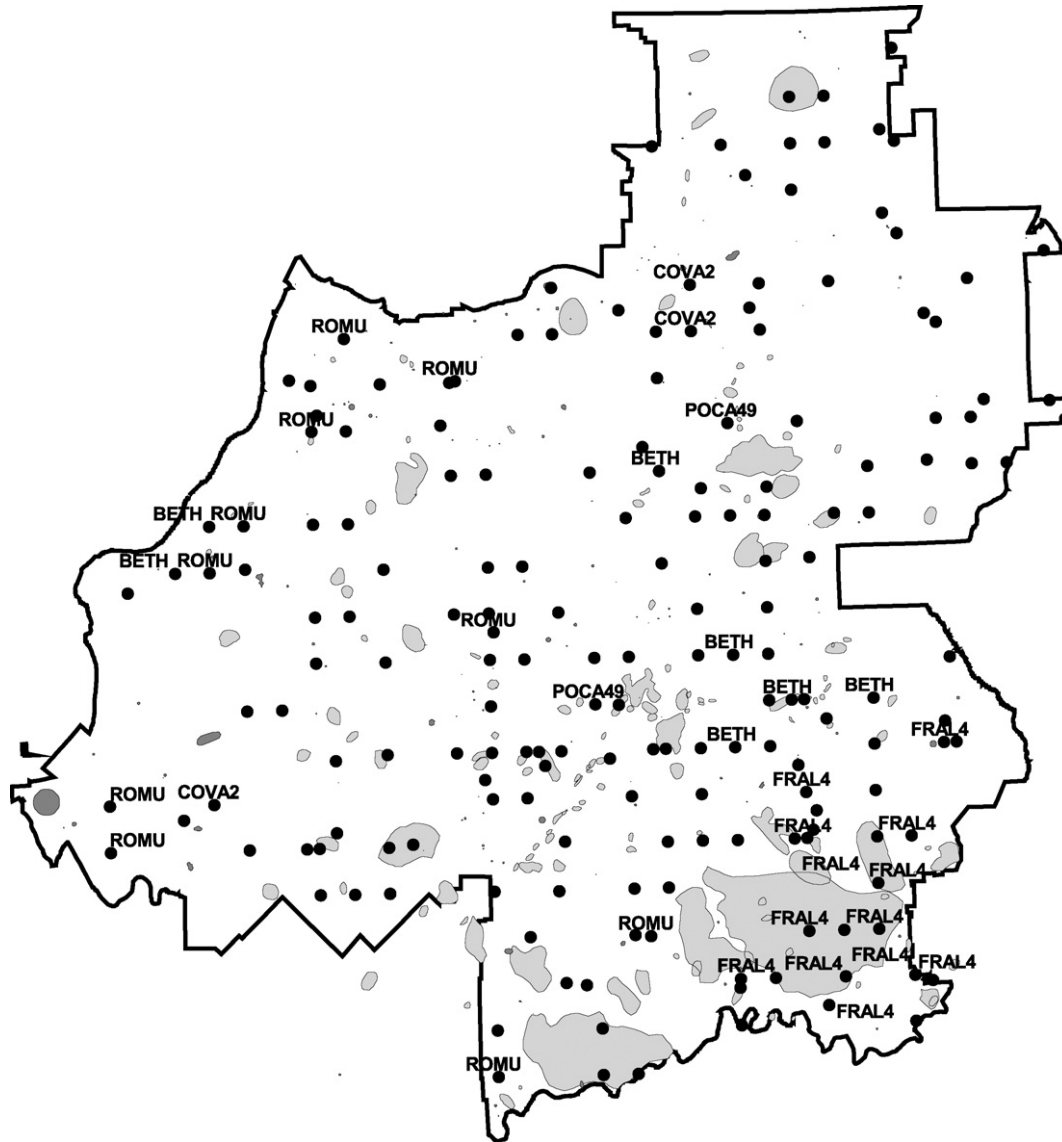
Fig. 3. Fires between 1923 and 1928 (light grey) and fires between 1980 and 2005 (dark grey – very few) as well as plot locations with primary invasive exotic species labeled. (BETH, *Berberis thunberjii*; COVA2, *Coronilla varia*; FRAL4, *Frangula alnus*; POCA49, *Polygonum caespitosum*; ROMU, *Rosa multiflora*).

significant. The closer a plot was to a planting site, the less likely an invasive species would be present. Removing distance to exotic planting, both exotic species richness ($\chi^2 = 4.63$; $p = 0.031$) and pH ($\chi^2 = 4.97$; $p = 0.026$) were significant. Invasion was more likely if the sites were rich in native and exotic (non-invasive) species and the soil was relatively alkaline (Table 3). Removal of distance to exotic planting also reduces the potential for overfitting our combined model. With three variables we need at least 30 samples with our variable of interest (invasive exotic species); we have 35 (Concato et al., 1993).

Running each biotic, abiotic, and disturbance logistic model separately, the only significant biotic variable using presence of all exotic species as a response variable was native species richness ($\chi^2 = 33.9$; $p \leq 0.0001$). Sites with high species richness were more likely to have exotic species. Removing native species richness did not unmask any other important biotic variables. No abiotic variables met the $p \leq 0.1$ criterion with presence of exotic species as the response variable. Presence of non-forest land on the plot ($\chi^2 = 8.96$; $p = 0.003$), stand age ($\chi^2 = 7.25$; $p = 0.007$), and beech bark disease mortality ($\chi^2 = 3.86$; $p = 0.050$) were significant

disturbance variables. The latter was true with all but the elm spanworm defoliator, which produced an unstable model (quasi-complete separation of data points was detected), with only slight differences in the χ^2 and p values (cherry scallopshell moth was presented here). Younger stands with non-forest land present and without beech bark disease mortality were more likely to have exotic plants present. It is important to point out that the combined occurrence of beech bark disease mortality with invasive exotic or exotic species richness was rare. Only 32 plots were impacted by beech bark disease mortality with invasive exotic plant species occurring in two of these. Removing beech bark disease mortality (and distance to nearest exotic species planting) from this model resulted in presence of non-forest land ($\chi^2 = 9.35$; $p = 0.002$) and stand age ($\chi^2 = 7.24$; $p = 0.007$) as still being significant.

Combining all variable types with $p \leq 0.1$ and presence of all exotic species as the response variable, native species richness ($\chi^2 = 30.2$, $p \leq 0.0001$), presence of non-forest land ($\chi^2 = 5.89$; $p = 0.015$), and stand age ($\chi^2 = 5.40$; $p = 0.020$) were significantly associated with presence of exotic plant species. Younger stands,
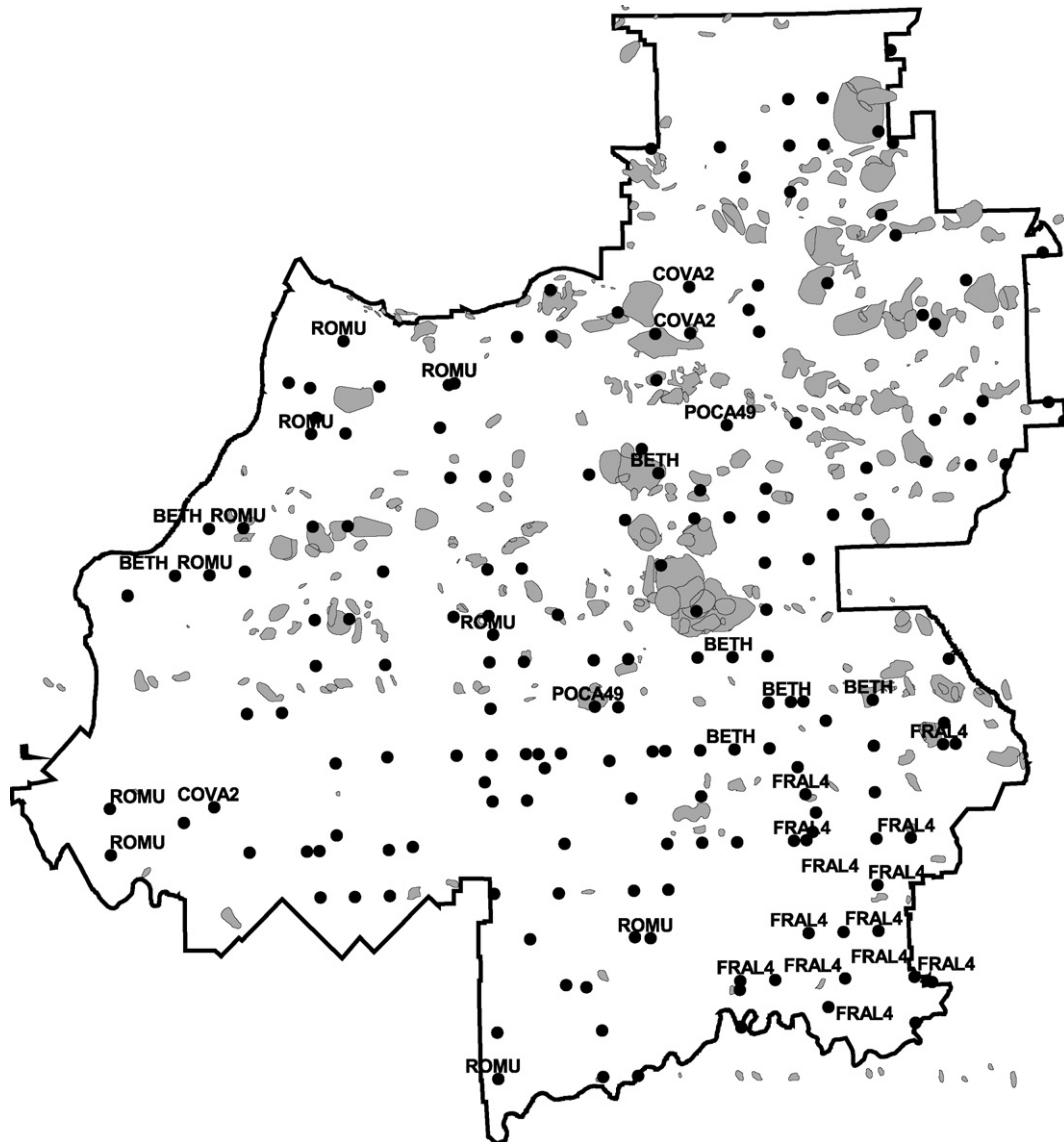
Fig. 4. Beech bark disease mortality from 2000 to 2005 (most of the mortality occurred in 2003) and location of the five exotic invasive species (BETH, *Berberis thunberjii*; COVA2, *Coronilla varia*; FRAL4, *Frangula alnus*; POCA49, *Polygonum caespitosum*; ROMU, *Rosa multiflora*).

stands rich in native species, and stands with non-forest land present were more likely to have at least one exotic plant species present. This model was the strongest of all the combined models with an adjusted R^2 of 0.43 (Table 4).

Thus, we can predict that for every 0.1 unit increase in native species richness, there is a 77% greater chance of an invasive exotic plant being present than not being present. However, this probability is based on a weak model (adjusted $R^2 = 0.24$). With more confidence (adjusted $R^2 = 0.43$), we could predict that for every 0.1 unit increase in native species richness, the presence of an exotic plant is 2.71 times more likely to occur than not occur.

We also ran both *R. multiflora* and *F. alnus* as response variables in their own logistic regression models. For *R. multiflora*, the most important biotic, abiotic, and disturbance variables were native species richness ($\chi^2 = 13.6$; $p = 0.0002$), soil pH ($\chi^2 = 7.58$; $p = 0.0059$), and number of standing dead trees ($\chi^2 = 5.33$; $p = 0.021$). Sites with more native species richness, more alkaline soils, and fewer standing dead trees were more likely to be invaded by *R. multiflora*. In the combined model for *R. multiflora*, native species richness ($\chi^2 = 10.7$;

$p = 0.0011$; odds ratio = 2.69 with 95% confidence limit = 1.58–5.35) and soil pH ($\chi^2 = 6.32$; $p = 0.012$; odds ratio 15.2 with 95% confidence limit = 1.92–147.8) remained significant. For *F. alnus*, the most important biotic, abiotic, and disturbance variables were the ratio of sapling density to tree density ($\chi^2 = 4.82$; $p = 0.028$), soil total nitrogen ($\chi^2 = 4.11$; $p = 0.043$), stand age ($\chi^2 = 6.89$; $p = 0.0087$), and fire ($\chi^2 = 9.02$; $p = 0.0027$). Sites with high sapling to tree density ratios, more soil nitrogen, that are younger, and have been historically burned were more likely to have *F. alnus* present. In the combined model for *F. alnus*, the sapling density to tree density ratio ($\chi^2 = 6.06$; $p = 0.014$; odds ratio = 1.32 with 95% confidence interval = 1.06–1.65) and fire ($\chi^2 = 12.8$; $p = 0.0003$; odds ratio = 17.5 with 95% confidence interval = 3.66–84.2) remained significant. The adjusted R^2 for the *R. multiflora* and *F. alnus* combined models were 0.37 and 0.30, respectively. However, given the small sample size for the variable of interest (each species), these models may be overfitted and are, therefore, less reliable. Nonetheless, running each of the independent variables separately resulted in the same variables being significant.
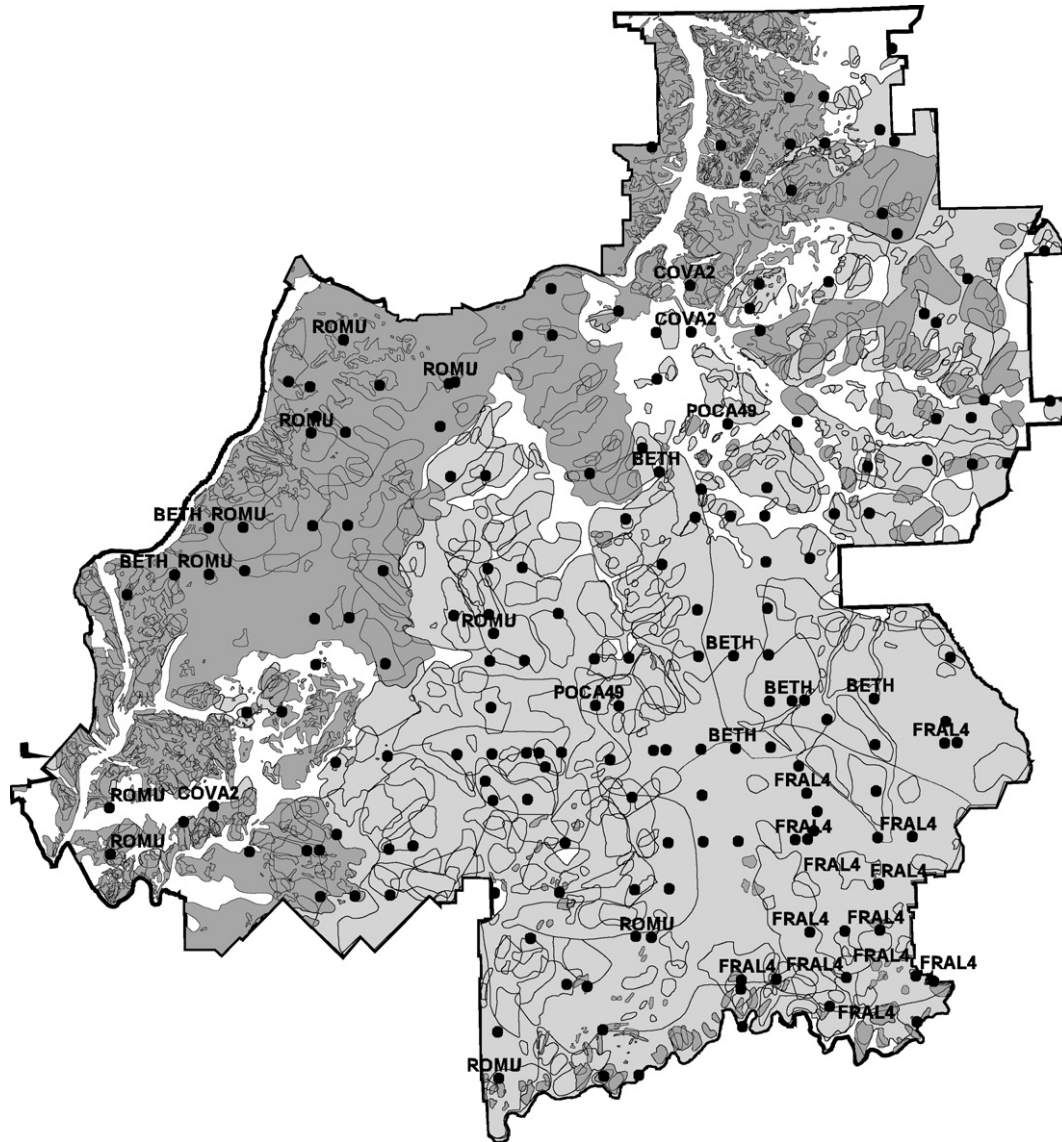
Fig. 5. Gypsy moth (light gray), elm spanworm, and cherry scallop moth defoliations (much overlap, both are dark gray) with the five exotic invasive and one exotic species (BETH, *Berberis thunberjii*; COVA2, *Coronilla varia*; FRAL4, *Frangula alnus*; POCA49, *Polygonum caespitosum*; ROMU, *Rosa multiflora*).

4. Discussion

4.1. General patterns

Invasive exotic and exotic species make up only 1% and 11%, respectively, of the ANF flora, using survey data from FIA plots which focus on forest interiors. A more comprehensive survey that includes road and trail surveys would likely increase the percentages, possibly reaching exotic species levels found in nearby herbaria (i.e., 29% in West Virginia University's herbarium; Huebner, 2003). Approximately, 30% of Pennsylvania's flora is believed to be exotic (Rhoades and Block, 2000) and 10.8% of the vascular plants in the conterminous U.S.A. are exotic, while 43.8% of Hawaii's flora is exotic (Vitousek et al., 1997). However, ANF exotic species levels were higher than in forest interiors of the Monongahela National Forest of West Virginia in which 1% of 80-year-old forest flora and 3% of 15-year-old clear cut flora were exotic and only 0.3% of the 80-year-old forests and 1% of the 15-year-old clearcuts were invasive exotic plants (Huebner and Tobin, 2006). The ANF exotic plant percentage was also higher than the

approximate 7% and 3% found in the MidAtlantic and Northeastern regional Forest Health Monitoring P3 plots (neither region of which included data from Pennsylvania or West Virginia), respectively (Stapanian et al., 1998) and deciduous woodlands of Calalonia (0.2%), the Czech Republic (1.0%), and Great Britain (3.1%) (Chytry et al., 2008). Despite this higher percentage of exotic species colonization compared to other eastern forests, the abundance data available confirms that ANF colonization by most invasive exotic species is still at early stages of establishment and has not yet escalated to a spread stage.

4.2. Important biotic variables

We predicted that native species richness would be the most important biotic variable. Our results support other studies that have shown a positive relationship between native and exotic species richness and invasion (Planty-Tabacchi et al., 1996; Wiser et al., 1998; Higgins et al., 1999; Lonsdale, 1999; Stohlgren et al., 1999; Huebner and Tobin, 2006; Belote et al., 2008). As in these studies, this positive relationship between native plant species
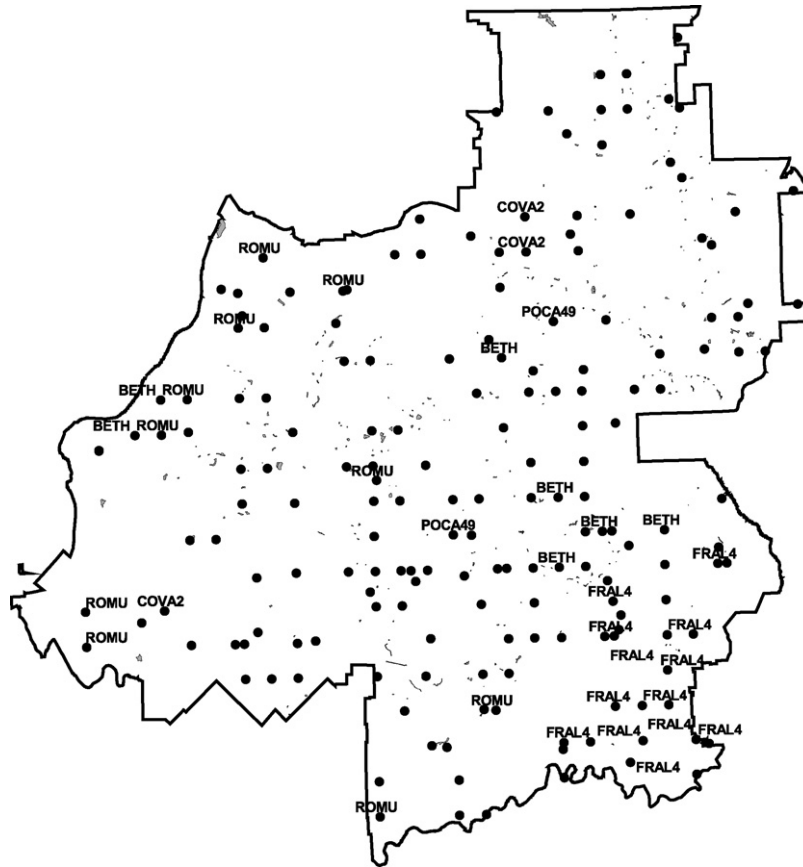
Fig. 6. Known plantings of exotic plant species and distribution of the five invasive exotic species and one exotic species (BETH, *Berberis thunberjii*; COVA2, *Coronilla varia*; FRAL4, *Frangula alnus*; POCA49, *Polygonum caespitosum*; ROMU, *Rosa multiflora*).

richness and both richness and presence of exotic invasive plants suggests that community saturation has not occurred, i.e., there are plenty of open niches and resources are abundant. Secondly, this relationship suggests that ANF's invasibility is currently being driven by immigration processes rather than competitive inter-actions among native and exotic species (Brown and Peet, 2003). At this stage, locating propagule sources may be the most efficient way of reducing invasive species spread in ANF. We also expected

the more species-rich forest type would be more likely to be invaded, but none of the forest types were significantly richer than any other. Density of potentially competing species in the sapling and overstory strata also does not appear to play an important role, except when evaluating *F. alnus* separately. Dominant native species, such as *Dennstaedtia punctilobula* (Michx.) Moore (hays-cented fern), which is known to prevent regeneration of native species (Horsley, 1993; McWilliams et al., 1996), may also prevent the establishment of invasive exotic plants. A preliminary analysis of quadrat cover data from 1999 to 2003 did not reveal a lack of invasion on plots with high fern cover (>70%; 4 plots with invasion and 15 without invasion) compared to sites with low fern cover

Table 3
Logistic regression showing the combined biotic, abiotic, and disturbance model using invasive exotic (IE) as a response variable and independent variables with $p \leq 0.1$ in the separate models

Model	Significant variables	Unit	Odds ratio	Confidence interval
	IE		IE	IE
Adj R^2 = 0.24				
N + pH + StAge + Dplant	N	0.1	1.77	1.30–2.50
	Dplant	1	6.79	1.85–25.01
Adj. R^2 = 0.10				
E + pH + StAge + Dplant	E	0.1	1.02	1.01–1.04
	Dplant	1	6.24	1.75–22.25
Adj. R^2 = 0.15				
N + pH + StAge	*N*	0.1	1.79	1.33–2.49
Adj. R^2 = 0.10				
E + pH + StAge	E	0.1	1.15	1.01–1.31
	pH	0.1	3.68	1.18–11.87

Variables listed here were significant at a $p \leq 0.05$. N = native species richness; E = exotic species richness (excluding invasive exotic species); StAge = stand age; Dplant = distance to exotic planting.

Table 4
Logistic regression showing the combined biotic, abiotic, and disturbance model using all exotic (AE) species as the response variable and independent variables with $p \leq 0.1$ in the separate models

Model	Significant variables	Unit	Odds ratio	Confidence interval
Adj. R^2 = 0.43				
N + NFP + StAge + Bbdm	N	0.1	2.71	0.95–3.97
	StAge	1	0.81	0.66–0.96
	NFP	1	4.30	1.40–15.2
Adj. R^2 = 0.43				
N + NFP + StAge	N	0.1	2.71	1.95–3.97
	StAge	1	0.80	0.66–0.96
	NFP	1	4.30	1.40–15.2

Variables listed here were significant at a $p \leq 0.05$. N = native species richness; StAge = stand age; NFP = presence of non-forest (yes or no); Dplant = distance to exotic planting; Bbdm = beech bark disease mortality.

(<10%; 10 plots with invasion and 45 without invasion), indicating a lack of invasive species propagules rather than an inability to compete. An experimental approach using abundant invasive plant seed is required to adequately determine the competitive impact of native interfering species on the establishment of invasive plants.

4.3. Important abiotic variables

We hypothesized that variables indicative of mesic and fertile site conditions would be the best predictors of site vulnerability to invasion by exotic plants. Our analyses only manifested one important abiotic variable, which was soil pH. Because pH is determined in part by base-forming cations, such as Ca, Mg, and NH_4, it is often used as a measure of soil fertility (Bigelow and Canham, 2002). More alkaline soils were indicative of the presence of invasive exotic plants and not exotic (non-invasive) plants. Thompson et al. (2001) also found a positive relationship between successful invasion and more alkaline soils in grassland systems. In fact, increasing soil acidity has been used in restoration efforts to inhibit invasion by unwanted plants (Owen and Marrs, 2000). However, the importance of soil pH was not shared by all exotics as a response variable, which may be indicative of a greater variety of species that have a wider range of soil pH tolerances, including *R. acetosella*, a calcifuge (Tyler and Strom, 1995). The Thompson et al. (2001) grassland study also showed that early invasion was closely related to both disturbance (increased bare ground and light) and alkaline soils, while increasing abundance of these species overtime was related only to soil pH. If we can assume that forest invaders behave similarly to grassland invaders, an increase in abundance of the invaders in the ANF is more likely to occur in more alkaline soils. However, the presence of *F. alnus*, which shows signs of local spread, was not related to soil pH but instead higher soil N. The prolonged presence of *F. alnus* may be manifesting a consequent change in soil composition, though it still may mean that soils high in nitrogen are more likely to be invaded by *F. alnus*. *F. alnus* is not an N-fixing species, however, other invasive exotics have been documented to increase soil N levels possibly via decomposition of leaf litter that is high in N and other nutrients (Ehrenfeld et al., 2001; Rodgers et al., 2008). As is problematic with many invasive species studies, not knowing the site conditions prior to the invasion, especially invasions in the spread stage, makes it impossible to be certain which came first—the site condition or the presence of the invader.

4.4. Important disturbance variables

As predicted, disturbance was important, but it only manifested itself strongly with stand age and the presence of non-forest land. There were several counterintuitive results involving the disturbance variables, including standing dead trees, beech bark disease mortality, and distance to the nearest propagule source. The counterintuitive relationship between beech bark disease mortality and proximity to a propagule source may be explained by a lack of data. While the presence of invasive exotic species was uncommon, it was not rare; the probability of occurrence was much greater than five times in a hundred trials, meaning a coefficient of variation over 50% (King and Zeng, 2001; Dixon et al., 2005). Nonetheless, the joint occurrence of invasive exotic plants and beech bark disease mortality or a nearby, known exotic planting was rare. The small area impacted by both beech bark disease mortality and exotic species plantings resulted in an underestimate of the probability of occurrence of two uncommon variables (i.e., invasive exotic plants and beech bark disease mortality) and an overestimate of the probability of an uncommon (invasive exotic) and common (no beech bark mortality or exotic plantings more than 1 km away)

variable (King and Zeng, 2001). Our research has revealed an important weakness of FIA data compared to research that stratifies samples equally using potentially important variables. Nonetheless, stands that suffer from beech bark disease mortality often have excessive beech bark sprouting, which may prevent invasion. Such sites would have a high sapling to tree ratio, but this variable was only significant when explaining the establishment of *F. alnus*.

Ironically, the known locations where exotic plants were deliberately planted within the ANF do not appear to be a significant propagule source. Several invasive species documented to have been planted, including *E. umbellata* and *C. orbiculatus*, were not found in these FIA plots. Likewise, *Fallopia japonica* (houtt.) ronse Decraene (Japanese knotweed), which is currently known to populate several roads and streams in the ANF (personal observation), was not found in a single FIA plot. The relatively small percentage of invasive exotic plants in the ANF may be due in part to a lack of propagule sources. However, the fact that invasive exotic plants were found is also indicative of existing seed sources that our study may not have measured, which may include other corridors (skid trails, landings, ATV and snowmobile trails, pipelines, and power lines). We also expected more standing dead trees to be indicative of a more open canopy or defoliation events, but this was not the case. The relationship between fewer standing dead trees and the presence of exotic invasive plants, may be explained by these variables' shared association with forest age or the stage of stand development (Castello et al., 1995; Sano, 1997). There was a trend (though not significant) for older stands to have more standing dead trees. Some of the older stands may be in or just coming out of an understory re-initiation stage in which large snags and gap formation are common, making invasion more likely. Likewise, some of the younger stands may be in a stem-exclusion stage in which tree mortality is high but gap formation is rare due to rapid canopy closure from surrounding trees, possibly reducing the likelihood of invasion. This discrepancy between standing dead trees and plant invasions further highlights the need for a more direct measure of light or gap formation in these stands.

Defoliation and other pathogenic events in the ANF have not yet resulted in a significant change in the current canopy structure (between 1999 and 2006) and any subsequent increase in light reaching the forest floor during this time period. Changes in canopy cover or foliar transparency that did occur did not make such sites more vulnerable to invasion by exotic plants. Moreover, the extensive road system in the ANF has not yet played a measurable role in increasing invasions into the forest interiors. Several studies have shown that forest edges serve as a barrier to invasion from roadside invasive species populations (Parendes and Jones, 2000) possibly due to decreasing light and pH as one goes from the roadside into the forest (Honnay et al., 2002). However, more shade-tolerant invasive species, such as *Microstegium vimineum* (Trin.) A. Camus (Japanese stilt grass), appear less likely to be deterred by forest edges (Huebner, 2007). While *M. vimineum* was not documented in the FIA plots, this species is known to be in nearby State Forests (personal observation), highlighting the importance of using these FIA plots to monitor for new invasions.

It was not surprising that fire was an unimportant disturbance variable, given that fires have been relatively infrequent in ANF. The spatial association of older fires and *F. alnus* invasion found in this study, while significant, may only be coincidental. Evaluations of fire records, *A. saccharum* die-back, and *F. alnus* invasions in other forests should be consolidated to see if similar patterns exist.

4.5. Scale effects

Our strongest variables, native and exotic species richness, soil pH, presence of non-forest land, and stand age were measured at

the same scale as the response variable. Plant and soil composition data are both tedious to collect and often spatially heterogeneous at fine scales. While one may predict from our results that exotic species are more likely to occur in alkaline soils within the more species rich areas ANF, gathering the data to spatially delineate these locations is labor intensive and costly. Consequently, using geospatial statistics, such as kriging, to predict plant invasions may not be realistic at the FIA intensive plot scale. There are examples of using kriging to successfully predict invasive plant species spread rates (Frappier et al., 2003), the location of weeds in agricultural fields (Cardina et al., 1995), and predicting wetland plants using water chemistry data (van Horssen et al., 1999), but these are at relatively fine scales with 1-m to 1-km between samples. These studies predict the spatial occurrence of plants that are common in the area in question. Even if we assume spatial data collected every 1200 ha for independent variables, such as soil pH, are adequate, a lack of invasive exotic plants at most of these points makes it difficult to refine the invasion gradients associated with each variable.

More importantly, a comparison of the significant variables associated with invasive exotic plants vs. all exotic plants may indicate that the patterns we see now may not be held constant as invasive exotic plants increase in number or abundance. While some invasive exotic plants, including *Berberis thungbergii* can change their surrounding environment (increase soil pH; Ehrenfeld et al., 2001; Rodgers et al., 2008) in such a way that facilitates further invasion, some other patterns may change. For instance, it is conceivable that extensive invasion of certain species, such as *M. vimineum* could increase fire frequency, which may also help perpetuate *M. vimineum*'s presence much like it does *Bromus tectorum* (cheat grass) in the Southwest (D'Antonio and Vitousek, 1992), but fire would not be the initial mechanism behind *M. vimineum*'s establishment. Our comparison of *R. multiflora* (representative of the early establishing invasive exotics) and *F. alnus* (potentially spreading, at least locally), did manifest differences in key variables with only *F. alnus* being associated with high soil nitrogen, high sapling to tree count ratios, and the occurrence of fire and not being associated with native species richness or soil pH. Consequently, it is important to distinguish between variables that predict for early establishment and those that may predict subsequent spread of invasive exotic plants.

We encourage FIA planners to continue similar intensive plot sampling, as conducted in the ANF in Pennsylvania, nationwide but also to consider adding plots such that key variables like disturbance type (i.e., history of being defoliated, burned, or harvested) and forest type have an adequate sample size for a given disturbance type, forest, province, or region. This stratified approach will give variables typically measured at a coarser scale a more equal standing with the variables measured at the same scale as the response variables. The latter may improve our ability to predict future new invasions in previously uninvaded forests or to locate existing infestations. Also, we hope to re-evaluate these plots in 10 years but know that presence/absence data tell us less about changing vegetation than measures of abundance (cover). Currently, estimates of cover only in the large subplots results in all but the most dominant species having similar abundance values, making it difficult to detect smaller changes in cover. Consequently, increases in invasive exotic species may not be detected until they actually dominate the subplots. We also encourage the FIA planners to return to measuring cover in the quadrats in order to better detect future increases or decreases in exotic and native species. This will become even more important as we try to define the variables associated with successful invasive plant species spread instead of early establishment.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2008.08.036.

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