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North American history of two invasive plant species: phytogeographic distribution, dispersal vectors, and multiple introductions

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Abstract

The North American historic phytogeographic distribution of mugwort (*Artemisia vulgaris*) and Japanese knotweed (*Polygonum cuspidatum*), two invasive perennial species introduced from Eurasia and East Asia respectively, was recreated using herbarium records. The putative initial introduction of these two species differs by c.a. 400 years, but their patterns of geographic distribution, introduction pathways, and local dispersal pathways are similar. Both species showed the expected logistic growth relationship between range size and the time following introduction, with lag phases of nearly 400 and 50 years for mugwort and Japanese knotweed respectively. The intrinsic growth rate was greater in Japanese knotweed than mugwort for the US, Canada, and North America. Both species were frequently found along waterway, railroad, and road rights-of-way. Introduction pathways differed, with Japanese knotweed commonly labeled as an ornamental escape (151 collections), while mugwort was commonly cited as an inadvertent component of ship ballast (20 collections). These potential founding populations were located across the final distribution for both species, suggesting anthropogenic large-scale dispersal across North America with local secondary spread. Range expansion appears to be active for both species in the US while nearing the carrying capacity in Canada. Managers of mugwort and Japanese knotweed can make use of this information on their range expansion dynamics and dispersal pathways by reducing anthropogenic dispersal and focusing resources on satellite populations and invasion corridors.

Introduction

One of the defining characteristics of an invasive species is anthropogenic introduction of propagules into novel habitats, often at great distances from the source. Despite the sizable human role in distributing non-indigenous species, we still know strikingly little about the mechanisms of successful establishment and future range expansion (Elton 1958; Sakai et al. 2001). Darwin (1859) suggested the explanation of the 'extraordinarily rapid increase and wide diffusion of (exotic) naturalized productions in their new homes' as simply a function of their 'geometrical ratio of increase'. This oversimplification of introduced species population dynamics, 'less destruction of the old and young...and nearly all the young have been enabled to breed' (Darwin 1859), has been debated by researchers since the publication of the *Origin*. The question remains: What mechanism(s) of introduction and secondary dispersal allow invasive species to expand their range so rapidly? Can we find answers to this and correlated questions by examining the historical record?

Recognizing the need to understand both how species initially arrive at a site and subsequently expand from that locus, many researchers have begun to turn to history. By understanding the minutiae of species autecology, their historic distribution in the introduced range, the details of dispersal pathways, and environmental limits to spread can lead to the identification of sites suitable to future invasion (Weber 1998). The interaction between the introduced species' characteristics and humans is especially apparent when the species has ornamental or crop value, which is the case for many invasive plant species (Bell et al. 2003). Initial dispersal of exotic species is closely associated with anthropogenic activity, but subsequent expansion from these foci can be the result of a variety of factors: environmental tolerance, availability of dispersal pathways, and diaspores reaching an appropriate site. The rate of range expansion is a function of the number and size of founding populations, with many small populations spreading faster than fewer large populations (Auld and Tisdell 1986). The ultimate number of established plants is not only a function of founding population dynamics, but is proportional to the probability of propagules finding a 'safe site' (Weber 1998). Successful establishment generally results in a population large enough to colonize additional locations from the founding loci. Obtaining this threshold population size has frequently been touted as the explanation for the oft observed lag phase following initial introduction (Kowarik 1995), which is most often viewed in the single dimension of time. A spatio-temporal evaluation of the distribution of an invasive species may better explain the characteristic lag phase followed by rapid range expansion.

Historical data on the phytogeographic distribution of invasive species in their introduced range can potentially elucidate numbers of independent introductions, dispersal pathways, and the ecology of the invasion process (Pysek and Prach 1995). However, detailed historic censuses of introduced plants often do not exist. Therefore, researchers have relied on collections residing in herbaria and historic floras for the region of interest. The cryptic invasion of the non-indigenous genotype of *Phragmites australis* (Cav.) Trin. *ex* Steudel was determined using historic herbarium records coupled with current distribution maps, elucidating a rapid extirpation of native genotypes across North America (Saltonstall 2002). The use of historic herbarium records has been used extensively in regions of Europe to reconstruct invasion processes and distribution (Pysek and Prach 1995; Weber 1998; Mihulka and Pysek 2001; Petrik 2003), but has been little utilized in North America (however, see Mack 1981; Toney et al. 1998).

This paper describes the spread and historic phytogeographic distribution of two perennial invasive species common in North America: mugwort (*Artemisia vulgaris* L.) and Japanese knotweed (*Polygonum cuspidatum* Sieb. *et* Zucc.; syn: *Fallopia japonica* (Houtt.) Dcne.) using herbarium collections. Both species are native to eastern Asia, with mugwort also being native throughout Europe, and were initially introduced into North America in contrasting fashion: mugwort accidentally via New World colonists and latter with ship ballast, and Japanese knotweed via deliberate introduction as an ornamental. These species were chosen to compare and contrast their historic distribution, range expansion dynamics, and pathways of dispersal at a continental scale due to their similar habitat preferences, yet different modes and times of introduction. The goals of this study were to (i) relate historic trends in geographical distribution to current extent, (ii) assess spreading dynamics using population growth models, (iii) parse out possible dispersal pathways and relate these to potential habitats upon which to focus management, and (iv) to assess the possible number of independent introductions, either intentional or accidental.

Methods

The study species

Japanese knotweed is native to eastern Asia, where it is commonly found as a colonizing species in lava flows (Beerling et al. 1994). This 'strong stout handsome bush' has been introduced across the globe as an ornamental, as the 'clouds of bloom' in late summer where touted as being 'very effective for bold mass effects' (Bailey

1916, p. 2743). Hindsight would prove valuable as this perennial has escaped cultivation in nearly every instance, becoming a serious invasive pest in Europe (especially in the United Kingdom) and North America. This invader generates staggering amounts of biomass with rhizomes reportedly burrowing through asphalt (Wade et al. 1996). Management strategies are at the forefront of many research efforts in the Northeastern US and the UK, yet are met with limited long-term efficacy (de Waal 1995; Child 2003).

Mugwort is a cosmopolitan species, occurring throughout Europe and central, southern, and eastern Asia (Barney and DiTommaso 2003). Historically mugwort was used as a medicinal – especially in East Asian pharmaceuticals – likely facilitating its wide geographic distribution on the Eurasian continent. While the first record of mugwort in North America indicates possible accidental introduction by Jesuits in the St. Lawrence region of Canada in the 16th century (Fernald 1900), modern inference of introduction loci indicates that ship ballast was a more common vector.

Japanese knotweed and mugwort produce a vigorous rhizome community, which serves as the primary means of establishment and also as a propagule source upon disturbance. However, seed production in the New World has been observed in the field with varying degrees of viability for both Japanese knotweed (Forman and Kesseli 2003) and mugwort (Barney and DiTommaso 2003), suggesting sexual reproduction contributes to recruitment as well. Upon introduction, both clonal invaders spread radially from the point of introduction (Barney et al. 2005). Japanese knotweed is a frequent invader of natural areas, while mugwort is becoming increasingly prevalent in native landscapes, previously being cited as a 'waste place' ruderal (Gray 1857; Gleason 1952).

Data source and analysis

Data on the distribution of mugwort and Japanese knotweed were obtained in 2003–2004 using the *Index Herbariorum*, a global database of public herbaria (http://sciweb.nybg.org/science2/ih/searchih.html). All herbaria listed in the United States and Canada were solicited for their collections of mugwort and Japanese knotweed. Of the 481 institutions (422 US, 59 Canadian) contacted, I received replies from 273 (56.7% of total), which included all major colleges/universities, museums, and research stations.

I received holdings from each institution in electronic form (spreadsheet or digital images of sheets), sheet copies via post, loans to CU, or site visits. I was able to see actual sheets or facsimiles for approximately 70% of the total collections, allowing taxonomic confirmation. A very low percentage were misidentified (<5%), suggesting that of the unseen 30% of the sheets, a vast majority were identified correctly. *Polygonum* species were identified using Zika and Jacobson (2003).

For the US, the finest resolution that I could generate was at the county scale, as most sheets did not have either specific site information or coordinates of collection sites, while the Canadian distribution was conducted at the regional municipality level (equivalent to US county). Collection dates were lumped into decadal increments (i.e., 1950 = 1950–1959) for ease of representation and analysis. The database was then thinned to represent only one entry per collection, as many collectors sent identical samples to multiple institutions. I assumed that once a species was collected in that political unit it was always there, allowing for a cumulative geographic spread (Pysek and Prach 1995), expressed as presence/absence.

To describe geographic range expansion following time since introduction, the population growth model proposed by Verhulst and Pearl – $\left(y = \frac{K}{[1+\exp^{(-t'r+\frac{x}{r})}]}\right)$ – was applied to the cumulative geography curves to assess the intrinsic growth rate (r), carrying capacity (K), and the time in which geographic range expansion begins to slow (t': i.e., the inflection point) for the US, Canada, and North America using SigmaPlot (version 9). Additionally, geographic spread was plotted as the number of new political units, and the area (km^2) of those political units, citing a population per decadal increment, which represents a rate (i.e., km^2 decade^{-1}) of large scale spread. The area represented does not represent actual area invaded, but the area of the respective political units. I did not include data for the current decade because it does not represent 10 full years of data.

The collection database was integrated into a geographic information system (GIS) using ArcGIS (version 9) for phytogeographic distribution representation. Data from 2001 were used for US county units and boundaries (US Geological Survey, 200208, countyp020: US Geological Survey, Reston, VA), and from 1996 for Canadian municipality units and boundaries (DMTI Spatial Inc., ESRI, Canada Regional Municipalities: ESRI® Data & Maps 2004, ESRI, Redlands, CA). Species distributions were represented at both the continental scale, as well as the regional scale, specifically Northeast US/Southeast Canada. I focused on the distribution in this particular region as this is where these species are most problematic and were initially introduced (Weston et al. in press).

In order to assess possible independent introductions and dispersal vectors, each sheet containing site characteristic information was categorized into one of the following groups: ballast (identified as being from ship's ballast), cultivated (identified as either an escape from cultivation, or as an ornamental), railroad (collected along a railroad right-of-way), road (collected along a roadway right-of-way), or waterway (collected on or near the bank of a drainage ditch, stream, river, pond, lake, or ocean). The ballast and cultivated sheets for each species were represented geographically, as they represent potential sites of unique independent introductions.

Results

Japanese knotweed

Japanese knotweed was collected at least once in 18.4% of conterminous US counties (577/3144) and 32.3% of Canadian municipalities (93/288) by the turn of the 21st century. The earliest US herbarium sheet indicates a 'cultivated' population of Japanese knotweed in Yorkville, New York in September 1873. The oldest Canadian sheets indicate three collections in 1901: Chilliwack (Fraser Valley Regional District), British Columbia; Longueuil (Champlain County), Quebec; and Niagara Falls, Ontario. There were very few collections of Japanese knotweed made in the US until 1920 when the number of 'infested' counties began to increase exponentially (Figure 1). According to the population growth equation Japanese knotweed colonization has yet to reach carrying capacity in North America ($K = 800$ political units) or the US ($K = 716$ political units) (Table 1). Contrastingly, infested political units in Canada appear to plateau in the 1970s (Figure 1), as the carrying capacity does appear to have been reached, at 93 political units. The intrinsic growth rate (r) of spread was higher in Canada (0.066) than the US (0.048) (Table 1), observed also in the rates of geographic spread in political units and area colonized (Figure 2).

The phytogeographic distribution of Japanese knotweed 30 years after the first North American collection is quite patchy, with most populations being concentrated in the Northeastern US, and disjunct populations scattered in the Southeast, Midwest, and Pacific Northwest US (Figure 3). By 1900, Japanese knotweed had been collected in 18 US counties and six Canadian municipalities. The first five decades of the 20th century were witness to an explosion in geographic distribution and regional density of Japanese knotweed populations. Populations were identified in 148 US counties and 29 Canadian municipalities, spanning locations 30–50° N latitude and (−)60° to (−)124° W longitude. Regions in the Midwest and the Pacific Northwest US and the Northeast US/Southeast Canada region saw a dramatic increase in new founding populations (Figure 3). By the millennium, Japanese knotweed range expansion increased even further, reaching the extremities of eastern Newfoundland (52° W) to Sitka, Alaska (54° N, −133° W) to southern California (34° N, −120° W). Populations were identified along the Pacific coast, stretching from Victoria, British Columbia south to Los Angeles, California. New to the final five decades of the 20th century was an additional cluster of populations in the inter-montane valleys of the Northern Rocky Mountains. Density in the Northeastern US/Southeast Canadian region continued to increase (Figures 3 and 4). By 2000, 71% of the counties in the Northeastern US (including Pennsylvania, New York, Maryland,

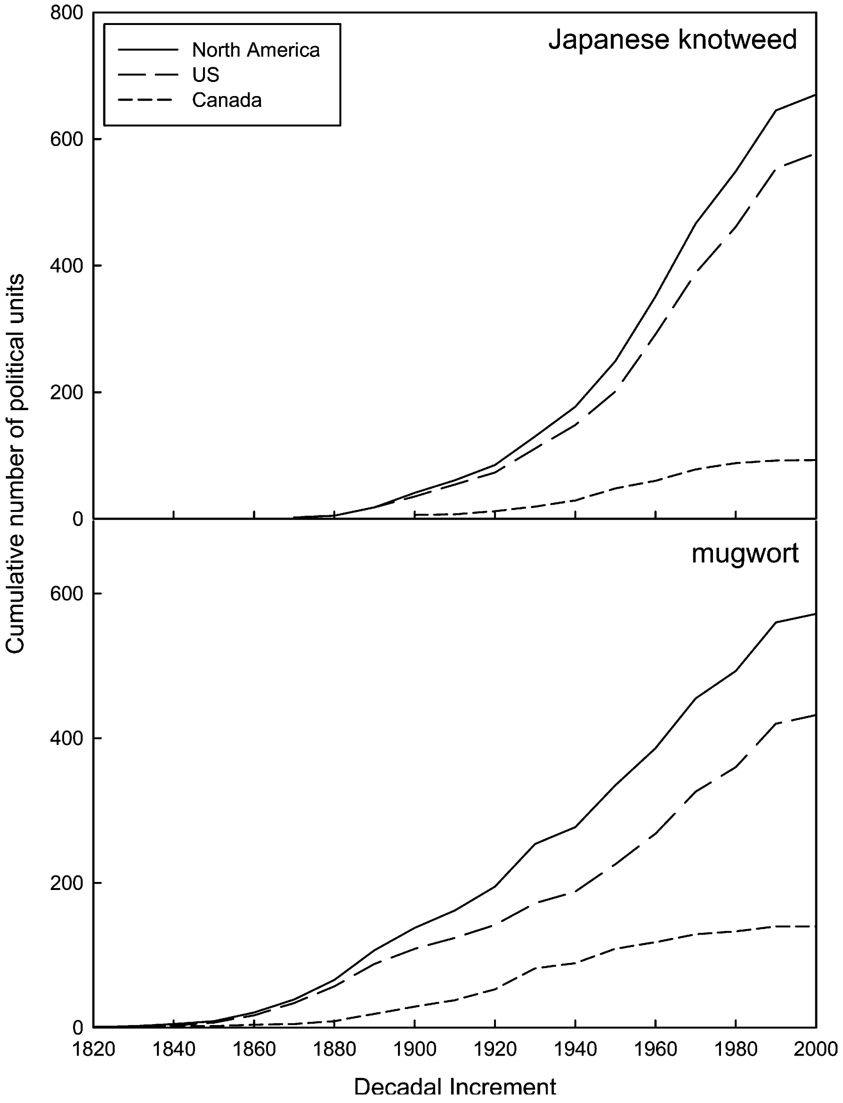

Figure 1. Cumulative number of political units (US counties or Canadian municipalities) per decade in which each species was collected (note difference in scale of the ordinate).

Table 1. Population growth parameters from fitting the Verhulst–Pearl equation to the cumulative number of political units citing a Japanese knotweed or mugwort population against collection decadal increments (from Figure 1).

		Model coefficients				
		t'	r	K	Observed number of political units infested by 2000	Adj R^2
North America	*P. cuspidatum*	1964	0.050	800.8	670	0.999
	A. vulgaris	1951	0.031	702.0	574	0.998
United States	*P. cuspidatum*	1967	0.048	715.8	577	0.999
	A. vulgaris	1968	0.027	632.2	432	0.996
Canada	*P. cuspidatum*	1951	0.066	99.2	93	0.999
	A. vulgaris	1928	0.052	143.7	140	0.999

The Verhulst–Pearl equation was modified to explicitly show the intrinsic growth rate (r), the carrying capacity (K in political units), and the point in which geographic spread begins to slow (t' in year).

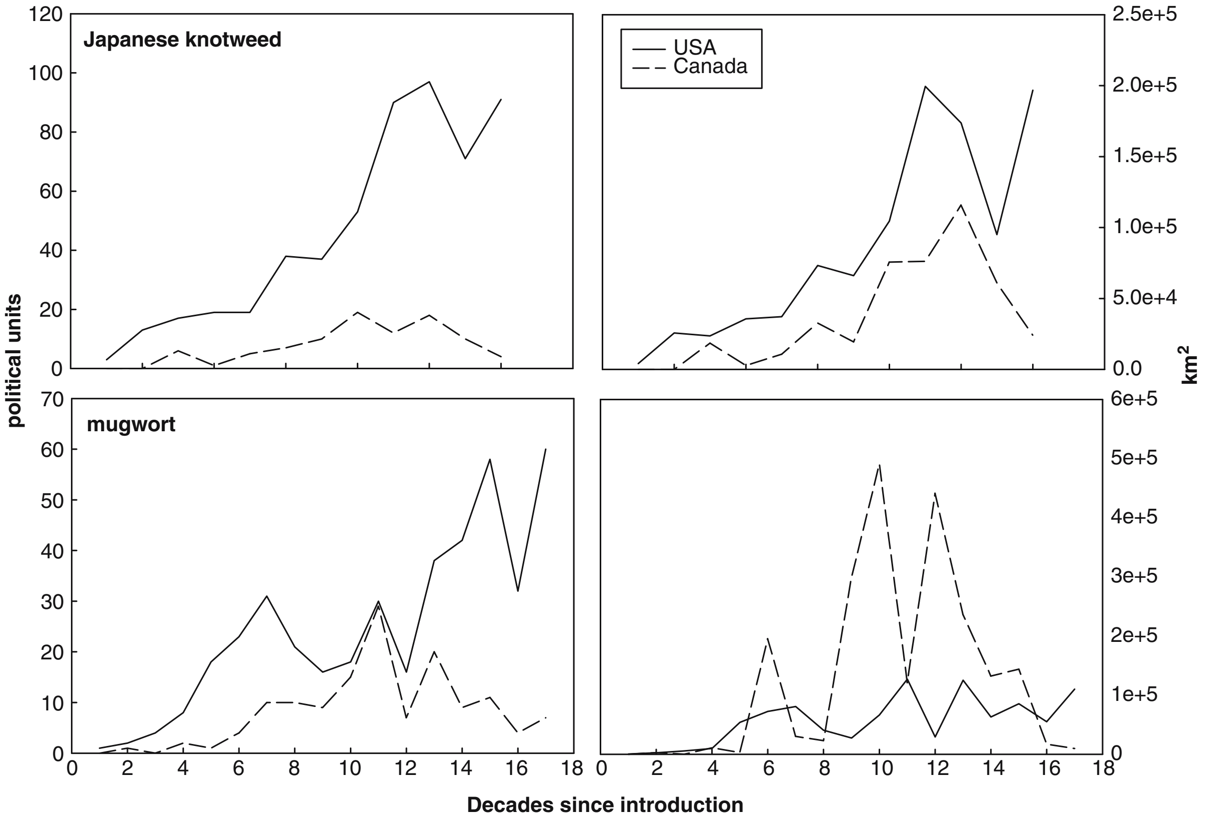

Figure 2. The number of newly colonized political units and area of those political units (km^2) in decadal increments (i.e., area$_{(t+1)}$ – area$_{(t)}$) for Japanese knotweed (top panels) and mugwort (bottom panels) in the USA and Canada.

and the New England states) claimed Japanese knotweed occupancy (Figure 4). In total, North America claims 670 separate political units (577 US counties and 93 Canadian municipalities) had been occupied by a Japanese knotweed population by 2000.

Of the unique Japanese knotweed sheets, 69% of US and 74% of Canadian collections contained collection site information. Of the 1212 unique Japanese knotweed collections citing a habitat characteristic, 776 fell within one of the chosen collection site categories (Table 2). The habitat types cited most frequently were waterways and road rights-of-way. A large proportion of the collections described the population as an escape from cultivation/ornamental. The single population described as growing from ship's ballast was found in Bronx, New York in 1901 (Figure 5). The 151 described 'cultivated' populations are as widely dispersed geographically as the entire species distribution in North America, ranging from Newfoundland to California and nearly everywhere in-between (Figure 5).

Mugwort

Mugwort was collected at least once in 13.8% of conterminous US counties (434/3144) and 48.6% of Canadian municipalities (140/288). The first North American herbarium record of mugwort was collected in Prince Edward County, Ontario in July 1825. The first mugwort record in the US dates to 1837 in Camden, NJ, and was misidentified as *A. canadensis* Michx. During the 40 years following the first collection, the number of newly identified populations was low (9 political units), with a dramatic increase in geographic spread following 1860 in the US and 1880 in Canada (Figure 1). According to the logistic growth model, large-scale mugwort geographic spread appears to

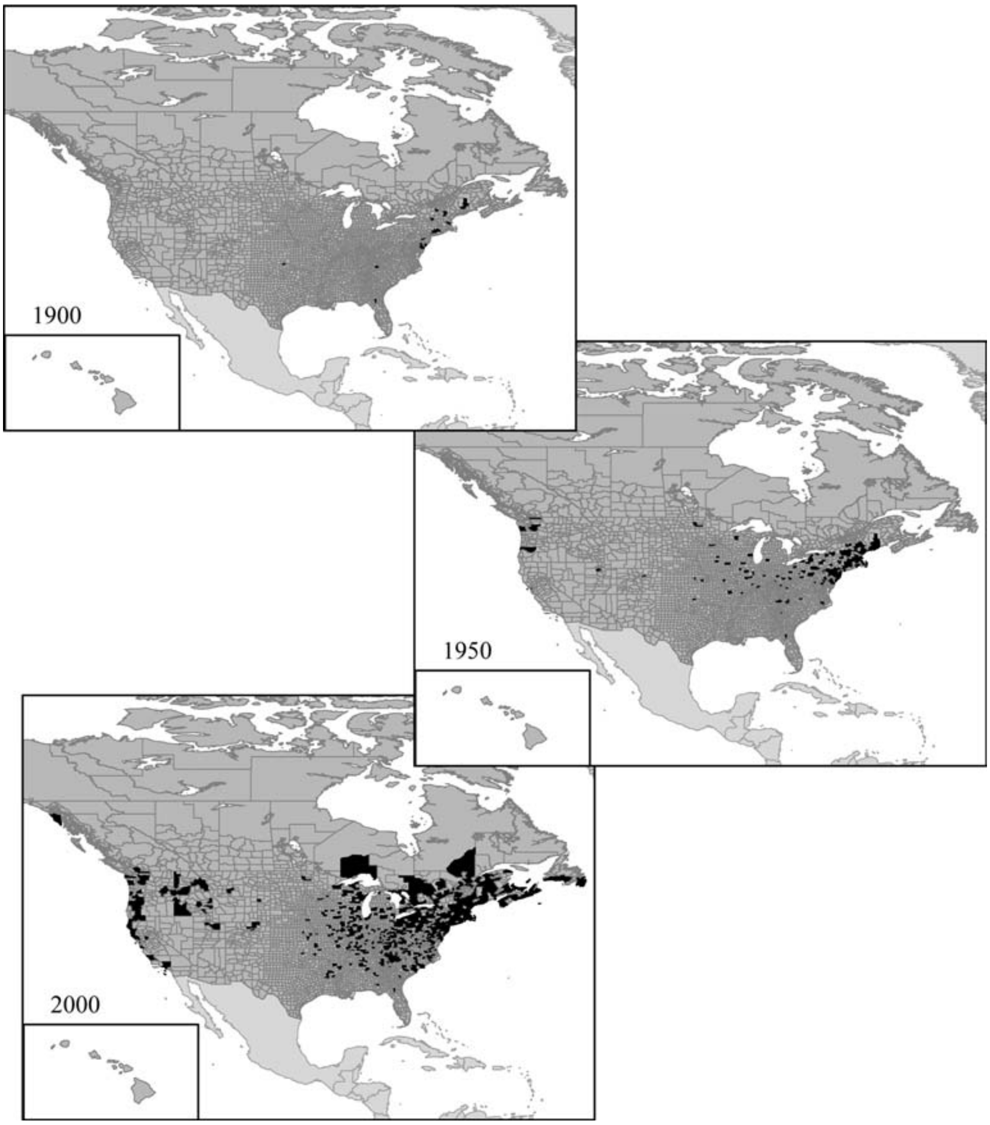

Figure 3. Distribution of Japanese knotweed in US counties and Canadian municipalities up to (a) 1900, (b) 1950, and (c) 2000.

be slowing in North America ($t' = 1951$), but has yet to reach the estimated carrying capacity (K) (Table 1). Mugwort range expansion should plateau at about 700 political units in North America, while the current number of infested counties resides at 574 (Table 1). Similar patterns are seen in the US, while in Canada mugwort is approaching the carrying capacity of about 140 political units. The number of newly colonized political units has steadily increased with time, while the area of these newly invaded political units shows no pattern (Figure 2).

The five decades following the first collected mugwort population in the 1820s saw little range expansion with nearly all populations existing in the east (Figure 6). By 1870 mugwort had been collected in 17 US counties and 4 Canadian municipalities. By 1940 mugwort populations appeared to be concentrated in the Northeastern US/Southeastern Canada with smaller disjunct patches across North America (Figure 6). By 1940 mugwort had been reported at locations as far north as the southern beaches of Hudson Bay (57° N), as far east as Newfoundland (−53° W),

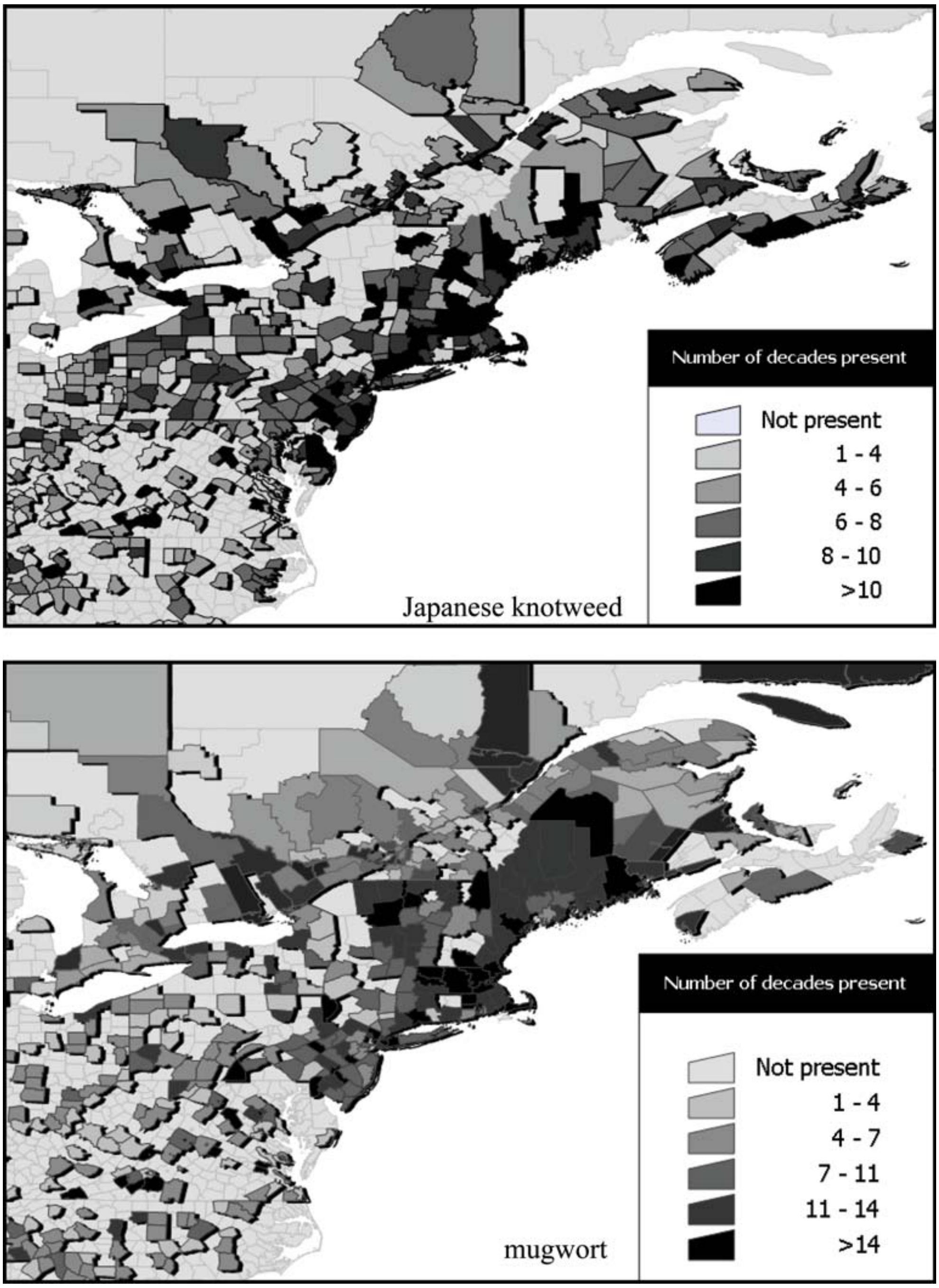

Figure 4. Distribution of Japanese knotweed and mugwort from initial introduction to 2000 in the Northeastern US and Southeastern Canada. Note different scales of shading between the two species.

and south to the Gulf Coast in Louisiana (29° N). By the turn of the millennium, the Southeastern and Northcentral US had been increasingly colonized by mugwort, while secondary expansion increased in the Northeast (Figures 4 and 6). A mugwort collection was made in the unlikely location of Port Brabant, Northwest Territory (39° N, −133° W) on the Beaufort Sea.

Table 2. Breakdown of all herbarium sheets containing site collection information parsed into deliberate and accidental dispersal modes. Values are shown as percentage of sheets with a description and the number of sheet in parentheses.

	Japanese knotweed				Mugwort			
	US		Canada		US		Canada	
Deliberate								
Cultivation	11%	(115)	19%	(36)	5%	(41)	2%	(10)
Accidental								
Ballast	< 1%	(1)	0%	(0)	2%	(17)	1%	(3)
Waterway	22%	(224)	17%	(33)	16%	(122)	17%	(75)
Railroad	9%	(95)	4%	(8)	11%	(83)	11%	(49)
Road	23%	(235)	15%	(29)	23%	(181)	22%	(101)
Net Total	66%	(670)	55%	(106)	57%	(444)	53%	(238)
Sheets with site descriptions	69%	(1017)	74%	(195)	61%	(777)	65%	(450)
All sheets	100%	1476	100%	264	100%	1277	100%	689

By the turn of the millennium, mugwort had been collected in 434 US counties and 140 Canadian municipalities including all five Hawaiian Islands. In the Northeastern US, 67% of the counties harbor at least one mugwort population (Figure 4).

Of the unique mugwort sheets, 69% of US and 65% of Canadian collections contained collection site information. Of the 1227 unique mugwort herbarium sheets with habitat descriptions, 682 fell within one of the five chosen categories (Table 2). In both countries the majority of the mugwort collection sites were described as roadway rights-of-way or along waterways (Table 2). Surprisingly, 11% of the sites were characterized as railroad rights-of-way in both countries. Sites characterized as either ship ballast or cultivated comprised a minor portion of the mugwort collections, but are important when considering the number of possible introductions. Figure 5 shows the wide geographic distribution of the ballast sites, occurring in the literal four corners of North America, while the sites characterized as escapes from cultivation are concentrated in the Northeast and Pacific Northwest, with outlier populations in Middle America (Figure 5).

Discussion

The cumulative number of political units in which mugwort and Japanese knotweed are found display the classic logistic growth form; a lag phase after initial introduction followed by exponential range expansion approaching a carrying capacity (Baker 1986). This relationship between range expansion, expressed as political units or area infested, and time after initial introduction has been documented in historic distribution recreations across wide-ranging spatial scales, using various data sources (e.g., herbarium records, floras, censuses) (Pysek and Prach 1995; Weber 1998; Lambrinos 2001; Huebner 2003). Many researchers argue the lag phase in the new range is a result of reaching a threshold population size to which further self-sustaining populations can expand outside the founding loci (Mack et al. 2000). Others suggest that founding populations are generally deficient in genetic variance, causing range expansion limitations, and that a lag phase results from time taken to acquire sufficient genetic variance to colonize and survive in new habitats (Lee 2002).

Invasive species with ornamental/agronomic value are often introduced on multiple occasions both in space and time (Baker 1986). The frequency, and more importantly, the phytogeography of these introductions can greatly hasten range expansion. Japanese knotweed, a popular ornamental in the 19th century, was collected as an escaped ornamental 115 times in North America by 2003. This number likely underestimates the actual status and geographic distribution of ornamental Japanese knotweed introductions, but still suggests a large number of intentional introductions of this noxious invader over large geographic areas. The geographic distribution of these cultivated populations spans the current

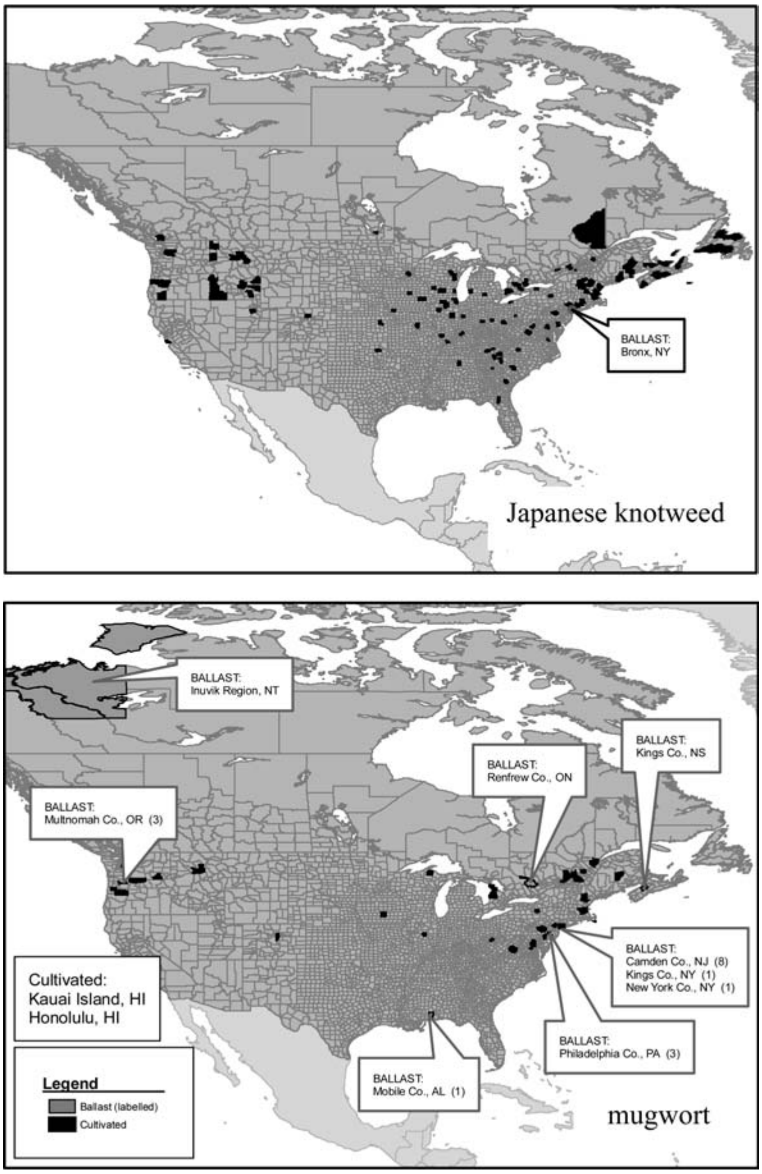

Figure 5. Distribution of sites specified as ship's ballast or cultivated escape for both Japanese knotweed and mugwort since time of initial introduction. These sites represent possible locations of independent introductions from the native range.

distribution, with a 'cultivated' herbarium specimen collected nearly every year since its introduction in 1873 (data not shown). Even with minimal genetic variation in these ornamental Japanese knotweed populations, each introduction can potentially increase the gene pool, and facilitate rapid geographic expansion. Japanese knotweed has an ornamental history in the United Kingdom as well, likely with multiple introductions, but no genetic variation has been detected (i.e., a single genet) (Hollingsworth et al. 1998). This suggests Japanese knotweed invasion in the United Kingdom is a product of broad environmental tolerance of a 'general-purpose genotype' (Schlichting 1986). Corroborating the putative multiple introductions at vast geographic scales of Japanese knotweed in North America with genetic analysis would allow for

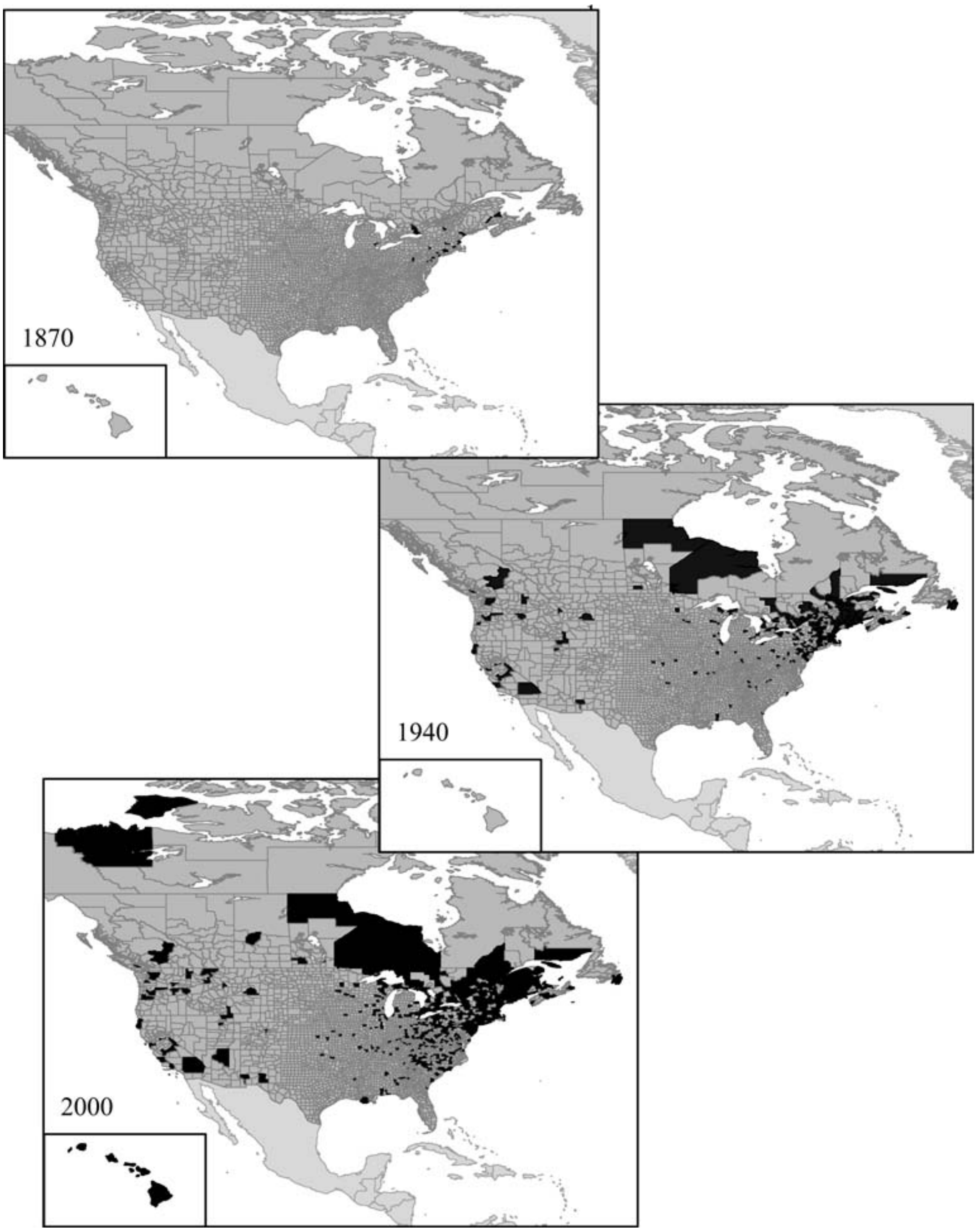

Figure 6. Distribution of mugwort in US counties and Canadian municipalities up to (a) 1870, (b) 1940, and (c) 2000.

conclusions to be drawn as to whether North American Japanese knotweed colonization is a result of genetic variation or a general purpose genotype.

An additional vector of new introductions is via ship ballast, as propagules stow away in ballast holds from ports across the globe (Holeck et al. 2004). Previous to the middle of the 20th century ballast consisted of soil and rocks from foreign ports, facilitating global transport of vascular plant propagules. The global nature of trade is bringing genetic material together that would otherwise never interact. This novel interaction could lead to the creation of new genotypes able to tolerate a variety of environmental conditions and perhaps out-compete native biota. Mugwort was introduced to at least six separate locations in North America via ship ballast, ranging from the arctic to both oceanic shorelines, and on multiple occasions in several of these locations. Floras of the Pacific Northwest touted mugwort as common to the eastern US and Canada, but 'known (locally) only from near ballast dumps at our largest ports' (Abrams and Ferris 1960; Gilkey and Dennis 1967). Mugwort was also cited as a cultivated escape across its introduced range. Therefore, both Japanese knotweed and mugwort large-scale range expansion was facilitated by numerous independent anthropogenic introductions, regardless of genetic relatedness.

The lag time for mugwort, assuming initial introduction in the 1500s by Jesuits, is about 400 years, while Japanese knotweed lag time is roughly 50 years. This large discrepancy could be explained as an initial mugwort introduction of 'benign' genotypes to relatively harsh environs followed by subsequent 'aggressive' introductions, ultimately generating sufficient genetic variance to initiate range expansion. An analogous sequence of events occurred with the common reed *Phragmites australis*, which was native to North America, but was subsequently displaced by an invasive European genotype after 40,000 years of benign residence (Saltonstall 2002). Alternatively, the lack of mugwort and Japanese knotweed range expansion in Canada could be explained by a lack of environmentally suitable habitats, likely due to minimum temperature and frost intolerance. Japanese knotweed is especially susceptible to late spring and early fall frosts, possibly explaining the low carrying capacity and restriction to southerly political units in wintry Canada. Both species appear to have reached the potential carrying capacity at the scale of municipalities in Canada, while in the US they remain in the exponential range expansion phase (Figure 1 and Table 1). The apparent lack of reaching the carrying capacity in the US can be partially explained as a result of missing information (i.e., species presence, but no herbarium collection). A model including environmental tolerances of each species could confirm the existence of suitable habitats (as political units) in which these species have yet to invade, corroborating range expansion as well as predicting locations providing suitable habitat for future invasions.

A species distribution classified as geographically disparate in the early stages of naturalization, followed by local spread from founding loci, is described as following the hierarchic diffusion model (Hengeveld 1989). This phytogeographic distribution pattern is most frequently found with intentional introductions (e.g., ornamentals) (Stuckey 1980; Weber 1998), but is likely the most common mechanism of spread for any introduced species across North America (Baker 1974). Long distance dispersal to and within North America is clearly anthropogenically mediated. Management can be focused on reducing future anthropogenically dispersed satellite populations – eradicating smaller units before they achieve local range expansion.

Range expansion from founding loci is a function of both existence of a dispersal vector and diaspores reaching an appropriate and safe site (Weber 1998). Several invasive species are known to spread along water corridors in central Europe, using the waterway as a dispersal vector (Pysek 1991; Pysek and Prach 1995; Dawson and Holland 1999). Japanese knotweed's winged achenes float and serve as a means of recruitment and range expansion (JN Barney, personal observation). Additionally, severed stem tissue of this species has been shown to regenerate downstream in the United Kingdom (de Waal 2001). Mugwort seed and rhizome tissue also can travel downstream and regenerate (JN Barney, personal observation). These two species appear to be profiting from the dynamics of moving water and its associated disturbances (i.e., floods and debris) to disseminate their propagules.

These invaders are also disseminating propagules along maintenance and traffic rights-of-way. Nearly 25% of collections of both species occurred along a roadside, while nearly 10% were found along railroad corridors. Conolly (1977) cites that secondary spread (i.e., expansion from founding foci) of Japanese knotweed in the United Kingdom was facilitated via colonization of river and railway embankments and along roadsides. Road and railroad rights-of-way are maintained regularly via mowing, which can move both seeds and vegetative tissue. This disturbance, in combination with the turbulence generated by passing vehicles (cars, trucks, trains), makes an opportunistic medium for propagule dissemination (Harrison et al. 2002; Gelbard and Belnap 2003). Waterways, roads, and railroads are the primary candidates for range expansion from founding foci for these invasive species, and should be considered when designing a management strategy for an area (Conolly 1977). A working knowledge of what is growing 'upstream' or 'down the road' can make for a more successful management plan.

The data upon which this analysis was based, herbarium collections, is subject to both temporal and spatial bias (Rich and Woodruff 1992). These biases are grounded in the collection frequency and priorities of individual institutions, accessibility of species, and species apparency (Rich and Woodruff 1992; Delisle et al. 2003). Public lands are more likely to be sampled (e.g., roads) than private landholdings, and showy species new to an area are more likely to be collected than inconspicuous species. Also, absence of evidence (i.e., no collection in a political unit) does not translate to evidence of absence. Despite these biases, herbarium records have been used to define conservation needs (MacDougall et al. 1998), document species changes (Willis and Moat 2003), and recreate species invasions at various spatial scales (Stuckey 1980; Reznicek and Catling 1987; Pysek 1991; Pysek and Prach 1995; Toney et al. 1998; Lambrinos 2001; Huebner 2003; Salo 2005). The probability of an individual being collected is dependent on the number of collectors in the field, which is a function of the population density of the area. Collections over the timescale of this study (1820–2000) coincide with population increases in most parts of the continent, especially in Northeastern US/Southeastern Canada. There is no accurate method of assessing the spatio-temporal collecting frequency (or the variation within) over North America as it is a function of a large number of interacting factors at smaller spatial scales. To reduce the variation in collection frequency per location this dataset only includes the first collection per political unit, which reduces temporal variation at each political unit. Additionally, the close alignment of invasive species with human activity (i.e., invaders are likely to be initially detected in anthropogenically modified landscapes in which they are introduced), and the large spatial scale of this study, minimizes site and regional collection variation respectively (Weber 1998).

Recreating the historic phytogeographic distribution of mugwort and Japanese knotweed using herbarium records showed that range expansion in both species was the result of several interacting factors. Intentional and accidental introductions, coupled with subsequent local radial expansion describe the geographic range expansion of both invading perennials. The intrinsic rate of spread was greater for Japanese knotweed, coupled with a shorter duration of exponential growth (i.e., t' was earlier). From this historic distribution I was able to parse out potential introduction vectors (e.g., ornamental and nursery trade) and corridors of invasion (e.g., road, railroad, and waterway rights-of-way). Range expansion was best approximated by the spatio-temporal distribution of independent introductions as ballast and ornamentals, followed by secondary range expansion. Additionally, it appears that the large-scale range expansion has ceased in Canada for both species, while remaining in the exponential phase in the US. Further studies of invasive species distributions could add information on the genetic variability that exists in these species, shedding light on the theory of multiple introductions of interacting genotypes. Both Japanese knotweed and mugwort continue to be distributed by the ornamental and herb trade in North America, potentially leading to the creation of 'novel invasive genotypes' via the interaction of naturalized and currently introduced genotypes. Legislation restricting the sale and movement of invasive species in both the US and Canada is severely lacking, with responsibility falling on plantsmen and land managers. Therefore, reducing the introduction of new genotypes and applying knowledge of species biology could be leveraged by land managers in an effort to minimize invasive species populations and preempt future invasions.

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