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The spread of woody exotics into the forests of a northeastern landscape, 1938–1999[1]

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HUNTER, J. C. AND J. A. MATTICE (Department of Biological Sciences, State University of New York College at Brockport, Brockport, NY 14420). The spread of woody exotics into the forests of a northeastern landscape, 1938–1999. J. Torrey Bot. Soc. 129:220–227. 2002.—This study documents changes in the distribution of non-native woody species from 1938 to 1999 within 30 forests of a 54 km^2 landscape in Monroe County, New York. Within these forests, the mean number of exotic species increased nearly three-fold from 1938 to 1999, and two species not naturalized within the landscape in 1938, *Lonicera morrowii* and *Rosa multiflora*, had become widespread by 1999. In 1999, the most abundant exotic was *Lonicera morrowii*, which had greater cover within forests on wetter portions of the landscape where much of the surrounding agricultural land had been abandoned. Though exotics accounted for < 10 % of relative cover within the shrub layer and < 1 % of the tree layer, their cover was higher in portions of some forests, especially near edges. In 1999, six species had covers > 25 % within patches > 100 m^2: *Acer platanoides*, *Crataegus monogyna*, *Ligustrum vulgare*, *Lonicera morrowii*, *Robinia pseudoacacia* and *Rosa multiflora*. These species in particular may represent on-going invasions that could alter this landscape's forested habitats.

Key words: Invasion, invasive species, introduced species, *Acer platanoides*, *Berberis thunbergii*, *Crataegus monogyna*, *Ligustrum vulgare*, *Lonicera morrowii*, *Prunus avium*, *Robinia pseudoacacia*, *Rosa multiflora*, *Salix fragilis*, *Sorbus aucuparia*.

Intentionally and accidentally, humans have transported thousands of plant species beyond their prior (native) range (Elton 1958; OTA 1993; Mack et al. 2000). In their new environs, a fraction of these introduced (exotic) species have "naturalized", their populations now persisting without human intervention. These naturalized species are the most rapidly changing portion of our floras, and additional species are continually being introduced and becoming naturalized (OTA 1993; Rejmanek and Randall 1994; Kowarik 1995).

Of recently naturalized species, some have rapidly changing ranges and rapidly changing local abundances (Nuzzo 1992; Catling and Porebski 1994; Sheeley and Raynal 1996). These expansions of range and abundance entail dispersal to, and successful establishment in, additional patches of habitat. Therefore, species with expanding distributions and increasing local abundance are referred to as "invasive" species (Pysek 1995a), and their invasions are having dramatic economic and ecological impacts, particularly where they have become abundant within a habitat (OTA 1993).

Documentation of invasions not only identifies invasive species and provides valuable information for resource managers, but also provides data for developing and testing models of the invasion process, for determining what site attributes contribute to the success of invaders and for identifying the traits that distinguish invasive from non-invasive species. Yet, of the hundreds of scientific papers dealing with plant invasions, relatively few are historical studies (Pysek 1995b). This is because historical records of species' distributions are very limited and generally at a regional scale. Most historical studies are based on herbarium records and floras (Nuzzo 1992; Catling and Porebski 1994; Sheeley and Raynal 1996). Unfortunately, such records are not very useful for documenting the changes in abundance and local distribution that are the direct product of the invasion process.

In contrast, our investigation was a landscape scale (10^1-10^2 km^2) study of change in the abundance and distribution of non-native plants. It was based on a unique data set, a census during the 1930's of the composition and structure of forests in Monroe County, New York. We re-

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located and re-inventoried 30 of these forests, documenting long-term changes in the distribution and abundance of woody exotics in the forests of a typical northeastern landscape.

Materials and Methods. STUDY SITE. Our study area was a 54 km^2 landscape in Monroe County, New York (Lat. 43°12′ Long. 77°56′). Its soils developed from glacial till on gently rolling terrain at 140–210 m elevation (Heffner and Goodman 1973). Mean annual rainfall is 81 cm. Mean January temperature is −5° C, mean July temperature is 21° C and the frost-free growing season lasts 150–180 days (NOAA 1994).

The landscape contains a mosaic of residential, agricultural, old field successional and forested lands. Most forests consist of young stands on recently abandoned agricultural land. Some however, are mature stands dominated by *Acer saccharum*, and *Fagus grandifolia*, with *Acer rubrum* also among the dominants in wetter areas, and with *Tilia americana* and *Fraxinus americana* abundant throughout. Most of these older forests have been selectively logged but never cleared for cultivation (Shanks 1966).

DATA COLLECTION AND ANALYSIS. We derived data on the historic flora and structure of the study area's older forests from a county-wide forest inventory conducted in the late 1930's (Shanks 1966; Unpublished data on-file at the Environmental Management Council, County of Monroe). All forests within the study area were described in 1938 and their locations marked on the County's tax assessment map. For each forest, the inventory included a list of woody species present, a cover estimate for each canopy species, typical heights and diameters for canopy trees, and notes on understory and herbaceous vegetation, logging history and grazing (Shanks 1966).

We used 1930 aerial photographs and the 1938 map of forest locations to relocate the forests inventoried in 1938. Of the 36 forests present in 1938, three no longer existed. We obtained access to 30 of the 33 remaining forests, and re-inventoried these in June and July of 1999. Forest areas ranged from 4 to 106 ha. Old stone walls marked the exact boundaries of all but portions of four forests, and for these boundaries the approximate location corresponded to roads.

In our re-inventory, we used methods similar to those of the 1938 inventory. In that inventory, after walking throughout a forest, Shanks, or his assistants, recorded a cover estimate for each tree species and a list of woody species in the forest (Shanks 1966). Each day, one to three forests were examined in this manner. In our 1999 re-inventory, we obtained comparable search times by crossing the forest interior at approximately 50 m intervals. We compiled a complete list of vascular plants for each forest with nomenclature following Gleason and Cronquist (1991). For each tree, shrub and woody vine species, cover was visually estimated within the tree, shrub (.5–3 m in height) and herbaceous layer (< .5 m). Besides estimating cover throughout the entire forest, we estimated the cover of each species in the band of forest within 10 m of the forest edge, and its cover in the forest's interior (> 10 m from an edge). The width of 10 m was chosen for the forest edge because it could be readily determined in the field and includes most of the narrow edge-influenced zone that Burke and Nol (1998) found in similar forests in Ontario. We also noted if a species covered > 25 % of the ground within any square area ≥ 10, 100 or 1000 m^2 (i.e., if it was locally dominant within the forest).

Beyond documenting long-term change, we evaluated if there was a correspondence between particular site attributes and the presence of exotics. Attributes evaluated were: forest area, surrounding land use (percent of forest perimeter bordering agricultural, successional and ruderal/horticultural vegetation), canopy disturbance, 1938 cover of elm (*Ulmus americana*), 1999 cover of sugar maple (*Acer saccharum*) and *Fagus grandifolium*, and soil properties (depth to water table, percent of soil < 2 mm, pH). These variables were selected because they could be quantified from readily available data sources (e.g., aerial photographs, prior inventory records, soil surveys) and similar variables have been related to the spread of exotics (Hutchinson and Vankat 1997; Stapanien et al. 1998; Mack et al. 2000)

The cover of *Acer saccharum* recorded during the 1999 survey and of *Ulmus americana* recorded during the 1938 survey were used as site attributes because of their relationship to disturbance history. *Acer saccharum* was the most abundant late successional species within these forests and its abundance has been negatively associated with exotic species cover in other studies (Hutchinson and Vankat 1997). *Ulmus americana* was the third most abundant canopy tree within these forests prior to the arrival of

Table 1. 1938 and 1999 Frequency and cover of exotic species of woody plants in forests (N = 30) near Brockport, New York. Relative cover values are the mean (± 1 SE) total cover (herb, shrub and tree layers combined) in forests where the species was present at that time. In 1938, cover values were recorded for tree species only.

	Frequency (%)		Relative Cover (%)	
Species	1938	1999	1938	1999
Solanum dulcamara	70	40	—	<1
Sorbus aucuparia	20	7	<1	1 ± 0.9
Prunus avium	20	80	<1	1 ± 0.2
Rosa canina	13	0	—	—
Crataegus monogyna	13	23	<1	2 ± 0.8
Pyrus malus	7	23	<1	<1
Robinia pseudoacacia	7	23	<1	1 ± 0.4
Catalpa speciosa	3	0	—	—
Picea abies	3	3	<1	<1
Lonicera morrowii	0	77	0	5 ± 1.5
Rosa multiflora	0	70	0	2 ± 0.8
Ligustrum vulgare	0	33	0	1 ± 0.5
Berberis thunbergii	0	23	0	<1
Salix fragilis	0	17	0	2 ± 0.7
Acer platanoides	0	7	0	11 ± 2.2
Ailanthus altissima	0	3	0	2
Alnus glutinosa	0	3	0	<1
Elaeagnus umbellata	0	3	0	<1
Prunus mahaleb	0	3	0	<1

Dutch elm disease. These trees died in the 1960's (J. Bobear, SUNY Brockport, personal communication), a time period not covered by the aerial photographs we examined.

We used a geographic information system to aid our analysis of relationships between the distribution of exotic species and forest area. From 1930 aerial photographs and the 1938 map of forest locations, we mapped the re-inventoried forests onto a U. S. Geologic Survey 7.5 minute quadrangle map. We then digitized the location of forest polygons to create an ArcInfo coverage.

In addition, from aerial photographs, we constructed a canopy disturbance history for each forest. By placing a dot grid upon the photographs (Avery and Berlin 1992), we estimated the area of gaps in each forest's canopy. A gap was defined as any break in the canopy layer > 2 m in diameter, filled with trees < 1/3rd the canopy's height. Percent of forest in canopy gaps was estimated from 1930, 1951 and 1999 photographs (1:1000 scale, on-file at County of Monroe, Rochester, NY).

From the 1999 aerials, we also estimated the percent of each forest's perimeter bordered by mature forest, successional vegetation (old fields/shrubland and successional hardwood forest), agricultural fields and other anthropogenic habitats (horticultural and ruderal vegetation). These determinations of adjacent vegetation types were checked later during our field work.

Using the County's soil survey (Heffner and Goodman 1973), the soil mapping units underlying each forest were identified and their relative area estimated with the aid of a dot grid (Avery and Berlin 1992). Based on these percents and the estimated engineering properties of each mapping unit (Heffner and Goodman 1973), a weighted average was calculated for each forest's soil pH, percent passing a 2 mm sieve, and depth of seasonal high water table.

Correspondence between site attributes and species' distributions was evaluated by Spearman rank correlation and principal components analysis (Zar 1999; Legendre and Legendre 1998). Prior to the principal components analysis, forest areas were log transformed and percentage variables were arcsine transformed, and then all variables were standardized to Z scores.

Results. In 1938, woody exotics were a minor component of the forest vegetation. Nine non-native species (7 trees, 1 shrub and 1 vine) were observed within the forests (Table 1). However, only one species (*Solanum dulcamara*) occurred in > 20 % of the forests, and none of the trees had > 2 % relative cover in the canopy of any forest. (Cover values were not recorded for shrub species in 1938.) On average,

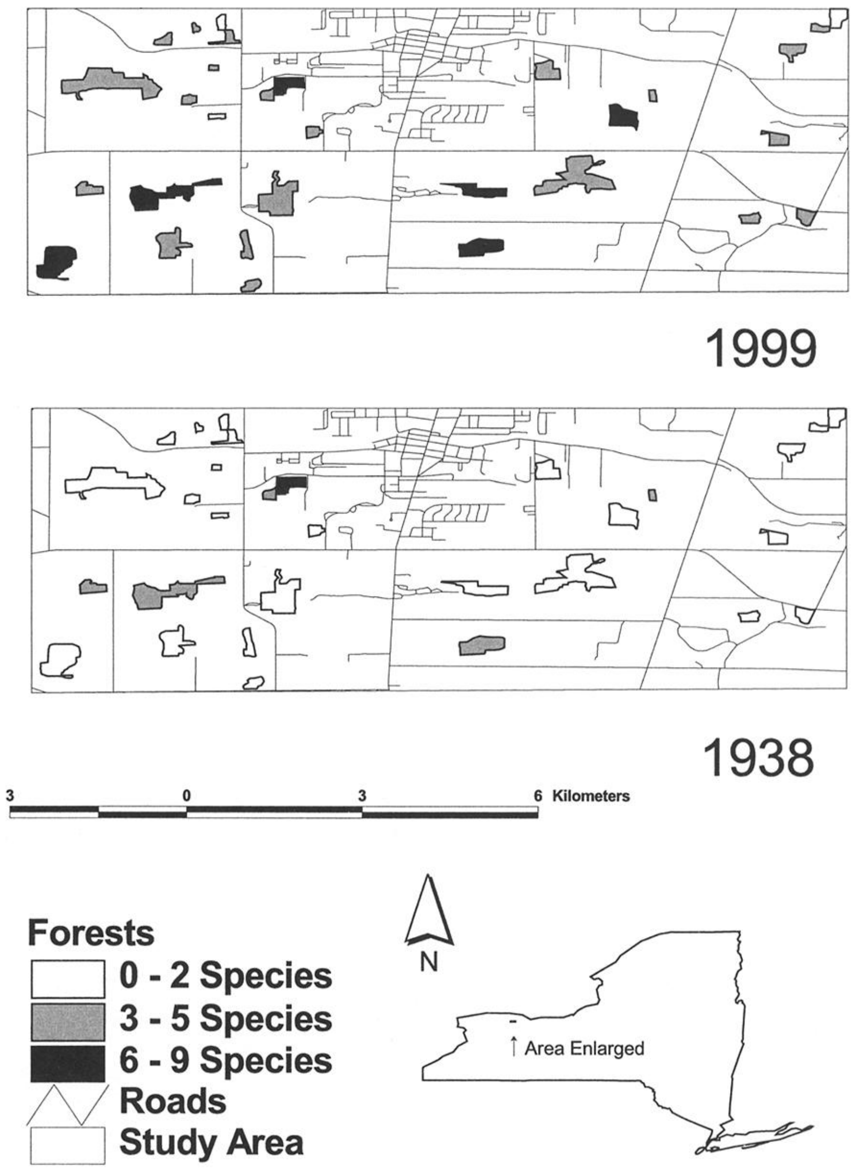


Fig. 1. Number of woody exotic species in 1938 and 1999 within 30 forests (4–106 ha) in the vicinity of Brockport, Monroe County, New York.

forests contained 1.6 ± .2 exotic species, and within the tree layer the relative cover of these species averaged .2 ± .06 %.

By 1999, the number of exotic species and their frequency within the forests were considerably greater (Fig. 1). Of the nine species present in 1938, four species decreased in frequency and four increased. The distribution of just two changed substantially: *Solanum dulcamara* decreased from 70 to 40 % of forests ($P < .025$, G test), and *Prunus avium* increased from 20 to 80 % of forests ($P < .001$, G test). However, ten additional species (4 trees and 6 shrubs) were observed in 1999 (Table 1). While three of these occurred in the outer 10 m of just a single forest (*Alnus glutinosa*, *Elaeagnus umbellata* and *Prunus mahaleb*), four were in > 20 % of forests (*Berberis thunbergii*, *Ligustrum vulgare*, *Lonicera morrowii* and *Rosa multiflora*). Thus, there were now both more exotic species and more species widely distributed than in 1938 (Fig. 2). On average, forests contained 4.4 ± .3 species

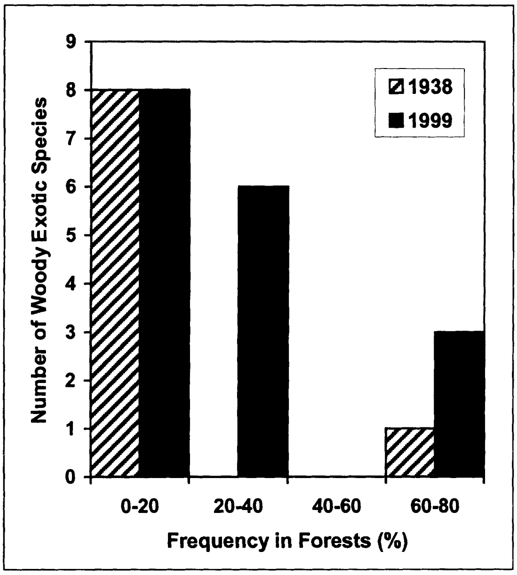


Fig. 2. Frequency in 1938 and 1999 of non-native woody species within 30 forests, Brockport, New York.

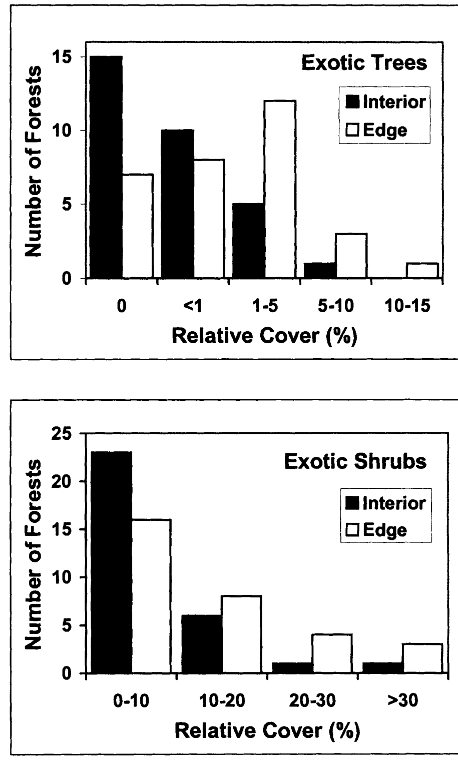
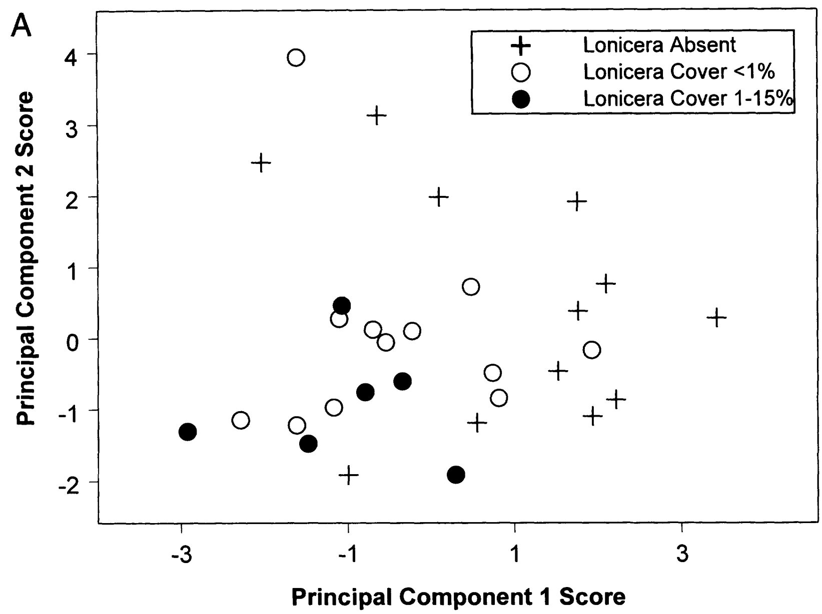


Fig. 3. Relative cover of exotic trees and shrubs within the interior and along the edge of 30 forests in Brockport, New York. Edge: forest area < 10 m from forest boundary; Interior: forest area > 10 m from boundary.

in 1999: 2 ± .2 species that were present in at least one forest in 1938 plus an additional 2.4 ± .2 species not observed in any forest in 1938. As a consequence, the number of exotics per forest had increased nearly three-fold over the 61 years (significant with $P < .001$, Wilcoxon paired-sample test).

Nonetheless, exotic species were still a minor component of forest vegetation in 1999. Within the tree layer, exotics had a relative cover of just .9 ± .2 % and within the shrub layer 7.6 ± 1.7 %. However, exotics were more abundant in some portions of the forests, particularly near edges (Fig. 3). Within 10 m of the forest edge, their relative cover within the tree layer was 2.2 ± .5 % versus .6 ± .2 % in the forest interior (difference significant with $P < .001$, Wilcoxon paired-sample test). Within the shrub layer, their relative cover was 11.7 ± 2.3 % near the edge versus 6.6 ± 1.5 % in the interior ($P < .001$, Wilcoxon paired-sample test). Also, six species had covers > 25 % within patches > 100 m^2: *Acer platanoides*, *Crataegus monogyna*, *Ligustrum vulgare*, *Lonicera morrowii*, *Robinia pseudoacacia* and *Rosa multiflora*. *Robinia pseudoacacia* dominated the tree canopy only where it appeared to have been planted. Of the others, only *Acer platanoides*, *Ligustrum vulgare* and *Lonicera morrowii* dominated patches in more than one forest. Patches of *Acer platanoides* occurred in two forests and consisted of several canopy individuals and a high density of understory saplings over areas 10^2-10^3 m^2. The shrub *Ligustrum vulgare* was locally abundant within both the herbaceous and shrub layers of six forests. The shrub *Lonicera morrowii* dominated patches, often at 100% cover, within 12 forests. Interestingly *Lonicera* seedlings and individuals < 50 cm were rare in most of these forests.

There was little correspondence between forest attributes or principal components derived from them and either the number of exotic species in a forest or the distribution of individual species among forests. Disturbance was the only attribute associated with the number of exotic species present. From 1930–1999, forest canopies experienced moderately high levels of disturbance. In 1930, canopy gaps occupied 23 ± 3.0 % of forest area, in 1951 16 ± 1.7 % and in 1999 12 ± 1.4 %, with half the forests having > 20 % of their area in gaps at one of these dates. Mean percent of area in gaps (1930–1999) was positively correlated with number of exotic species in 1999 ($P < .01$, $r_s = .482$), as was



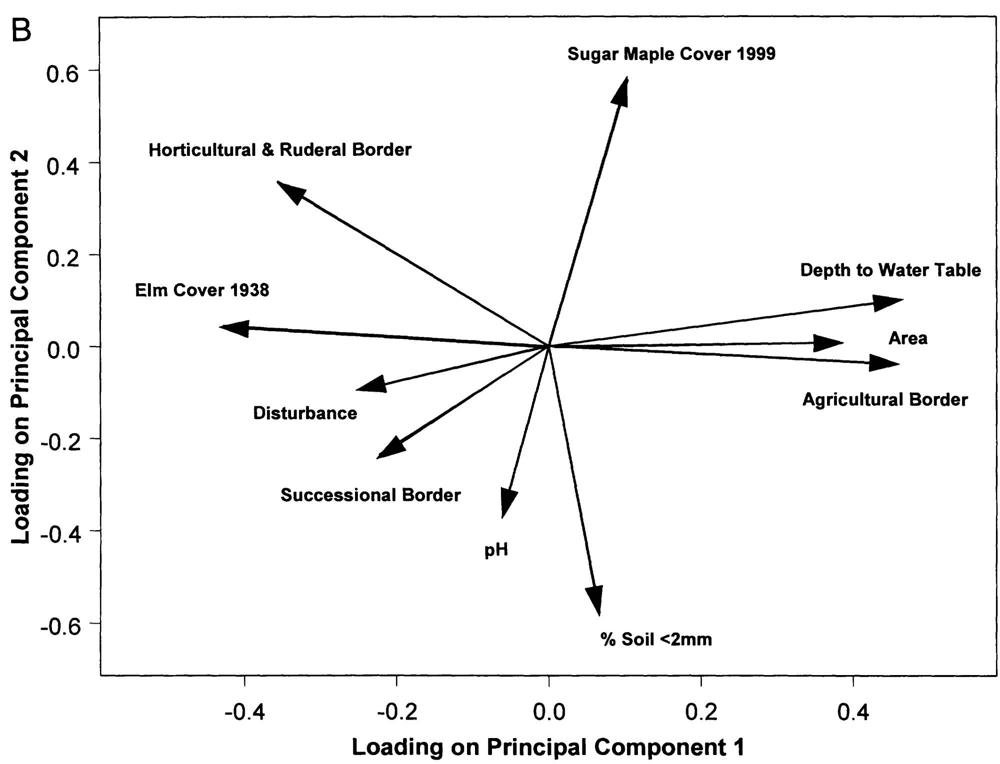


Fig. 4. A) Correspondence of *Lonicera morrowii* cover and scores on first two principal components for 30 forests at Brockport, New York; B) Loadings on the first two principal components for site attributes of 30 forests at Brockport, New York. Sugar maple cover = 1999 cover of *Acer saccharum*, Depth to water table = mean depth to seasonal high water table, Area = forest area, Agricultural border = percent of forest perimeter bordered by Agricultural lands, % soil < 2 mm = mean percent of soil particles passing through a 2 mm sieve, Successional border = percent of forest perimeter bordered by old fields/shrublands and forests < 60 years old, Disturbance = mean percent of canopy in gaps, 1938 Elm cover = 1938 cover of *Ulmus americana*, Horticultural & ruderal border = percent of forest perimeter bordered by horticultural and ruderal vegetation.

percent of area in gaps in 1999 ($P < .02$, $r_s = .454$).

Except for *Lonicera morrowii*, the abundance of individual species was not associated with any forest attribute or principal component derived from them. However, *Lonicera morrowii* was the only species that was both abundant and widespread (Table 1), and accounted for most cover by exotics. Its abundance was negatively correlated with forest scores along both the first and second components resulting from the principal components analysis of forest attributes ($P < .005$ and $P = .05$, Spearman rank correlation, Fig. 4a). Negative scores on the first axis were associated with smaller forests with a lower percent of their border in agricultural use, shallower depths to water table, and a higher percent of elm cover in 1938 (Fig. 4b). Negative scores on the second axis were associated with higher pH, a greater percent of soil < 2 mm and a lower cover of sugar maple (Fig. 4b). Overall, forests with negative scores on both components were in wetter portions of the landscape where much of the surrounding agricultural land had been abandoned or converted to other uses.

Discussion. Within these forests, more nonnative woody species were observed in 1999 than in 1938. This increase could be due merely to our 1999 species lists being more complete than the 1938 lists, but this possibility is unlikely to account for much of the increase. First, most of these species would not be overlooked easily. They are conspicuous and were widely planted as ornamentals in the 1930's, and thus probably familiar. Second, as of the 1930's, *Lonicera morrowii* and *Rosa multiflora* were not included in regional floras (Beckwith and Macauley 1896; Zenkert 1934) and probably not widely established, while in 1999 these were two of the most widespread species. More likely, the greater number of exotics in the 1999 data reflects an actual increase within these forests.

Though the number of exotic species had increased, most of these taxa were still uncommon and seem unlikely to become more abundant within these forests. Of the 17 species observed in 1999, six either occurred in fewer forests than in 1938 or were near the edge of just a single forest. Eight others had become more frequent yet still were not abundant in any forest. For example, *Prunus avium* was in six forests in 1938 but in 1999 it had not attained > 5 % cover in any of them (nor in any other forest). Thus, based on current distributions and the past 61 years change, only *Lonicera morrowii* and perhaps *Acer platanoides*, *Ligustrum vulgare*, or *Rosa multiflora* seem likely to become more abundant in the near future.

These results were similar to those of several other studies reporting a low abundance of exotics within mature deciduous forests, or an association between exotics and disturbance or forest edges (Brothers and Spingarn 1992; Burke and Nol 1998; Stapanian et al. 1998; Goldblum and Beatty 1999). However, using historic or current patterns to predict future abundance is unreliable, particularly because during the initial stage of invasion species are at low abundance (Kowarik 1995; Mack et al. 2000). Furthermore, historic events can aid invasions. For example, in this study, changes in human land use and disturbance caused by Dutch elm disease may have aided invasion of forests by *Lonicera morrowii*. Thus, to an extent, most species observed could be increasing in abundance or represent a potential future invasion. In fact, five of these species have been reported as spreading through forests and other habitats in the northeast: *Acer platanoides* (Wyckoff and Webb 1996), *Ailanthus altissima* (Knapp and Canham 2000), *Berberis thunbergii* (Ehrenfeld 1997; Silander and Klepis 1999), *Lonicera morrowii* (White et al. 1993; IPC 2000), and *Rosa multiflora* (Robertson et al. 1994).

Whether most of the exotics or virtually none represent on-going invasions, locally abundant species, such as *Lonicera morrowii*, *Ligustrum vulgare*, and *Acer platanoides*, should be of particular concern. These species already have demonstrated the ability to occupy a large portion of the space at local sites within at least some forests. Through expansion of existing patches and formation of additional patches, these species could become abundant throughout forest understories, and many invasions proceed in this manner (Moody and Mack 1988). Monitoring the establishment, persistence and expansion of exotic-dominated patches could identify such on-going invasions, as well as provide insight into the invasion process.

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