Landscape Position Influences the Distribution of Garlic Mustard, an Invasive Species

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Abstract - We investigated the distribution and abundance of *Alliaria petiolata*, an invasive biennial, with respect to historical land use, and examined environmental conditions to look for correlations with distribution patterns. Sixty currently forested plots in Cuyahoga Valley National Park, OH were chosen based on 1959 land use: agricultural (open) versus forested. Plots were analyzed for Garlic Mustard distribution, abundance, invasion area, and incursion distance. Garlic Mustard distribution did not vary with historical land use, but did vary significantly with distance from rivers and with elevation. Polygon area:perimeter values were also correlated with invasion. These results differ from studies done with Garlic Mustard in New England where historical land use appeared to be a larger factor in distribution. These results suggest the importance of landscape corridors in biological invasions and can be used to identify areas with greater potential for invasive species in this region.

Introduction

Invasive species are considered the second greatest threat to biodiversity today (Wilson 2002). These species have the ability to displace native species through competition or disease, and can often cause changes in the community structure and degrade the environmental health of the landscape (Mack and D'Antonio 1998, McCarthy 1997, Williamson 1996). Currently, 5–25% of the vascular species in the United States today are considered invasive (Vitousek et al. 1996). Over $130 billion per year is spent to control the spread and impacts of these species (Evans 2003). Research regarding invasive species will not only increase general knowledge regarding these plants' biology and ecology, but can also allow land managers to increase the efficiency of their control programs and may ultimately mitigate the extent of the damage done by aggressive nonnative invading plants. The management applications of this research are extremely useful and are of great importance to the discipline of conservation biology (Coblentz 1990).

While all communities are more or less able to be invaded by exotic plants (Williamson 1996), landscape disturbances often play a major role in biological invasions (Inderjit 2005, Nuzzo 1999). The extent of human presence has been proven to be a major contributor to biological invasions, possibly due to humans artificially increasing propagule abundance (Williamson 1996). Some recent work has explored the influence of long-term historical land use on the spread and distribution of invasive plants (Lundgren et al.

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2004; Kristina Stinson, Harvard Forest, Petersham, MA, pers. comm.), building on substantial research supporting the influence of historical land uses on stand-scale and large-scale (e.g., landscape) species composition as well as abiotic conditions (Foster 1992, Guggenberger et al. 1994, Hall et al. 2002, Motzkin et al. 2002, Verheyen et al. 1999). Most of this work has been done in the New England area, a region with soils developed on bouldery till, though some research on historical land use has been done in Wisconsin and in Europe (Guggenberger et al. 1994, White and Mladenoff 1994).

Alliaria petiolata (Bieb.) Cavera and Grande (Garlic Mustard) is an invasive Eurasian herbaceous plant, first recorded in Long Island, NY in 1868 (Nuzzo 1993). It can limit the biodiversity of a forest understory through competition and also demonstrates allelopathy, disrupting mycorrhizal associations (Roberts and Anderson 2001, Stinson et al. 2006, Wolfe and Klironomos 2005). Byers and Quinn (1998) demonstrated that Garlic Mustard populations display phenotypic plasticity in biomass allocation and flowering phenology between habitats, which allows for successful establishment in a variety of light, moisture, and soil conditions. Habitat variation also influenced the survivorship and seed germination of populations. Sites in their study were strongly distinguished by differences in pH, calcium content, nitrogen content, and percent organic matter, among other factors. Historical human activity has also been shown to influence similar soil nutrients; at least some of the differences may be due to fertilization of agricultural fields (Koerner et al. 1997, Verheyen et al. 1999). These results lead to the hypothesis that lasting abiotic differences resulting from historical agriculture will cause the differential distribution and survival of Garlic Mustard.

This study investigates the distribution of Garlic Mustard in the Cuyahoga Valley National Park with relation to 1959 land use. The objectives of this investigation were to determine 1) if historical land use has influenced the current distribution or abundance of Garlic Mustard in the Cuyahoga Valley National Park and 2) if selected environmental variables can be used to explain any trends discovered.

Materials and Methods

Species description

Garlic Mustard behaves strictly as a biennial in the United States with a first-year rosette and a second-year flowering and fruiting plant (Nuzzo 2000). Seeds are produced in siliques on the tops of the stems and average 350 seeds per plant, though extremely stout plants can produce up to 7000 seeds (Nuzzo 1999). Seeds usually germinate into rosettes in mid-spring; second-year plants usually bolt in mid-spring and are fully grown within approximately one month (Anderson et al. 1996). In northeastern Ohio, mature seeds dehisce from the siliques around late July. Seed dehiscence is quickly followed by senescence, and seed rain is normally limited to within 1–2 meters of the mother plant. (Anderson et al. 1996, Nuzzo 2000). Garlic Mustard has been present in Ohio since at least 1927, and specimens were recorded in proximity to Cuyahoga Valley National Park in 1959 (# 13724 and 63474, The Ohio State University Herbarium).

Site description

The Cuyahoga Valley National Park is located in northeastern Ohio (41°17'N, 81°34'W) in Cuyahoga and Summit counties and is approximately 135.95 km^2. The dominant soil series are Ellsworth silt and loam (3.20 km^2), rough broken land (1.55 km^2), and Glenford silt and loam (0.77 km^2). The Park stretches from Bedford, OH to Akron, OH. The majority of the area is deciduous hardwoods, with dominant communities being *Quercus* spp. (oak)/*Carya* spp. (hickory), *Acer* spp. (maple)/oak, and maple/*Plantanus occidentalis* L. (Sycamore) (based on National Park Service GIS data). The river valley was the site of the Ohio and Erie Canal, created in 1827 and abandoned in 1913. Previous to 1974, the area consisted of a matrix of privately owned farms and forest patches, some owned by the Cleveland Metropolitan Park District. In 1974, the area was designated by the national government as a national recreation area (Cockrell 1992, ODNR 2006). The area was established as a National Park in 2000 (Cross 2002) and includes several metropolitan parks and two ski resorts. Sections of private land are also embedded within the Park. The Cuyahoga River valley itself consists mainly of alfisols on glacial till with shale and sandstone bedrock between 480–205 million years old (Cockrell 1992, NRCS 2007). The average annual temperature is 9.78 °C, and the area receives an average of 98.30 cm of rain each year (for comparison, Worcester, MA, near the region studied by Lundgren et al. [2004], has an average temperature of 8.4 °C and has an annual precipitation of 124.59 cm; NOAA 2005). This area presents an opportunity to examine the influences of historical land use on the distribution of an invasive plant in a culturally heterogeneous landscape with more fertile soils and different climatic conditions than most other areas previously studied.

For this study, we chose the year 1959 as a reference point for historical land use in the Cuyahoga River valley region. The National Park GIS staff had already created detailed 1959 land-use maps of the Park, allowing for accurate delineation of currently forested areas into areas that were either open or forested fifty years ago. This date corresponds well to post-peak agriculture use and the subsequent abandonment of farmland and reestablishment of forest cover in Ohio as described by Simpson et al. (1994). These trends are seen in the Cuyahoga River valley; in 1959, the area currently designated as national park had 38.84 km^2 of agricultural land and 77.88 km^2 of forested land; today the area has only 8.44 km^2 of agriculture and maintained open areas and 95.70 km^2 of forest (Figs. 1a, 1b). During this time, there was a net increase in urban and other land uses of 12.58 km^2. As most remaining agriculture was abandoned when the Park was commissioned in 1974, there has been adequate time for forest regrowth (other than in select patches used for educational and recreational purposes). This reversal of land-use trends is roughly equivalent to that which occurred in 1830 as described in studies conducted in the Massachusetts area (Foster 1992, Hall et al. 2002).

Experimental methods

Historical and present land use in the Cuyahoga Valley National Park was determined using files provided by the National Park staff. Using

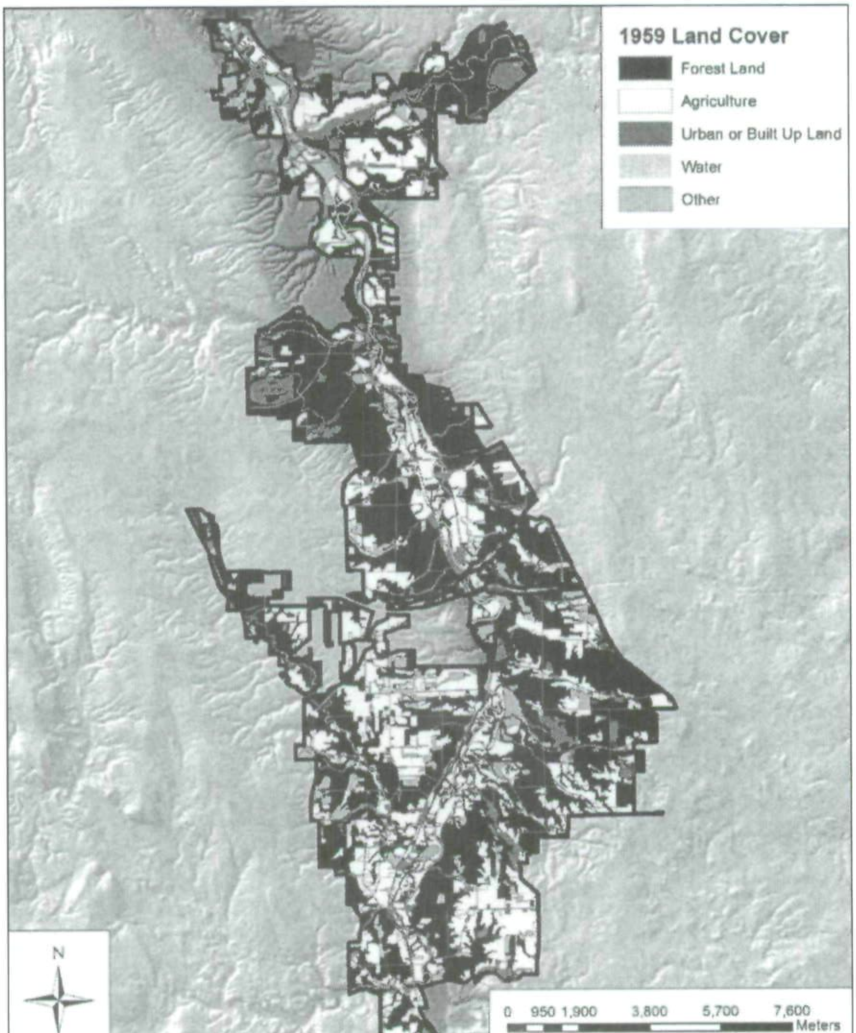

Figure 1a. Land cover of Cuyahoga Valley National Park in 1959.

ArcMap 9.1, polygons were created and divided into two categories based on their 1959 status: agricultural (open) or wooded. All polygons are currently forested. Each polygon extended at least 150 m along a trail edge and at least 50 m into the forest interior to establish a buffer from other land-use categories or mapping inaccuracies. Study polygons, thirty in each category, were then randomly selected, each at least 1 km from its nearest neighbor. Study plots inside the polygons, each 2500 m^2 in area, were selected along the trails present through the polygon using the centroid function on ArcMap and satellite photographs of the area. Plots were rectangular in shape, extending 100 m long along the trail edge and 25 m into the forest. Trails, which are pervasive throughout the Park, were used

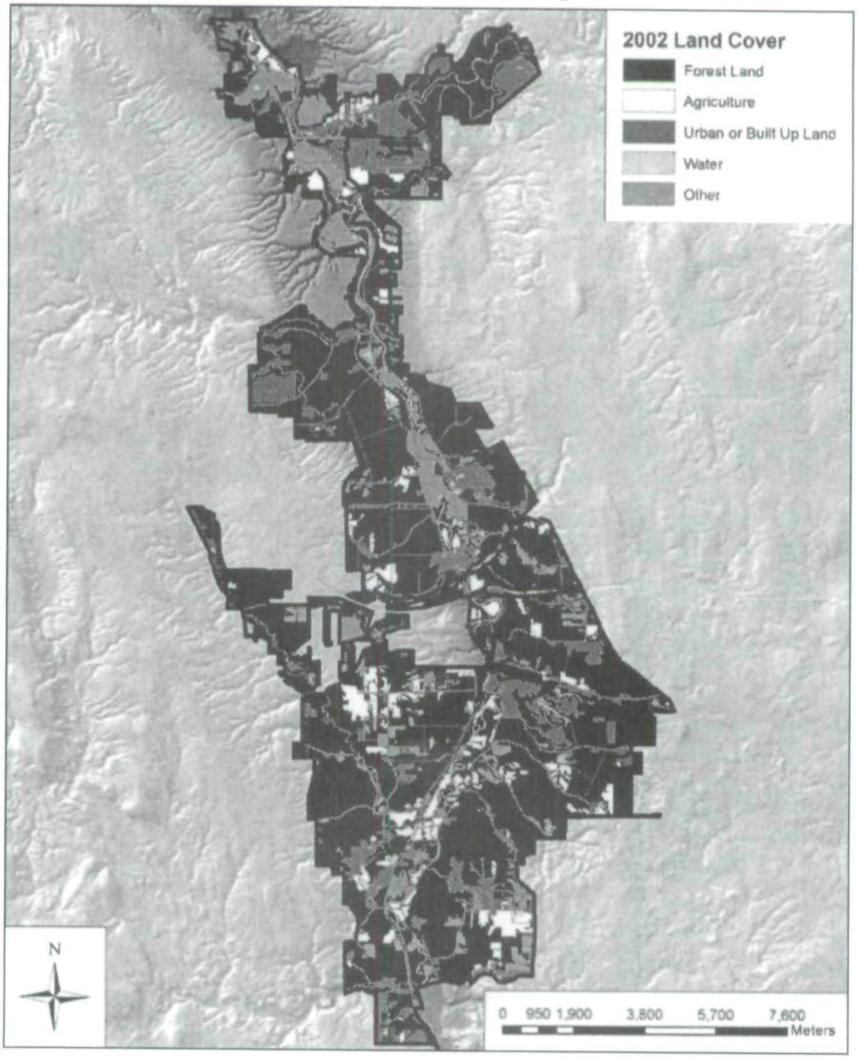

Figure 1b. Land cover of Cuyahoga Valley National Park in 2002.

as plot boundaries in order to eliminate them as a variable during analysis. Roads and pathways are well-known corridors for invasion (Lundgren et al. 2004, Parendes and Jones 2000), so all sites are at a high risk of modern invasion. Thus, there is no way to test for the effects of agriculture on historical Garlic Mustard invasion. The current study examines only whether abiotic or biotic changes in areas that were historically agricultural have created conditions that facilitate invasion and establishment.

Plots were surveyed on foot, and any Garlic Mustard found was divided into edge populations, located between the trail edge and the outer treeline, or forest populations, extending into the forest past the outer treeline. Population boundaries inside study plots were delineated as zones without individual plants for 15 m, which is appropriate given the normally short dispersal distance of Garlic Mustard (Anderson et al. 1996, Nuzzo 2000). Maximum incursion of the population into the forest and maximum length along the plot were recorded. Visual measurements of the abundance of the population were made as the percent of the population's maximum area covered by Garlic Mustard in the following classes: <1.0%, 1.0–3.0%, 3.1–5.0%, 5.1–15.0%, 15.1–25.0%, 25.1–50.0%, 50.1–75.0%, or >75.0%. Percent canopy cover was measured at the center of each plot at 5-m intervals from the trail edge using a convex spherical densiometer, and qualitative assessments of canopy composition, stand structure, topography, soil moisture, and common understory vegetation were recorded. Major disturbances such as power lines, roads, etc., were avoided by requiring a minimum of a 25-m forested buffer to the rear of each plot. Slope and aspect were determined from a digital elevation map using ArcMap, and plot distances from rivers and roads were determined using GIS layers created by the National Park.

Chi-square analyses were performed on population presence or absence with respect to land use. Edge and forest environments were very similar and were therefore merged prior to the analysis of environmental and plot data. ANOVA tests were run on population invasion class, incursion distance, and invasion area with respect to land use and with respect to the study polygon area:perimeter ratio, aspect, slope, canopy cover, distance from roads, distance from rivers, and elevation. All analyses were done using SYSTAT 9.

Results

The results of all χ^2 analyses and ANOVAs are listed below in Table 1. Land use was not correlated to Garlic Mustard presence, invasion class, invasion area, or incursion distance. Mean polygon area:perimeter ratio differed between agricultural and forest land uses (30.35 and 59.91, respectively). The average slope in degrees also differed between agricultural and forested land use (10.73 and 27.80, respectively). Garlic Mustard presence varied significantly with both distance from rivers and elevation. The mean distance to rivers of plots lacking Garlic Mustard was 825.0 m (± 423.7 m SD) and to plots occupied by Garlic Mustard was 483.6 m (± 365.4 m) (Fig. 2). Similarly, plots lacking Garlic Mustard had a significantly higher average elevation (274.4 ± 120.63 m) than did plots occupied by Garlic Mustard (246.3 ± 38.0 m) (Fig. 3). River distance and elevation were strongly correlated ($P = 0.001$, $F = 12.39$, $r^2 = 0.176$). Analysis of covariance showed that both elevation and river distance were still significant after removing the effects of the covariant. Area:perimeter ratio was significantly correlated to incursion distance and remained correlated ($P = 0.027$, $F = 9.61$, $n = 7$) after removing sites invaded 25 m into the forest interior; this adjustment was done to avoid bias in regression analysis caused by plot size limits. Slope was not significantly correlated to invasion area when historical land use was used as a covariate.

Discussion

This study investigated the hypothesis that lasting abiotic differences in forest stands that were used in historical agriculture would cause a differential distribution and survival of Garlic Mustard. As land-use history was not found to influence any properties of Garlic Mustard populations, this differential distribution does not seem to have occurred in the Cuyahoga valley. This finding is contrary to contemporary research in the New England region (DeGasperis and Motzkin, in press; Lundgren et al. 2004), as well as much of the research associated with long-term

Table 1. Results of plot analysis for land use and environmental influence. Asterisks indicate significant results ($P < 0.05$).

Site or environmental factor		Land use ($n = 60$)	*Alliaria petiolata* presence ($n = 60$)	Invasion class ($n = 28$)	Incursion distance ($n = 28$)	Invaded area ($n = 28$)
Area:Perimeter ratio	$P =$	0.000*	0.124	0.679	0.004*	0.100
	$F =$	26.62	2.44	0.66	10.02	2.90
Aspect	$P =$	0.912	0.680	0.549	0.597	0.287
	$F =$	0.01	0.17	0.85	0.29	1.18
Slope	$P =$	0.000*	0.695	0.180	0.150	0.049*
	$F =$	30.30	0.16	1.66	2.20	4.26
Canopy cover	$P =$	0.618	0.582	0.955	0.628	0.932
	$F =$	0.25	0.31	0.24	0.24	0.01
Road distance	$P =$	0.212	0.052	0.137	0.780	0.345
	$F =$	1.59	3.92	1.86	0.08	0.93
River distance	$P =$	0.057	0.002*	0.923	0.103	0.159
	$F =$	3.76	11.01	0.31	2.85	2.10
Elevation	$P =$	0.218	0.001*	0.393	0.283	0.073
	$F =$	1.55	13.03	1.10	1.20	3.48
Land use	$P =$	N/A	0.301	0.113	0.869	0.813
	$F =$	N/A	1.06	2.69	0.03	0.06

vegetation composition done by various researchers (e.g., Foster 1992). There are three main possibilities for this finding: phenotypic variability, edaphic factors, and scale of disturbance.

First, phenotypic plasticity in plants, and plants' ability to spread over wide geographic ranges, are topics of much ongoing research (Sultan 2000). Donohue (2005) reviewed seed dispersal, flowering, and germination time in *Arabidopsis thaliana* (L.) Heynh. (Mouseear Crest) and showed how the timing of each characteristic can influence itself or interact with other life-history traits to manipulate the environment the

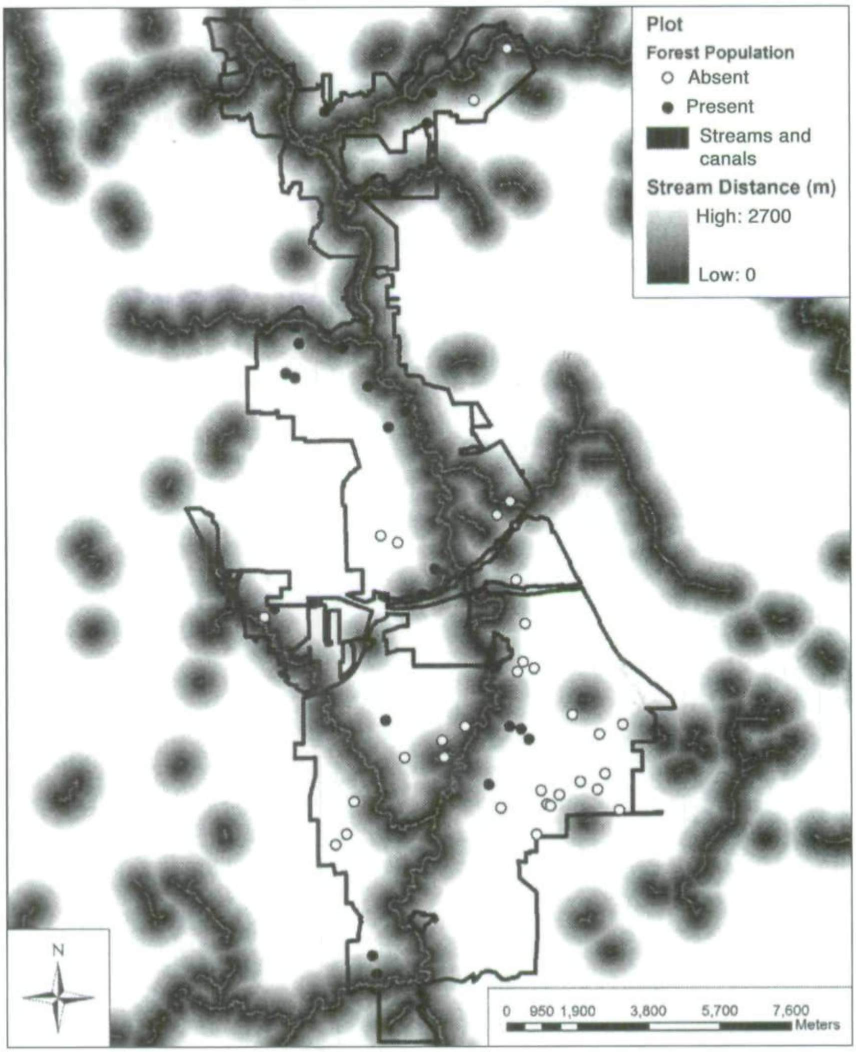

Figure 2. Garlic Mustard population distribution in relation to distance from rivers. Coloration extends to one standard deviation past the mean distance from rivers for plots occupied by Garlic Mustard.

organism experiences in future generations. This plasticity in phenology, which then determines the environment of the organism, has been termed niche construction and influences the phenotypic expression and natural selection pressures on a given life-history trait (Donohue 2005). Byers and Quinn (1998) examined the demographic variation in Garlic Mustard in four contrasting habitats in New Jersey and found flowering time and biomass allocation to vary significantly among habitats, concluding through common garden experiments that the plants responded to the range of habitats mainly through phenotypic plasticity. Thus, plasticity in

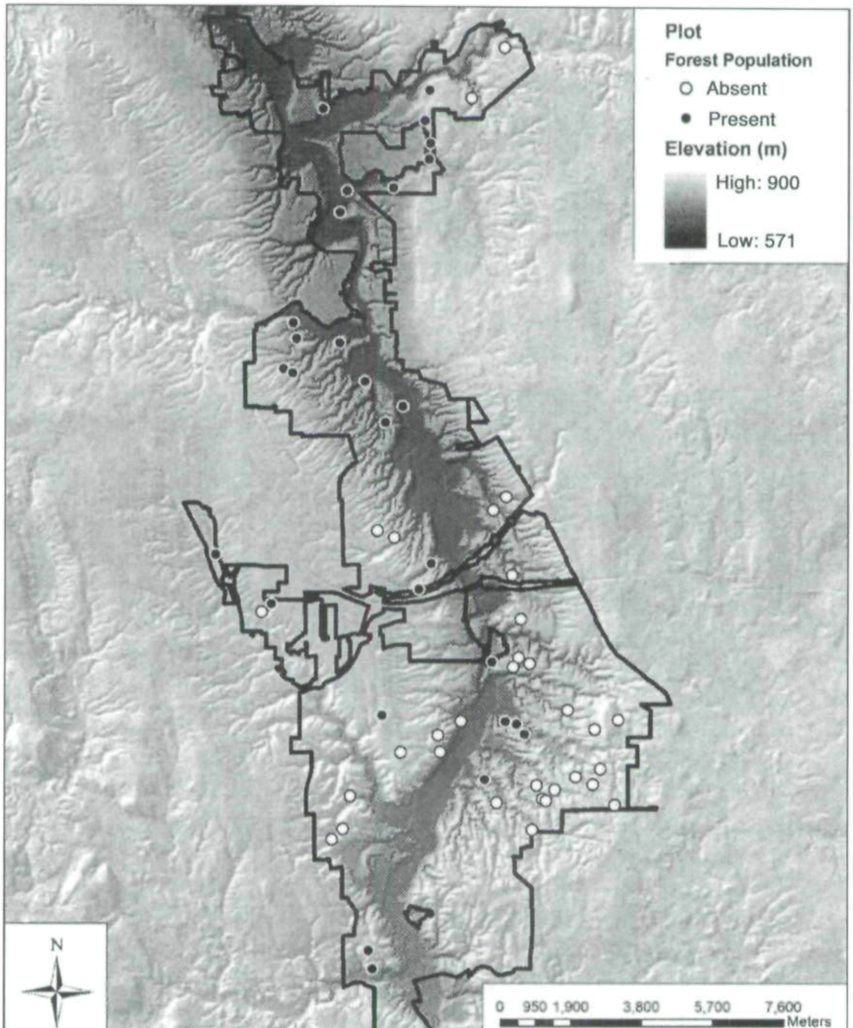

Figure 3. Garlic Mustard population distribution in relation to elevation. Coloration extends to one standard deviation past the mean elevation of plots occupied with Garlic Mustard.

phenology by Garlic Mustard in this region may allow it to overcome any environmental pressures from varying historical land uses. In addition to niche construction, invasive plants are known to alter the nutrient dynamics of soils through allelopathy, changing primary productivity rates, or changing ecosystem processes (Ehrenfeld 2003, Lundgren et al. 2004, Rice 1984, Vanderhoeven et al. 2005). If a small invasive population has been established for a long enough period of time, it is possible it may alter the soil characteristics and promote its own spread.

Second, the "soil signature" of soils in Ohio, mainly alfisols, is very different compared to the rockier soils in New England, which are inceptisols or entisols). Alfisols, which generally have a higher percent base saturation and total cation exchange and have a finer texture than entisols and inceptisols (Gardiner and Miller 2003), can lead to different plant communities in relatively similar climates, and this difference may hold some important implications for invasive species distributions.

Third, some studies (Anderson et al. 1996, Nuzzo 1999) cite Garlic Mustard's ability to capitalize on one-time microdisturbances through phenotypic plasticity and self-fertilization. Therefore, disturbances that create distinct microhabitats, such as treefalls or steep shaded slopes, may be enough for Garlic Mustard to establish a population and spread. Future studies may find that different limiting factors may control distribution at different spatial scales (e.g., the factors at play in a treefall versus those on an entire landscape), obscuring their effects.

As mentioned above, the presence of paths along study plots should encourage the establishment of Garlic Mustard at all locations, limiting inferences to long-term abiotic or biotic differences in historically farmed or forested sites. Surveys of areas that lack paths may show different conclusions, though this result is unlikely due to the factors mentioned above. In addition, it would be difficult to locate plots without trails, as most historically agricultural areas within the Park are in close proximity to roads and pathways.

Garlic Mustard incursion distance was negatively correlated with polygon area:perimeter ratio (r^2 = 0.527; Table 1). This correlation remained significant even after removing sites with a 25-m incursion distance. This measurement is limited due to the plot size, but may hold some importance when relating Garlic Mustard's "approach and retreat" advance from disturbances (Nuzzo 1999), as the edges created by historical agriculture can change many environmental conditions and may facilitate modern invasions (Alston and Richardson 2006, Brothers and Springarn 1992, Foster 1992, Saunders et al. 1991).

Garlic Mustard population distribution was found to increase with decreasing elevation. This result would suggest that the relatively minor changes in elevation, approximately 100 m, play some role in the distribution of Garlic Mustard. This influence has been documented for individual species and community composition in other areas, including floodplains (discussed below), and can be due to competition with other plants or differing abiotic variables which may constrain a species' vertical distribution and realized niche (Funk et al. 2004, Lenssen and de Kroon 2005, Leyer 2005, Welch et al. 2006). It is also possible that forest populations of Garlic Mustard, despite any phenotypic plasticity, require a long-term seed dispersal agent to exist in forest interiors. Data by Stinson et al. (unpubl. data) suggest that forest populations of Garlic Mustard in New England may be serving as sink populations, and Nuzzo (1999) found the rate of spread to be partially dependent on the establishment of satellite populations. While the mechanism for the spatial pattern observed in this study is not elucidated, it is possible that seed transport by gravity or surface water runoff may be responsible as a seed source for populations at lower elevations and that populations may have a source-sink dynamic. This dynamic may be especially important for populations in historically wooded areas, which are often on steeper slopes than previously farmed landscapes (see above). While not conclusive, this finding holds implications for land managers and for future studies.

Garlic Mustard population distribution was also negatively correlated to river distance. This finding seems intuitive when coupled with the elevation data, as Cuyahoga Valley National Park is innately related to the river valley and its topography, and elevation and river distance are strongly correlated (see above). Still, past research suggests this finding may imply some additional spatial patterning based on location or habitat variation. The role of water in biological invasions is multifaceted. Observed rates of spread by Garlic Mustard are well above values predicted using simple expulsion from the mother plant, indicating a long-term dispersal agent. Water transport has been identified as a long-distance seed vector for riparian flora (Andersson et al. 2000, van Eck et al. 2005,Vogt et al. 2004) as well as for Garlic Mustard (Nuzzo 1993). Rivers may also serve as corridors for shorter term, distance-dependent seed transport, and can serve to connect otherwise fragmented communities (Kudoh and Whigham 1997, Thomas et al. 2006, Vogt et al. 2004). Campbell et al. (2002) found a strong correlation between predicted dispersal rates and an analytical model for river-aided seed dispersal and offers this relationship as an opportunity to predict the invasion of alien species and to compare with actual invasion rates. Garlic Mustard has a short-lived seed bank (Baskin and Baskin 1992, Nuzzo 1999), and yearly floods may be important to both long-distance spread and forest interior incursion. In addition, the Cuyahoga River valley and its tributaries likely serve as preferred routes for wildlife and human movement, combining the topography, river presence, and human presence in the area to create a passive corridor for seed dispersal. Thus, it may be useful to consider elevation as a proxy for distance from major dispersal corridors in this geographical context.

However, rivers may also serve to change the abiotic conditions, mainly risk of drought, and thereby limit species' distribution; some studies on the elevation-related phenomena discussed above are found in conjunction with floodplain environments (Lenssen and de Kroon 2005, Leyer 2005). Also, Byers and Quinn (1998) found higher survivorship, earlier flowering phenology, and higher germination rates of Garlic Mustard in floodplain environments compared to drier environments. While the present study did not examine the roles of rivers in Garlic Mustard spread, the Cuyahoga River's importance in this study area cannot be ignored and should be a point of study in this and other areas.

This study examined the influence of historical land use on the distribution and abundance of Garlic Mustard in a river valley environment in northeast Ohio. While historical land use did not appear to have any influence, other environmental factors in the region may be limiting the distribution of Garlic Mustard populations. These trends warrant further studies and may prove useful to land managers targeting the floodplains to limit the spread of Garlic Mustard into forest interiors.

In addition to this functional but proximate finding, a more broad-scale conclusion can be drawn. Studies on invasive plant distributions, and species distributions in general, like those discussed above, are often somewhat contradictory. Some studies favor abiotic site conditions (Byers and Quinn 1998, Lenssen and de Kroon 2005, Leyer 2005) or interspecies competition (Lenssen and de Kroon 2005, Vilà and Weiner 2004) as the range-limiting factor. Other studies attribute geographic limits to seed dispersal limitations (Andersson et al. 2000, van Eck et al. 2005, Vogt et al. 2004). In addition, disturbance levels are often believed to favor invasive species dispersal (Inderjit 2005, Nuzzo 1999, Williamson 1996). Historical land use, explored in the present study, has proven to be a very strong variable in determining New England plant species composition with both native and invasive species (Degasperis and Motzkin in press, Donohue et al. 2000, Foster 1992), but does not appear to play a major role in the Cuyahoga River valley region. While each of the above variables, in addition to others not mentioned, certainly plays a role in any given case, it may be prudent to advise land managers and scientists to take a cautionary stance before assigning a specific variable as a limiting factor in an invasive species' niche or as the main factor in its competitive abilities. In fact, the limiting variables appear to change depending on the species (Davis 2006), ecoregion (K. Stinson et al., unpubl. data), and habitat (Byers and Quinn 1998). In the future, a comprehensive understanding of the invasive species of interest, and specifically its behavior in the region of interest, should be obtained by land managers before expending limited resources for its control or extermination. This precaution will allow their efforts to be more effective and lasting, conserving our ecosystems' functionality and biodiversity.

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Literature Cited

Alston, K.P., and D.M. Richardson. 2006. The roles of habitat features, disturbance, and distance from putative source populations in structuring alien plant invasions at the urban/wildland interface on the Cape Peninsula, South Africa. Biological Conservation 132:183–198.

Anderson, R.C., S.S. Dhillon, and T.M. Kelley. 1996. Aspects of the ecology of an invasive plant, Garlic Mustard (*Alliaria petiolata*), in central Illinois. Restoration Ecology 4(2):181–191.

Andersson, E., C. Nilsson, and M.E. Johansson. 2000. Plant dispersal in boreal rivers and its relation to the diversity of riparian flora. Journal of Biogeography 27(5): 1095–1106.

Baskin, J.M., and C.C. Baskin. 1992. Seed germination biology of the weedy biennial *Alliaria petiolata*. Natural Areas Journal 12:191–197.

Brothers, T.S., and A. Sprigarn. 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. Conservation Biology 6(1):91–100.

Byers, D.L., and J.A. Quinn. 1998. Demographic variation in *Alliaria petiolata* (Brassicaceae) in four contrasting habitats. Journal of the Torrey Botanical Society 125(2):138–149.

Campbell, G.S., P.G. Blackwell, and F.I. Woodward. 2002. Can landscape-scale characteristics be used to predict plant invasions along rivers? Journal of Biogeography 29:535–543.

Coblentz, B.E. 1990. Exotic organisms: A dilemma for conservation biology. Conservation Biology 4(3):261–265.

Cockrell, R. 1992. A green shrouded miracle: The administrative history of Cuyahoga Valley National Recreation Area, Ohio. National Park Service Midwest Regional Office, Omaha, NE. Available online at http://www.nps.gov/history/history/online_books/Cuyahoga/toc.htm. Accessed June 27, 2007.

Cross, R. 2002. A "stealth" park slips under the radar screen. Chicago Tribune, June 9, 2002. Available online at http://www.chicagotribune.com/travel/chi-020609cuyahogaside,1,679541.story?coll=chi-900siteindex-fea. Accessed June 27, 2007.

Davis, A.S. 2006. When does it make sense to target the weed seed bank? Weed Science 54:558–565.

DeGasperis, B.G., and G. Motzkin. In press. Windows of opportunity: Historical and ecological controls on *Berberis thunbergii* invasions. Ecology.

Donohue, K. 2005. Niche construction through phenological plasticity: Life-history dynamics and ecological consequences. New Phytologist 166:83–92.

Donohue, K., D.R. Foster, and G. Motzkin. 2000. Effects of the past and the present on species distributions: Land-use history and demography of wintergreen. Journal of Ecology 88:303–316.

Ehrenfeld, J.G. 2003. Effects of exotic plant invasions of soil nutrient cycling processes. Ecosystems 5:503–523.

Evans, E.A. 2003. Economic dimensions of invasive species. Choices 18(2):5–9.

Foster, D.R. 1992. Land-use history (1730–1990) and vegetation dynamics in central New England, USA. Journal of Ecology 80:753–772.

Funk, D.W., L.E. Noel, and A.H. Freedman. 2004. Environmental gradients, plant distribution, and species richness in arctic salt marsh near Prudhoe Bay, Alaska. Wetlands Ecology and Management 12:215–233.

Gardiner, D.T., and R.W. Miller. 2003. Soils in Our Environment. Prentice Hall, Upper Saddle River, NJ. 656 pp.

Guggenberger, G., B.T. Christensen, and W. Zech. 1994. Land-use effects on the composition of organic matter in particle-size separates of soil: I. Lignin and carbohydrate signature. European Journal of Soil Science 45:449–458.

Hall, B., G. Motzkin, D.R. Foster, M. Syfert, and J. Burk. 2002. Three hundred years of forest and land-use change in Massachusetts, USA. Journal of Biogeography 29:1319–1335.

Inderjit. 2005. Plant invasions: Habitat invisibility and dominance of invasive plant species. Plant and Soil 277:1–5.

Koerner, W., J.L. Dupouey, E. Dambrine, and M. Benoît. 1997. Influence of past land use on the vegetation and soils of present day forest in the Vosges mountains, France. Journal of Ecology 85:351–358.

Kudoh, H., and D.F. Whigham. 1997. Microgeographic genetic structure and gene flow in *Hibiscus moscheutos* (Malvaceae) populations. American Journal of Botany 84(9):1285–1293.

Lenssen, J.P.M., and H. de Kroon. 2005. Abiotic constraints at the upper boundaries of two *Rumex* species on a freshwater flooding gradient. Journal of Ecology 93: 138–147.

Leyer, I. 2005. Predicting plant species' responses to river regulation: The role of water-level fluctuations. Journal of Applied Ecology 42:239–250.

Lundgren, M.R., C.J. Small, and G.D. Dreyer. 2004. Influence of land use and site characteristics on invasive plant abundance in the Quinebaug Highlands of southern New England. Northeastern Naturalist 11(3):313–332.

Mack, M.C., and C.M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. Trends in Ecology and Evolution 13(5):195–198.

McCarthy, B.C. 1997. Response of a forest understory community to experimental removal of an invasive nonindigenous plant (*Alliaria petiolata*, Brassicaceae). Pp. 117–128, *In* J.O. Luken and J.W. Thieret (Eds.). Assessment and Management of Plant Invasions. Springer-Verlag Publishing, New York, NY. 324 pp.

Motzkin, G., D.A. Orwig, and D.R. Foster. 2002. Vegetation and disturbance history of a rare dwarf Pitch Pine community in western New England, USA. Journal of Biogeography 29:1455–1467.

National Oceanic and Atmospheric Administration (NOAA). 2005. Comparative climatic data for the United States through 2006. Available online at http://www1.ncdc.noaa.gov/pub/data/ccd-data/CCD_2006.pdf. Accessed July 19, 2007.

Natural Resources Conservation Service (NRCS). 2007. Distribution maps of dominant soil orders. Available online at http://soils.usda.gov/technical/classification/orders/. Accessed June 27, 2007.

Nuzzo, V. 1993. Distribution and spread of the invasive biennial *Alliaria petiolata* (Garlic Mustard) in North America. Pp. 137–145, *In* B.N. McKnight (Ed.). Biological Pollution. Indiana Academy of Science, Indianapolis, IN. 261 pp.

Nuzzo, V. 1999. Invasion pattern of the herb Garlic Mustard (*Alliaria petiolata*) in high-quality forests. Biological Invasions 1:169–179.

Nuzzo, V. 2000. Elemental stewardship abstract for *Alliaria petiolata* (*Alliaria officinalis*) Garlic Mustard. The Nature Conservancy, Elemental Stewardship Abstracts, Arlington, VA.

Ohio Department of Natural Resources (ODNR). 2006. History of Ohio's canals. Available online at http://www.ohiodnr.com/water/canals/canlhist.htm. Accessed November 18, 2006.

Parendes, L.A., and J.A. Jones. 2000. Role of light availability and dispersal in exotic plant invasion along roads and streams in the H.J. Andrews Experimental Forest, Oregon. Conservation Biology 14(1):64–75.

Rice, E.L. 1984. Allelopathy. Academic Press, New York, NY. 422 pp.

Roberts, K.J., and R.C. Anderson. 2001. Effect of Garlic Mustard (*Alliaria petiolata* [Bieb.] Cavara & Grande)] extracts on plants and arbuscular mycorrhizal (AM) fungi. American Midland Naturalist 146:146–152.

Saunders, D.A., R.J. Hobbs, and C.R. Margules. 1991. Biological consequences of ecosystem fragmentation: A review. Conservation Biology 5(1):18–32.

Simpson, J.W., R.E.J. Boerner, M.N. DeMers, L.A. Berns, F.J. Artigas, and A. Silva. 1994. Forty-eight years of landscape change on two contiguous Ohio landscapes. Landscape Ecology 9(4):261–270.

Stinson, K.A., S.A. Campbell, J.R. Powell, B.E. Wolfe, R.M. Callaway, G.C. Thelen, S.G. Hallett, D. Prati, and J.N. Klironomos. 2006. Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. PLoS Biology 4(5):e140.

Sultan, S.E. 2000. Phenotypic plasticity for plant development, function, and life history. Trends in Plant Science 5(12):537–542.

Thomas, J.R., B. Middleton, and D.J. Gibson. 2006. A landscape perspective of the stream corridor invasion and habitat characteristics of an exotic (*Dioscorea oppositifolia*) in a pristine watershed in Illinois. Biological Invasions 8:1103–1113.

Tikka, P.M., H. Högmander, and P.S. Koski. 2001. Road and railway verges serve as dispersal corridors for grassland plants. Landscape Ecology 16:659–666.

Van Eck, W.H.J.M., H.M. van de Steeg, C.W.P.M. Blom, and H. de Kroon. 2005. Recruitment limitation along disturbance gradients in river floodplains. Journal of Vegetation Science 16:103–110.

Vanderhoeven, S., N. Dassonville, and P. Meerts. 2005. Increased topsoil mineral nutrient concentrations under exotic invasive plants in Belgium. Plant and Soil 275:169–179.

Verheyen, K., B. Bossuyt, M. Hermy, and G. Tack. 1999. The land-use history (1278–1990) of a mixed hardwood forest in western Belgium and its relationship with chemical soil characteristics. Journal of Biogeography 26:1115–1128.

Vilà, M., and J. Weiner. 2004. Are invasive species better competitors than native plant species? Evidence from pair-wise experiments. OIKOS 105:229–238.

Vitousek P.M., C.M. D'Antonio, L.L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. American Scientist 84(5):468–479.

Vogt, K., L. Rasren, and K. Jensen. 2004. Water-borne seed transport and seed deposition during flooding in a small river-valley in northern Germany. Flora 199: 377–388.

Welch, B.A., C.B. Davis, and R.J. Gates. 2006. Dominant environmental factors in wetland plant communities invaded by *Phragmites australis* in East Harbor, Ohio, USA. Wetlands Ecology and Management 14:511–525.

White, M.A., and D.J. Mladenoff. 1994. Old-growth forest landscape transitions from pre-European settlement to present. Landscape Ecology 9(3):191–205.

Williamson, M. 1996. Biological Invasions. Chapman and Hall Publishing, London, UK. 244 pp.

Wilson, E.O. 2002. The Future of Life. Knopf (Random House) Publishing, New York, NY. 229 pp.

Wolfe, B.E., and J.N. Klironomos. 2005. Breaking new ground: Soil communities and exotic plant invasion. BioScience 55(6):477–487.