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Fruit type, life form and origin determine the success of woody plant invaders in an urban landscape

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Abstract The spread of alien plant species is a critical ecological event worldwide, but the forces that control this spread are not well documented. Alien plant species are well known to disrupt ecological services of native ecosystems, change the composition of native habitats, and often lead to the extirpation of native flora and fauna. Here, we report on life history patterns of plant species with rapidly spreading and declining ranges in North America's major urban region. We tested for differences in life history traits between the 466 native and alien woody flora of the New York metropolitan area. We also examined the relationship between life history traits and change in distribution in the New York metropolitan area between 1900 and 2000. Native and alien species of the New York metropolitan area differ with respect to pollination vector and breeding system. However, pollination vector and breeding system are not associated with success, defined here as increasing range spread in the urban environment; instead, fruit type (dispersal), life form and origin are important determinants of success. Alien species that are deciduous trees, shrubs or vines with fleshy fruit are the most successful in increasing their distribution in this urban landscape. Newly introduced species with these characteristics are expected to have a better chance at establishing in similar urban landscapes and should be targets for intensive management. The ability to predict which alien species will become invasive is also a valuable tool for the prevention of invasions by newly introduced plant species.

Keywords Biological characters · Life history · Invasive species · Alien plants · Urban ecology · Dispersal · New York metropolitan area

Introduction

As the world becomes more and more urbanized, there is increasing concern over the loss of natural habitats and native species as well as the introduction of alien species. Alien plant species are well known to disrupt ecological services of native ecosystems, change the composition of native habitats, and often lead to the extirpation of native flora and fauna (Williamson 1996; Myers and Bazely 2003). Cities act as immigration hubs

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for alien species; they have rich alien floras and serve as sources of alien species for surrounding suburban and rural areas (Pyšek 1998). Urbanization brings about substantial changes in native terrestrial plant communities due to habitat destruction and the introduction of alien species (Robinson et al. 1994). These changes often include the dominance of alien invasive plant species within native plant communities and the biotic homogenization of urban habitats (McKinney and Lockwood 1999), causes of much concern worldwide. Despite these issues, biological invasions in urban regions have been poorly studied. Understanding the patterns of alien species spread in urban landscapes is critical to the task of managing for ecological integrity.

Urban regions have unique habitats and constraints on the persistence and spread of plant species. Invasive non-indigenous plant species tend to succeed in urban, fragmented landscapes, but the mechanisms for their success are not well characterized. The number of alien species present in an urban flora is related to the degree of human-mediated disturbances. For example, the majority of the alien flora of Berlin became established in the last 150 years concurrent with industrialization (Kowarik 1990). In eastern and mid-western cities in the United States, alien and native species richness was related to the date of city settlement (Clemants and Moore 2003). In central Europe, the number and relative contribution of alien species to the flora increased with city size (Pyšek 1998). Distribution patterns of alien species are also related to land use, industries, the presence of botanical gardens and horticultural trade (Gilbert 1989).

While interactions with the environment clearly affect the ability of an alien species to succeed and become invasive in urban landscapes, the characteristics of the species should be the main predictor of range expansion (Reichard and Hamilton 1997). The ability of a species to establish and invade new areas should be related to traits that generally influence reproduction and survival (Myers and Bazely 2003). Plants with life history traits that allow rapid population growth, efficient pollination, dispersal and reproduction in fragmented landscapes would be expected to succeed. Therefore, it should be possible to use these general life history traits to determine which species are most associated with the ability to persist and spread in an urban landscape. Relating range size to these life history traits allows for the prediction of invasive success (Reichard and Hamilton 1997).

Some urban centers have published floras dating back at least 100 years, and these allow one to study the history of species change during rapid urbanization. It is essential to document changes in floras from the onset of urbanization as this may reveal critical features that are associated with a species ability to persist in urban landscapes (Robinson et al. 1994). Outside of Europe, however, there are very few complete floras documenting the success of introduced plant species over time (Pyšek 1998). For the New York metropolitan area, the Brooklyn Botanic Garden has a complete list of the woody flora and a measure of how much each species has changed in distribution between 1900 and 2000 (Clemants and Moore 2005). Using this extensive data set, we examine the hypothesis that some plant species are predisposed via their life history traits to be more successful in an urban landscape. The link between life history traits and invasiveness has been widely debated, but very few studies have been made specifically in urban regions (but see Robinson et al. 1994). Most past studies of the relationship between life history traits and invasion success only qualitatively identify invasive species. In contrast, we use a direct measure of the distribution change in the New York metropolitan area of each species in the flora over 100 years. The results from this study may enable us to make generalizations about which species will successfully persist, spread or decline as a region undergoes urbanization and which species will become invasive. The results will also allow us to gain a better understanding of the mechanisms of biotic change associated with plant invasions and help us manage against invasions in urban landscapes.

Methods

The New York Metropolitan Flora Project (NYMF) is a comprehensive project aimed at documenting the entire flora in the New York metropolitan area. The flora includes only vascular plants and only established populations that grow without cultivation (Moore et al. 2003). The region covered in this project includes 25 counties in New York, New Jersey and Connecticut within approximately an 80-km radius of New York City (Moore et al. 2003). This area covers ~19,800 km^2 (Moore et al. 2003) and includes the most densely human populated region in the United States with a population of ~21.2 million (Hobbs and Stoops 2002). The New York metropolitan area was divided into 964 5 × 5 km blocks using the New York Transverse Mercator Grid, the same grid system used in the *Atlas of Breeding Birds of New York State* (Andrle and Carroll 1988). Presence of a plant species, based on herbarium collections, field observations and published data, was recorded in each 25 km^2 block (Moore et al. 2003). For more information on the species data collection pertaining to the NYMF please see Moore et al. (2003).

We selected life history traits that could be determined from published floras and were likely to influence a species distribution. For each species, life history traits were assigned in five categories: origin (native or exotic), fruit type, breeding system, life form, and pollination vector (Table 1). Fruit type is an important determinant of dispersal ability for woody plant species. The distribution of plants in anthropogenically disturbed habitats depends on effective dispersal (Hodkinson and Thompson 1997). Reproductive attributes have been shown to be determinants of invasiveness (Reichard and Hamilton 1997). Life form is strongly correlated to species range sizes (Kelly 1996; Reichard and Hamilton 1997) and success in urban areas (Robinson et al. 1994). The type of pollination vector (i.e., wind, insect, bird, etc.) can also determine range size (Kelly 1996; Kelly and Woodward 1996). Traits assigned were based on descriptions of each species in five of the region's most comprehensive floras (Rehder 1940; Hough 1947; Fernald 1950; Dirr 1983; Gleason and Cronquist 1991). A total of 466 species were characterized.

In order to assess the change in range in the New York metropolitan area for each species between 1900 and 2000, a change statistic was used (Clemants and Moore 2005). The NYMF includes records of species distribution from the late 1800s to the present. Records of species occurrences after 1988 were greater due to an increase in collection effort when the NYMF project was initiated. Records before 1988 were based only on herbarium collections, field observations and published data as described above. Therefore, a species may show an increase in range from 1900 to 2000 due to collection effort only and using an absolute measure of change in recorded range size would be biased towards sampling effort. Instead, the change statistic was used, which is a measure of relative change in recorded range size and was calculated using the methods described in Telfer et al. (2002). This method minimizes sampling bias (Telfer et al. 2002).

Table 1 Representation of life history traits in the flora of the New York metropolitan area

Category	Trait	Number	%
Origin	Native	281	60.3
	Alien	185	39.7
Fruit type	Wing	107	23.0
	Dry	80	17.2
	Fleshy	246	52.8
	Nut	33	7.1
Life form	Coniferous tree	24	5.2
	Coniferous shrub	4	0.9
	Broad-leaved deciduous tree	133	28.5
	Broad-leaved deciduous shrub	247	53.0
	Broad-leaved vine	27	5.8
	Broad-leaved evergreen shrub	29	6.2
	Parasitic shrub	2	0.4
Breeding system	Dioecious	81	17.4
	Monoecious	93	20.0
	Hermaphroditic	283	60.7
	Polygamous	9	1.9
Pollination vector	Bird	1	0.2
	Insect	340	73.0
	Wind	103	22.1
	Insect/wind	22	4.7

Percentages and numbers are out of a total of 466 species, the total number of species in the woody flora not including hybrids

The number of blocks each species was present in was counted for two time periods, 1900–1950 and 1951–2000. These counts were then calculated as proportions by dividing the number of blocks a species was present in by the number of blocks in the total survey area. The proportions were logit-transformed and a weighted least squares linear regression model was fitted to the relationship between the counts for each time period (Clemants and Moore 2005). This line represents the change of the average species. The standardized residual for each species from the regression line provided the change index, or the relative change in range (Telfer et al. 2002). If a species was recorded in fewer blocks than the average species, then its range decreased between 1900–1950 and 1951–2000 and its change index was negative. If a species was recorded in more blocks than the average species, then its range increased between the two time periods and it had a positive change index. The change index was calculated for only species with more than five observations in each time period, resulting in change indices for 224 species. For more information on the methods of calculating the change index, including the specific model, and a complete list of the 224 species' change indices, consult Clemants and Moore (2005).

Statistical analysis

Log-likelihood χ^2-tests (G-statistic) and Fisher's exact test (FREQ procedure in SAS Version 9.1, SAS Institute, Cary, NC, USA) with Bonferroni adjusted alpha levels of 0.0125 per test to avoid an inflated Type I error rate, were performed to examine differences of life history traits between alien and native species ($n = 466$). We used the general linear model procedure (GLM) in the SAS statistical package (Version 9.1, SAS Institute) to perform analysis of variance with Tukey's multiple comparisons test (PDIFF, MEANS, and LSMEANS options) on change index and life history categories to determine which traits best explained variation in the change index ($n = 224$) and which life history syndromes were significant for change. Normality of the change index data was confirmed using the Shapiro–Wilk statistic ($W = 0.996$, $P = 0.8495$).

Some studies of the correlation between plant species ranges or invasiveness and life history have stressed the importance of using phylogenetically independent analyses (e.g., Crawley et al. 1996, 1997; Kelly 1996). This is because closely related species in a flora are more likely to have the same life history attributes and this may result in certain attributes over represented not because of habitat requirements but because of taxonomic relationships (Kelly 1996). We chose not to isolate taxonomic relationships in our analysis, so that the data set presented in this paper is a complete, unweighted representation of trends for all species in the New York metropolitan woody flora and the relationship between changes in distribution and life history characteristics for each species present. Many other studies have used the relationship between life history and invasiveness to successfully predict which species will become invasive (e.g., Rejmánek 1996; Reichard and Hamilton 1997) without isolating taxonomic relationships.

Results

Native species accounted for 60.3% of the 466 woody species in the New York metropolitan area; alien species accounted for 39.7% of the flora (Table 1). We found that the most common (52.8%) fruit type in the complete flora was fleshy fruit. The majority of species had a perfect breeding system (60.7%). Gymnosperms accounted for only 6.1% of the woody flora. The most common (53.0%) life form was the broad-leaved deciduous shrub class. Insect pollination was the most common (73.0%) form of pollination. Bird pollination was very rare in the flora, represented by only one species (*Campsis radicans* (L.) Seem. Ex Bureau).

We found significant differences between the life history traits of the alien and native flora in the New York metropolitan area (Table 2).

Table 2 Life history differences between alien and native species in the New York metropolitan flora using log-likelihood χ^2-tests (G-statistic) and Fisher's exact test

Category	χ^2			Fisher's exact test
	G	*df*	*P*	*P*
Fruit type	9.80	3	0.0203	0.0240
Life form	12.61	6	0.0497	0.1160
Breeding system	13.68	3	0.0034*	0.0030*
Pollination vector	15.04	2	0.0005*	0.0006*

P-values with an asterisk are significant after Bonferroni adjustment of $P < 0.0125$

The alien and native flora significantly differed in breeding systems and pollination vectors. The native flora had a greater frequency of dioecious, monoecious, and wind pollinated species. The alien flora had a greater frequency of hermaphroditic species and insect pollinated species. There was a trend for the alien and native flora to differ with respect to fruit type and life form, but these results were not significant after Bonferroni correction. The native flora had a greater frequency of nut-bearing species and deciduous shrubs. The alien flora had a greater proportion of species with dry fruit and deciduous trees. Fisher's exact test produced similar results, with a significant difference between alien and native species for fruit type, breeding system, and pollination vector (Table 2). However, only breeding system and pollination vector were significant after Bonferroni correction

The change index differed significantly among life history traits (Table 3). Life history traits within the life history categories of origin, fruit type and life form significantly differed (Table 3). The change index did not differ significantly among traits within breeding system and pollination vector. The interaction effect of fruit type and origin on change index was also significant (Table 3).

Tukey's Studentized Range (HSD) test identified particular life history traits within each life history category that significantly differed and were associated with an increase (positive change index) or decrease (negative change index) in distribution in the urban landscape over the past 100 years. Alien species increased in distribution $(\overline{X} = 0.4672)$ and were significantly different ($P < 0.05$) from native species, which decreased in distribution $(\overline{X} = -0.1198)$. Within the fruit type category, nut-bearing species $(\overline{X} = 0.3558)$ had a significantly ($P < 0.05$) higher change index than species with other types of dry fruits $(\overline{X} = -0.3836)$. Deciduous trees $(\overline{X} = 0.3558)$ had a significantly higher change index ($P < 0.05$) than deciduous shrubs $(\overline{X} = -0.1951)$, coniferous trees $(\overline{X} = -0.6084)$, or evergreen shrubs $(\overline{X} = -0.8013)$. Broad-leaved (deciduous, semi-evergreen, or evergreen) vines $(\overline{X} = 0.3424)$ were significantly different ($P < 0.05$) from evergreen shrubs.

Table 3 Results of change index ANOVA of life history categories

	F	*df*	*P*
Overall model	2.71	25	<0.0001
Origin	18.68	1	<0.0001
Fruit type	3.45	3	0.0175
Life form	4.32	5	0.0009
Origin*fruit type	3.46	2	0.0333

Only results significant to $P < 0.05$ are displayed

We also tested if particular life history syndromes, combinations of life history traits, were significantly successful (increased distribution) or unsuccessful (decreased distribution), as measured by the change index (Table 4). Alien, fleshy-fruited, broad-leaved vines and alien, fleshy-fruited, deciduous shrubs, and trees were significantly successful (ex. *Celastrus orbiculata* Thunb., *Rosa multiflora* Thunb. Ex Murray, and *Morus alba* L., respectively). Of the native species, deciduous trees with winged fruits (ex. *Acer negundo* L., *Populus deltoides* Marsh.) and nut-bearing deciduous trees (ex. *Quercus alba* L., *Quercus rubra* L.) were significantly successful. Native, fleshy-fruited evergreen shrubs were significantly unsuccessful (ex. *Arctostaphylos uva-ursi* (L.) Spreng., *Vaccinium macrocarpon* Aiton).

Discussion

The proportion of native and alien species in the New York metropolitan flora (60.3 and 37.9%, respectively) is similar to floras of cities in the United States (Clemants and Moore 2003) and Europe (Kowarik 1990; Pyšek 1998). In a study of eight cities in the eastern and mid-western United States, including New York City, the percentage of alien species ranged from 19.3 to 45.7% (Clemants and Moore 2003). The flora of Berlin, Germany consists of 58.6% native species and 41.4% alien species (Kowarik 1990). In floras of 54 Central European cities, the average representation of alien species was 40.3% (Pyšek 1998).

In addition to changes in species distribution, the quality of urban plant communities with worldwide increased urbanization is a major direction in the changing pattern of life on earth and needs more attention. The flora of the highly

Table 4 Significant life history syndromes as determined by post hoc Tukey's multiple comparison tests on LS means after change index ANOVA of life history categories

Origin	Fruit type	Life form	Change index (mean)	LS mean ± SEM	*P*
Alien	Fleshy	Broad-leaved vine	1.15	1.24 ± 0.44	0.0048
Alien	Fleshy	Broad-leaved deciduous tree	0.97	1.08 ± 0.49	0.0283
Alien	Fleshy	Broad-leaved deciduous shrub	0.51	0.66 ± 0.28	0.0194
Native	Wing	Broad-leaved deciduous tree	0.53	0.68 ± 0.24	0.0058
Native	Nut	Broad-leaved deciduous tree	0.48	0.71 ± 0.30	0.0184
Native	Fleshy	Broad-leaved evergreen shrub	-1.03	-0.99 ± 0.44	0.0253

urban landscape of the New York metropolitan area may differ in the proportion of life history traits represented from other studies of worldwide distributions and countrywide distributions of temperate regions. This is a subject for further research, but some patterns do emerge. In the New York metropolitan flora, there is a large representation of monoecious and dioecious breeding systems (Table 1). Yampolsky and Yampolsky (1921) found in 121,492 species of flowering plants (woody and herbaceous) worldwide that monoecy and dioecy were represented in only 5 and 4% of the flora, respectively. The percentages reported in our study include 28 gymnosperms. However, with the exclusion of gymnosperms, the proportion of monoecious and dioecious species in the flora is still high; close to 20% for both breeding systems. In NC, USA, 3.5% of species are dioecious (Bawa 1980) and only 3% of flowering plants are dioecious in the British Isles (Briggs and Walters 1997). Williamson and Fitter (1996) found that 4% of native and naturalized British angiosperms and gymnosperms are dioecious and 8% are monoecious. These percentages include both woody and herbaceous plants. The frequency of dioecy is greater in woody plants than in herbaceous plants. Trees (12%) and shrubs (14%) have a much greater frequency of dioecy than herbs (1%) in the flora of North Carolina (Bawa 1980). This may account for the differences between our percentages and those in other studies.

The frequency of pollination vectors in the New York metropolitan area may be similar to other temperate regions. In Great Britain, 63% of the flora is insect pollinated and 25% are wind pollinated (Williamson and Fitter 1996). This is similar to our results in which we found that 73% of woody plants in the New York metropolitan area are insect pollinated and 22% are wind pollinated.

We show here that the alien and native species in the New York metropolitan flora differ in life history traits and also that success (defined as an increase in range size) in the metropolitan area is associated with particular life history traits. In the ecological literature, there are some conflicting results indicating different life history characteristics associated with alien, invasiveness status, or greater range size depending on the geographic region and the data analyzed. Our data indicate that of the New York Metropolitan flora, nut-bearing species and deciduous trees and vines have the greatest increase of range, regardless of native or alien origin. The success of many woody invaders in both disturbed and undisturbed habitats has been positively correlated with vertebrate dispersal (i.e., fleshy fruits) (Rejmánek 1996) and prolific regeneration by seed (Gilbert 1989). Invasive plants are also likely to produce small and numerous seeds, have efficient dispersal abilities, and support generalist mutualisms (Myers and Bazely 2003). However, some studies focused on the flora of Great Britain have not found a relationship between dispersal mode and invasion success (Crawley et al. 1996, 1997) or range size (Kelly 1996). Seed characteristics are important determinants of demographic success. Invasive alien plant species in the United Kingdom have large seeds and persistent seed banks (Crawley et al. 1996, 1997). Invasive *Pinus* species tend to have a short juvenile period, small seed mass and short intervals between large seed crops (Rejmánek and Richardson 1996).

Life form may also be an important determinant of success. Trees in Great Britain have larger range sizes than shrubs (Kelly 1996) and trees on the urban island of Staten Island, New York succeeded better than shrubs or vines after over 100 years of urbanization (Robinson et al. 1994). Evergreen leaves are associated with non-invasiveness in North America (Reichard and Hamilton 1997). This is confirmed in the New York Metropolitan area where evergreen shrubs have decreased in range.

Although our analysis did not find any correlation between pollination vector or breeding system and distribution change, we did show that the alien and native flora differ in their pollination and breeding systems. We show that alien species, regardless of distribution change, tend to be insect pollinated. Successful alien species in the United Kingdom are insect pollinated (Crawley et al. 1996, 1997; Williamson and Fitter 1996) and flowering time is temporally separated from native species (Crawley et al. 1996, 1997), but wind pollinated species have larger ranges than insect pollinated species (Kelly 1996; Kelly and Woodward 1996). Perfect flowers have been associated with invasiveness (Reichard and Hamilton 1997) and the alien flora of New York has a greater than expected frequency of hermaphrodism. Local and regional abundance is related to breeding system in some cases (Kunin and Shmida 1997). However, at the global scale, breeding system and abundance are not related (Kunin and Shmida 1997) and in the flora of the British Isles, successful invasion was not related to breeding system (Crawley et al. 1996, 1997). Although we found differences in breeding system and pollination vector between alien and native species, these differences did not translate to an increase or decrease in range. Breeding system should be an important determinant of distribution change, but we may need to examine breeding systems more subtly, such as self-compatibility versus self-incompatibility species groupings (e.g., Kunin and Shmida 1997).

Seed dispersal is possibly the most important trait determining spread in the New York metropolitan area. Those species capable of long distance dispersal will ultimately be the species to increase range and maintain metapopulations in the fragmented habitats of urban landscapes. In temperate deciduous forests, long distance spread is possible for wind dispersed and animal dispersed trees. However, wind dispersal usually transports seeds farther than animal dispersal (Clark et al. 1999). In the New York Metropolitan area, bearing nuts was a significant predictor of spread. Nut-bearing species, such as oaks are spread long distances by blue jays (Johnson and Webb 1989) so it is not surprising that nut-bearing species show an increase in range. Other species that increased in range included those native species with winged fruits. These wind dispersed native species, such as *A. negundo* L. and *P. deltoides* Marsh., are also early successional species that easily establish in disturbed habitats common to urban areas. Fleshy fruits, common to many alien successful species, are dispersed primarily by birds in the urban landscape. Birds have been found to be important dispersal agents of fleshy-fruited invasive shrubs (Bartuszevige and Gorchov 2006) and fleshy fruits easily disperse across the urban landscape to the most urbanized habitats such as ecologically restored landfills (Robinson and Handel 1993).

We show in this study that successful alien and successful native species differ in life history traits. It is unclear why alien species with fleshy fruits were successful and native species that exhibited an increase in range were nut bearing or had winged fruits. Success in the urban landscape may ultimately depend both on species' life history characteristics and the ecological amplitude of individual species. Thompson et al. (1995) found differences between alien and native flora (woody and herbaceous species combined) of expanding ranges of England, Scotland, Ireland and the Netherlands. Successful alien species were clonal, had short-lived seed banks, and were polycarpic perennials with leafy canopy structure. Successful native species in these North Western European countries had long-lived seed banks. Unlike the flora of the New York metropolitan area, wind dispersal was not a trait of successful native species (Thompson et al. 1995).

Ecological amplitude of individual species also plays role in success in the urban landscape. Successful alien and native species in the New York Metropolitan area may be more adaptable to the environmental conditions common in habitats subjected to urban pressures, such as changes in climatic and soil differences, pollution, and changes in habitat composition and structure.

Urban areas are warmer, have a longer growing season, lower humidity and higher average precipitation than adjacent rural areas (Gilbert 1989). Soils are also impacted by urbanization and have unique structural and chemical properties (Hollis 1991; Craul 1994) that would affect the composition of plant species. These changed urban factors favor only some species. Native species that have increased distribution between 1930 and 1999 in Great Britain were species adapted to anthropogenically disturbed habitats, such as roadsides, waste ground, railway right-of-ways, and hedgebanks (Preston et al. 2002). Increasing species of both native and alien origin in four NW European countries were fast growing species characteristic of nutrient rich habitats, but alien species were found more commonly in wasteland and dry habitats (Thompson et al. 1995).

Habitat destruction and changes in habitat structure and composition of remnant habitats also affects the success of species. In the New York metropolitan area, the overabundance of white-tailed deer in suburban areas has caused great changes to the structure of remnant habitats. Overbrowsing by deer impacts many woody species (Côté et al. 2004), particularly native shrubs and may have caused the contraction of ranges of many native species in the New York metropolitan area. Loss of wetland habitat in the New York metropolitan area may be an additional cause of range contraction, particularly of hydrophytes such as species in the Ericaceae family (Clemants and Moore 2005). Similarly, species in Great Britain that exhibited a contraction of range between 1930 and 1999 were primarily species of rare and low-nutrient habitats such as heathlands and bogs (Preston et al. 2002).

The most striking result of our study was that alien species have a significantly higher increase in range than native species in the urban landscape. The focus of much invasive ecology research asks the question of why alien species succeed better in particular habitats than native species. In an urban region such as the one studied here, the success of alien species may be attributed to a variety of factors. First, alien species may positively respond to different environmental or landscape factors than native species (Clemants and Moore 2003). High levels of disturbance in urban regions facilitate the survival and spread of introduced species (Gilbert 1989). Second, alien species may be able to become invasive because of the lack of enemies in the new range (Keane and Crawley 2002; Vilà et al. 2005). Third, alien species may represent a novel life form in the invaded community, allowing them to become dominant (Mack 2003). Fourth, many alien species that are good colonizers in their native ranges would be expected to have the ability to colonize similar habitats elsewhere. Finally, alien species may be predisposed by their life history for rapid spread as the region became more urbanized. Examinations of alien species that were introduced and became established versus alien species that were introduced but did not become established would allow us to understand better how life history allows alien species to become established and spread.

The success of alien species may also be related to human mediated propagule pressure. We did not measure propagule pressure, which may influence a species ability to succeed in the urban environment. The increased availability of propagules, due to cultivation and continual introduction by humans, increases the likelihood of establishment and persistence of particular species (Williamson 1996; Rouget and Richardson 2003; Lockwood et al. 2005). Propagule pressure may be especially important for woody species, as most non-indigenous woody species have been introduced for horticultural uses (Reichard 1997), but the importance of the role of man in the dispersal of alien plants has not been well studied primarily due to the lack of data on the quantity and location of cultivation of horticultural species. In the New York metropolitan area, data on the continual introduction, cultivation and sale of woody species is not available at this large scale and therefore it was not possible to take this sort of propagule pressure into account in this study.

Many of the most successful alien plants in the New York metropolitan area, such as *Ampelopsis brevipedunculata* (Maxim.) Trautv., *Elaeagnus umbellata* Thunb., and *C. orbiculata* Thunb., have been introduced and cultivated for horticultural purposes. However, not all well known ornamental plants have increased in range, such as

Hibiscus syriacus L. and *Ligustrum vulgare* L. These species continue to be cultivated and, despite widespread horticultural introductions, have decreased in range. There are also many other alien species, both woody and non-woody, that have been introduced to the New York Metropolitan area and have not become invasive. In addition, there are some widespread native species (ex. *Gaylussacia baccata* (Wangenh.) K. Koch., *Liquidambar styraciflua* L., *Populus grandidentata* Michx.), that despite their commonness, have changed very little in range size, indicating that propagule pressure may not be the most important mechanism for range increases in the New York Metropolitan area.

Introduction by people is certainly the most important factor determining the species richness of the alien flora (Crawley et al. 1997), but may not be the only factor determining success once a species is introduced. While propagule pressure certainly affects the range of introduction and the success of particular introduced species (Williamson and Fitter 1996), life history characteristics associated with human importation, such as showy flowers (insect pollination), colorful fruits (animal dispersal) and adaptation to disturbed areas should also be life history traits associated with reproductive success and efficient dispersal that enables establishment and spread into new environments. Therefore, although those species favored by humans will initially be introduced in greater quantities, their ability to escape cultivation, such as via dispersal by animals, and establish new populations relies ultimately on their life history characteristics, which were examined here.

Many studies have attempted to generalize the characteristics of invading species with the hope of being able to identify and stop certain species from initial introduction (e.g., Crawley et al. 1996, 1997; Rejmánek and Richardson 1996; Williamson and Fitter 1996). These attempts at characterizing invasive species by their life history traits have had mixed success (Mack et al. 2002). However, for woody plant species, prediction of invasiveness using life history traits has been shown to be successful and is recommended for use in import regulations (Mack et al. 2002). Our study is unique in that we have confirmed particular life history syndromes, as successful (increased distribution) or unsuccessful (decreased distribution) in a major urban region. Urban regions are often the epicenter of invasions (Pyšek 1998), so examinations of the trends of successful and unsuccessful species in urban regions results in accurate predictions for which species can be expected to become invasive. We found that alien deciduous shrubs, trees and broad-leaved vines with fleshy fruits were the most successful over time in the urban landscape. Particular caution should be used before importing woody alien plant species that are deciduous and animal dispersed. By understanding which life history traits are associated with chronic invasiveness, authorities can focus both prevention and eradication efforts on those species presenting the greatest risk to biodiversity, habitat degradation and ecological services.

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