Regional and Historical Influences on Exotic Plant Invasions

The Ecological Drivers of *Alliaria petiolata* Invasion in Western Massachusetts

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Abstract

Alliaria petiolata is an herbaceous biennial herb that was introduced to New England over a century ago, and has since spread across North America. *A. petiolata* frequently grows along forest edges, but can also invade intact forest communities, an unusual ability for an invasive plant. Much is known about *A. petiolata*'s ecology at the scale of the local ecosystem, but there has been little work on the importance of spatial, temporal, and environmental factors at the regional scale. The studies presented here are based on field surveys of *A. petiolata* in the Connecticut Valley and Berskshire Valley ecoregions of western Massachusetts. A history of human impact from agricultural land use could be playing a role in the distribution of *A. petiolata* in these ecoregions. The goal of the studies is to determine the historical, geographic, and environmental influences on *A. petiolata*'s occurrence and performance and to draw lessons for thinking about invasive plants on the regional scale.

The survey included 175 roadside, forested plots, across the two ecoregions, and across areas with wooded and cleared pre-introduction land cover. Data on *A. petiolata* occurrence and abundance, community structure, and soil moisture was collected in the field. Additional site-specific data on land fragmentation, climate, and geology was obtained using GIS datalayers from MassGIS. Multiple logistic regression and MANOVAs were used to determine which factors had the greatest impact on *A. petiolata* occurrence and abundance.

Results show that *A. petiolata* has a higher occurrence in the Berkshire Valley than in the Connecticut Valley that cannot be accounted for by environmental differences between the ecoregions. There are no differences between ecoregions in abundance. Pre-introduction land use history does not appear to have a significant effect on *A. petiolata* distribution at the regional scale. Latitude stands out as an important environmental variable, as *A. petiolata* is more prevalent in more southern sites. This is most likely related to the history of invasion rather than climate-related factors, which were taken into account. Among other environmental variables, different factors appeared to be important for the different processes of establishment at a site, establishment in the forest understory, and abundance in the understory. These findings lead to the general conclusion that history and geography, in addition to environment, are important considerations in studying plant invasions at the regional scale.

Acknowledgements

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Chapter I - Introduction

The Invasive Species Phenomenon

> Nowadays we live in a very explosive world, and while we may not know when or where the next outburst will be, we might hope to find ways of stopping it or at any rate damping down its force. It is not just nuclear bombs and wars that threaten us…there are other sorts of explosions…ecological explosions. An ecological explosion means the enormous increase in numbers of some kind of living organism – it may be an infectious virus like influenza, or a bacterium like bubonic plague, or a fungus like that of the potato disease, or a green plant like the prickly pear, or an animal like the grey squirrel. I use the word 'explosion' deliberately, because it means the bursting out from control of forces that were previously held in restraint by other forces… Ecological explosions differ from some of the rest by not making such a loud noise and in taking longer to happen. That is to say, they may develop slowly and they may die down slowly; but they can be very impressive in their effects, and many people have been ruined by them, or died or forced to emigrate.
>
> - Charles S. Elton, 1958, *The Ecology of Invasion by Animals and Plants* (Elton 1958)

Biological invasions occur when organisms make their way into new, often distant ecological communities where their descendents persist, proliferate, and spread (Elton 1958). Such invasions are not a novel or exclusively a human-driven phenomenon, but humans are no doubt responsible for accelerating the process, expanding its scope, and exacerbating the effects, often to our own detriment. As a human problem, non-native biological pests have been around since the birth of agriculture and trade at the dawn of civilization. In 1958, Charles Elton first recognized the large scope of the potential issues raised by this massive biogeographic rearrangement. With today's global trade networks, there are few places on the planet free of organisms introduced by people (Mack et al. 2000), and one study has attributed a minimum of $120 billion in annual economic damages to the 50,000 invasive species in the United States (Pimentel et al. 2005).

The ecological consequences of invasive species are also non-trivial, as invasive organisms are at least partially responsible for nearly half of all endangered and threatened species in the U.S., and ecologists predict that biotic invasions, along with climate change, will be among the foremost drivers of biodiversity loss in the coming century (Simberloff et al. 2005). Invaders are capable of altering fundamental ecosystem properties such as plant productivity, the dominant species in a community, nutrient and water cycling, and the physical features of a landscape (Mack et al. 2000).

Though the consequences of invasive species can be characterized as dire, or even apocalyptic in Elton's colorful description, they also present unique opportunities to study a variety of ecological and evolutionary processes relating to species distribution and abundance (DeGasperis and Motzkin 2007). The bulk of research in the ecology of biological invasions has occurred only in the last few decades (Mack et al. 2000). Some broad principles have emerged relating to the characteristics that make species good invaders, the attributes of habitats that are susceptible to invasion, and the processes by which invaders establish and spread. But there is a lack of definitive synthesis, generalization, and predictive ability in the science, as every species appears to be a unique case study in invasion biology (Mack et al. 2000; Mack et al. 2007). In this young field that has significant bearing on human concerns there is ample opportunity to expand our understanding.

Approaches to the Study of Invasive Plants

Many different approaches have been taken to studying invasive plants. Most studies focus on a single species (Cavers et al. 1979; Anderson et al. 1996), but some compare two or more species (Morrison et al. 2007), and others look at hundreds (Aronson et al. 2007).

From both a scientific and applied point of view, developing an ability to predict invasions is important. This has often been done by looking either at the characteristics that make species good invaders (Williamson and Fitter 1996), or attributes that make habitats invasible (Naeem et al. 2000), though examining the habitat-species match can be particularly informative (Meekins and McCarthy 2001; Welk et al. 2002). From the applied side, research in the control and management of invasive plants is also important (Blossey et al. 2001; Slaughter et al. 2007), as is information on the impacts of exotics on native plant communities (Stinson et al. 2007). The effects of invasives on abiotic processes like nutrient cycling and hydrology have also been documented (Ehrenfeld 2003). In the evolutionary context, adaptive responses to new environments and phenotypic plasticity have been documented and widely discussed (Maron et al. 2004; Richards et al. 2006). More recently, attention has been drawn to the population genetics of invasive plants (Meekins et al. 2001; Bossdorf et al. 2005)

These approaches involve the study of invasive plants from ecological, evolutionary, and conservation perspectives, but it is also possible to more fully emphasize the spatial and temporal aspects of invasion biology through biogeography and historical ecology. Such an approach allows invasions to be viewed as something more than just a biological phenomenon by putting them in a larger geographic and historical context. Mack et al. emphasize the need for spatially explicit case histories of how invasions unfold, and argue that time-series maps are one of the most effective ways for both scientist and the public to understand invasions (Mack et al. 2000; Mack et al. 2007). The studies presented here emphasize the geographic and historical aspects of invasion biology in attempting to answer the question of what drives a plant to invade a given area. This question is approached by looking at the regional and historical land use effects on an invasive herb in western Massachusetts. We will see that this approach also has implications for the population biology and evolutionary ecology of the study species.

Biological invasions typically progress through the phases of introduction, establishment, and then integration into the new landscape, with each stage unfolding on successively larger scales. To fully understand the dynamics of invasions it is necessary to study them at all levels of spatial hierarchy (Mack et al. 2007). At the global and continental level, species ranges and potential ranges can be mapped out with ecological niche models based primarily on physical factors such as temperature and precipitation (Peterson 2003). At the level of the local ecosystem, small-scale disturbance and inter-species interactions tend to drive plant invasions (Wiser et al. 1998). In between the local and continental is the regional scale, which is particularly important in studying invasions because the regional scale is where patterns of invasibility and spread are most likely to emerge and it is the scale at which humans usually deal with invasives (Lonsdale 1999; With 2002). Regions are defined as broad geographical areas with common geophysical attributes and spheres of human activity (Foreman 1995). Our focus here will be on patterns of plant invasion that are visible at the regional scale.

Plant invasions are widely recognized to be facilitated by disturbances such as logging, fires, or grazing (Hobbs and Huenneke 1992). One of the most profound forms of landscape disturbance at the regional scale is human land use change (Foster et al. 1998). Broad-scale land use change over the past three centuries has been implicated in influencing the distributions of both native and non-native plants in New England and elsewhere (Peterken and Game 1984; Motzkin et al. 1999; Donohue et al. 2000; Aragon and Morales 2003; Von Holle and Motzkin 2007). These studies have demonstrated that historical land use changes are a vital part of understanding the process of plant invasions. DeGasperis and Motzkin have shown that abandonment of agricultural land can facilitate an invasion at the local scale both by creating a window of opportunity during the post-abandonment period and by leaving a persistent legacy of biotic and edaphic change (DeGasperis and Motzkin 2007). It remains to be seen whether this process of land use change-induced facilitation of invasion holds widely and at the regional scale.

Study Area

The studies presented here were conducted in the Massachusetts portions of the Connecticut River Valley and Western New England Marble Valleys (Berkshire Valley) ecoregions (EPA Level IV designation; see Figure 1.1). Ecoregions are regions of relative homogeneity in ecological systems and relationships between organisms and their environment, based primarily on soils, land use, land surface form, and potential natural vegetation (Omernik 1987). The ecoregions used in these studies consist of flat to rolling plains in parallel, north-south running valleys that are easily distinguished from their surroundings by geology and topography. Geologically, these valleys have been shaped by repeated glaciation and accompanying deposits. Both areas contain white pine, hemlock, and transition hardwoods with species characteristic of both the northern hardwood and central hardwood vegetation zones (Westveld et al. 1956). Like most of New England, the landscape in these regions has undergone broad-scale change in the 350 years since the beginning of European settlement. Throughout the valleys, land-cover was converted from forest to a mosaic of pasture, tilled fields, and woodlots.

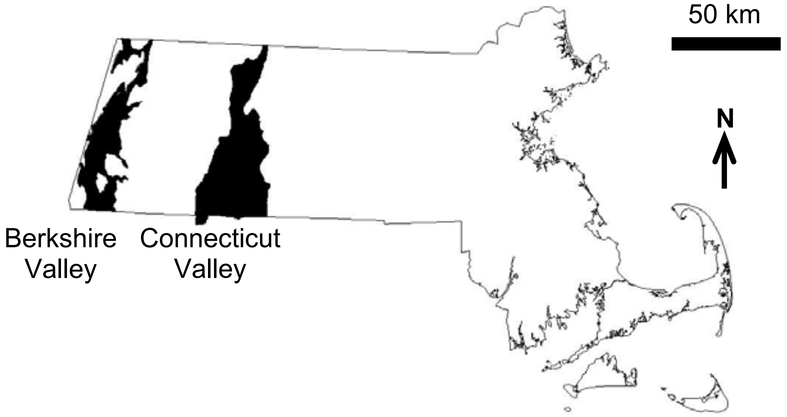

Figure 1.1: The Massachusetts portions of the Berkshire and Connecticut Valley ecoregions. Both extend south into Connecticut and the Berkshire Valley extends north into Vermont while the Connecticut Valley extends north along the Vermont-New Hampshire border.

Agriculture peaked in the region during the mid-1800s, and the subsequent abandonment of much farmland led to reforestation, though with lasting changes in forest composition and soils (Foster et al. 1998; Foster and Aber 2004).

The Connecticut Valley ecoregion sits between the Worcester Plateau to the east and the Berkshire Highlands to the west, with elevation ranging from 30 to 150 meters. Bedrock is primarily sedimentary, especially carbonate, though there are a number of basalt ridges (Griffith et al. 1994). Soils and surficial geology range from excessively-drained, sandy outwash to silty, alluvial, flood-plain sediment, and mixed till (Griffith et al. 1994). The ecoregion has a relatively mild climate with 3671 annual growing degree days, temperatures ranging from -3.9ºC to 22.1ºC, and annual precipitation averaging 109 cm (Hall et al. 2002). The area spans the transition hardwoods-white pine-hemlock and central hardwoods-white pine-hemlock vegetation zones (Westveld et al. 1956). The rich soils and accessibility provided by the Connecticut River led to early settlement of the Valley in the 1600s (Foster and Aber 2004). Modern land-cover includes farmland, discontinuous forests, and concentrated urban development dominated by the city of Springfield and its suburbs.

Forty kilometers west of the Connecticut Valley is the Berkshire Valley, drained by the Hoosic and Hausatonic Rivers, and running between the Berkshire Highlands to the east and the Taconic Mountains to the west. This sedimentary and carbonate lowland, ranging in elevation from 180 to 370 meters, is topographically and geologically well-differentiated from the surrounding highlands made up of more resistant bedrock (Griffith et al. 1994). Soils and surficial geology are loamy, mesic, mixed till, deposits (Griffith et al. 1994). The Berkshire Valley has a colder and wetter climate than the Connecticut Valley, averaging 3271 annual growing degree days with temperatures ranging from -5.5ºC to 20.5ºC and 122 cm of precipitation (Hall et al. 2002). This climate difference is reflected in vegetation, as the ecoregion spans the transition hardwoods-white pine-hemlock and northern hardwoods-hemlock-white pine zones (Westveld et al. 1956). Due to the Berkshire Valley's more remote location relative to accessible coastal areas, European settlement did not occur until the 1700s (Foster and Aber 2004). Current land-cover is mixed agriculture, woodland, and urban, similar to the Connecticut Valley, but with considerably lower population density.

Study Species

Alliaria petiolata is a prevalent invasive plant in New England that has the ability to colonize multiple habitats and will be the study organism used here to look at the historical, regional and environmental determinants of invasion.

Alliaria petiolata [M. Bieb.] Cavara & Grande (garlic mustard) is an obligate biennial herb belonging to the mustard family (Brassicaceae). The plant's native range extends across much of Western Eurasia and also includes parts of Central and South Asia and North Africa (Nuzzo 1993; Welk et al. 2002). First recorded in North America on Long Island, New York in 1868 (Nuzzo 1993), *A. petiolata* was probably introduced by European colonists as an edible garden herb and for its perceived medicinal value (Grieve 1985). It has since spread across at least 34 states and 4 Canadian provinces, and is most abundant in the Northeast and Midwest (Nuzzo 2000). In both its native and North American ranges, *A. petiolata* grows under a wide variety of light and soil conditions and in several floristic communities, but it tends to be most common and successful in partial light and damp soil along deciduous forest edges, hedgerows, and riparian areas (Cavers et al. 1979; Byers and Quinn 1987; Nuzzo 1993; Meekins and McCarthy 2001). *A. petiolata* is also found in floodplains, ruderal communities, eutrophic areas, along roadsides and railroad tracks, and in urban areas, and is thus considered disturbance-adapted (Cavers et al. 1979; Nuzzo 1993).

A. petiolata life history starts when seedlings germinate in early spring, developing into rosettes that can survive the winter to grow flower stalks the following spring. Flowering occurs in late spring or early summer and flowers can be self or insect pollinated (Anderson et al. 1996). *A. petiolata*'s sole means of reproduction is by its seeds, which require cold stratification to break dormancy (Cavers et al. 1979). Seeds are produced in siliques that ripen and disperse in the late summer as the plant dies (Cavers et al. 1979). Each individual is capable of producing several hundred seeds that are dispersed by gravity, soil disturbance, water (especially flooding), and animals, particularly humans (Cavers et al. 1979; Nuzzo 2000). Anthropogenic seed dispersal can occur as a result of roadside mowing and other landscaping activity, as well as by automobiles and trains (Nuzzo 2000).

Study Questions

The two studies presented here analyze the results of regional-scale field surveys of *A. petiolata* occurrence and abundance on forest edges in an attempt to determine the historical, regional, and environmental factors that control *A. petiolata*'s invasion pattern in western Massachusetts. The historical component is incorporated by looking at land use history and comparing sites with different pre-introduction land cover. The regional component involves comparing sites in the two ecoregions of study to look at inter-regional differences. Anthropogenic, geophysical, and ecological factors are also considered. Chapter II focuses on the limitations to *A. petiolata*'s dispersal and establishment ability by examining variation in occurrence by ecoregion and land use history, while taking into account environmental factors.

Chapter III focuses on *A. petiolata*'s ability to colonize a site by assessing its ability to establish in the forest understory from the forest edge, and by examining its abundance in the understory once established, also taking into account environmental factors. Together these studies should help create a clearer picture of how *A. petiolata* invasions work in a temperate, deciduous, regional-scale landscape that has a history of human-induced disturbance.

Chapter II - Regional, Historical, and Environmental Variation in *Alliaria petiolata* Occurrence

Introduction

Alliaria petiolata was first recorded in Massachusetts in Cambridge in 1938, but it was not until 1960 that samples were collected in the western part of the state, in the Connecticut River Valley town of Northampton (Mehrhoff et al. 2003). The first herbarium specimens from the Berkshire Valley are from 2001, but based on its current prevalence in the region, *A. petiolata* was almost certainly there decades earlier (D. Carpenter, pers. observ.). In fact, it has been suggested that *A. petiolata* is currently more common in the Berkshire Valley than in the Connecticut Valley (K. Stinson, pers. observ.). The study presented in this chapter is a field survey that aims to establish the regional-scale distribution of *A. petiolata* and characterize any ecoregional differences in its occurrence.

Recent work has shown that land use history can play an important role in determining non-native plant distributions in New England on both the local and regional scale (DeGasperis and Motzkin 2007; Von Holle and Motzkin 2007). Land that was cleared for uses that involve soil disturbance, such as agriculture, tends to have a higher occurrence of invasive plants. It may be the case that land use history plays a role in *A. petiolata*'s regional distribution in western Massachusetts, a role that could help explain ecoregional variation in occurrence. This study attempts to test this hypothesis by making use of historical records of land use prior to the introduction of *A. petiolata*, and by characterizing differences in occurrence between areas with different historical land covers.

There are many environmental factors that could also influence *A. petiolata*'s distribution by either limiting its dispersal or by limiting the availability of suitable niches. Anthropogenic landscape characteristics, such as fragmentation, can be important in creating dispersal corridors and favorable habitat for forest edge species like *A. petiolata* (Nuzzo 1993; With 2002). Climatic variables play an important role in limiting species' distributions, including *A. petiolata*, which requires moderate amounts of rainfall and sunlight, and a sufficient growing season (Welk et al. 2002). Soil moisture is likely to play a significant role in *A. petiolata* germination, survival, and growth, as seeds and rosettes are drought sensitive (Meekins and McCarthy 2001). Geological factors can affect soil properties such as hydrology, nutrient retention, and acidity that in turn influence vegetation cover (Ricklefs and Miller 2000; Hall et al. 2002). Forest community composition, which has been shown to influence invasion pattern (Wiser et al. 1998), could also play a role in *A. petiolata* distribution. In addition to characterizing any regional or historical differences in *A. petiolata* occurrence, this study seeks to identify which environmental factors best predict *A. petiolata* presence.

The aforementioned anthropogenic, geophysical, and ecological factors may correspond with, or be independent of ecoregion and land use history. By looking at regional and historical variation in the environmental variables, we should be able to answer the question of whether regional and historical differences in *A. petiolata* occurrence are the result of underlying environmental factors, or are caused by other spatial and temporal processes.

Methods

To investigate the regional, historical, and environmental factors contributing to *Alliaria petiolata* distribution in present day forests and forest edges, currently wooded roadside sites were selected following a stratified random sampling design. Sites were stratified by ecoregion (Connecticut Valley versus Berkshire Valley, see Figure 2.1a) and by historical (pre-*A. petiolata* introduction) land cover (wooded versus open). All sites were surveyed for *A. petiolata* occurrence and site-specific environmental data relating to anthropogenic, geophysical, and ecological phenomenon was collected.

Site Selection

Potential sites within the two study regions were selected according to four criteria. First, only areas with known historical land cover were considered (see Figure 2.1c). Historical land cover data was obtained from digitized municipal land surveys from the 1830s (Harvard Forest 2002; Hall et al. 2002). Land cover was classified as either wooded or open, with the open category including areas that were plowed, pasture, or residential. Second, potential sites were restricted to the roadside edges of currently wooded areas. Areas were considered wooded if they had continuous forest cover for at least the past 35 years (see Figure 2.1d). This was determined using digitized land use/land cover maps going back to 1971 and digitized forest harvest records going back from 2003 to 1984 (MassGIS 2002a, b; Kittredge et al. 2003; McDonald et al. 2006). Roadside forest edges were delineated by overlaying the land cover datalayers and a Massachusetts road datalayer (MassGIS 2002c) in ArcView 3.2 (ESRI 1996). Third, areas of roadside forest edge had to be large enough to accommodate a 25 × 100m plot, with the 100m sides of the plot oriented along and parallel to the roadside edge, and with 25m buffers of forest on the three non-edge sides of the plot (See Figure 2.2). Fourth, potential sites were required to be at least 1km away from one another in order to avoid sampling redundancy.

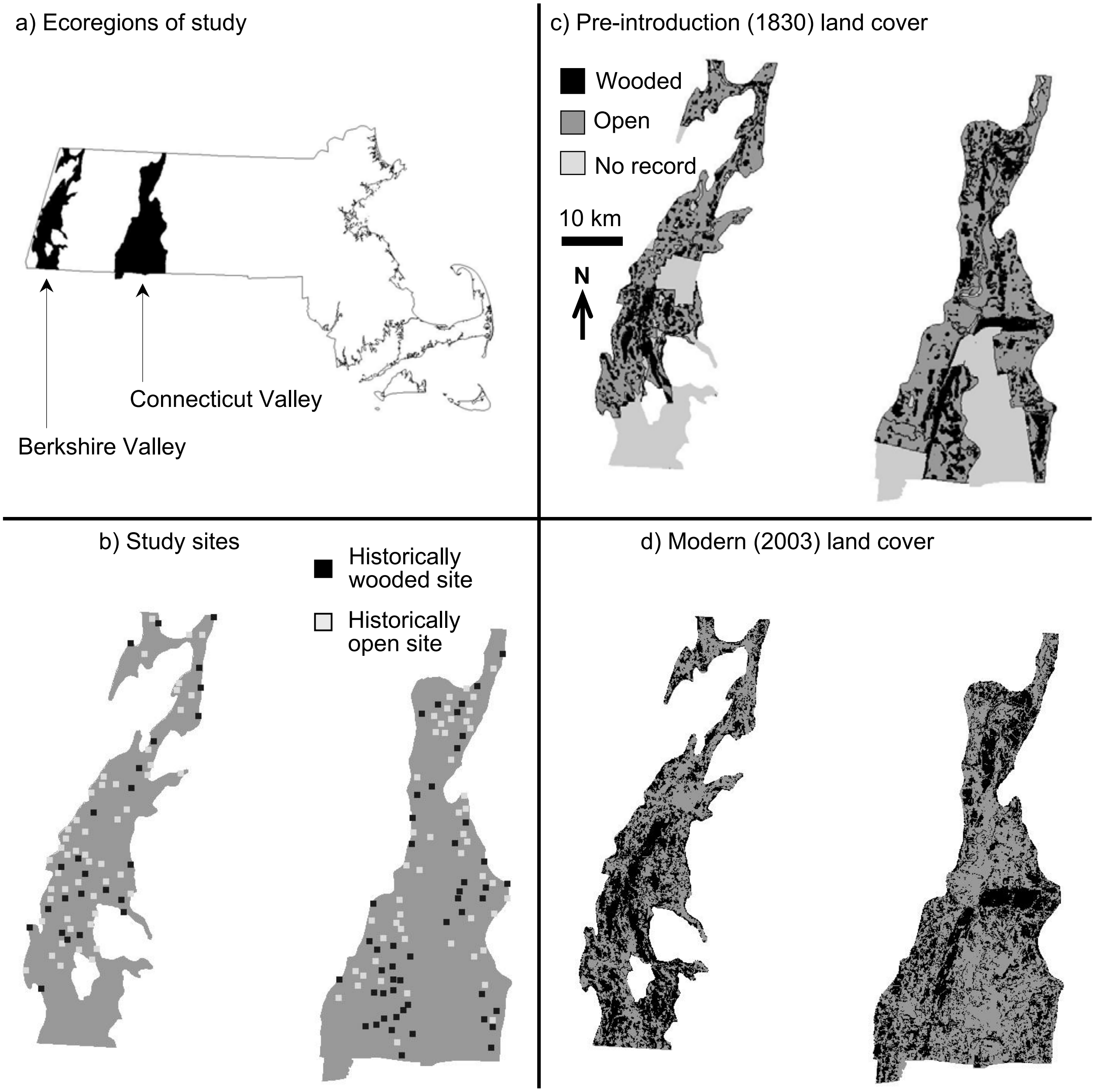

Figure 2.1: Maps of the Connecticut and Berkshire Valley ecoregions depicting (a) location of ecoregions within the political boundaries of Massachusetts, (b) location and historical land cover status of randomly selected survey sights, (c) land cover according to township land surveys from 1830, (d) modern land cover according to land use maps and forest harvest records covering the period 1971-2003.

The pool of eligible sites was divided into four categories based on ecoregion (Connecticut Valley and Berkshire Valley) and historical land cover (wooded and open), and fifty sites were randomly selected for field sampling from each category, except for Berkshire

Valley wooded sites (see Figure 2.1b). For historically wooded sites in the Berkshire Valley, only 25 sites met the criteria and all were used.

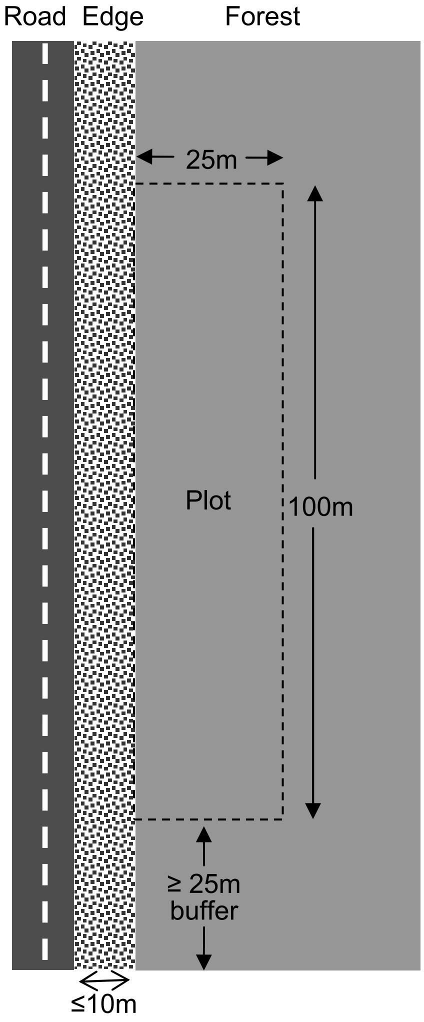

Figure 2.2: Design of survey sampling plots. A plot consists of a 25 × 100m tract of woodland, with one long boundary along a roadside edge, and at least 25m of woods on all other sides. The edge area between the woodland boundary and the road was no greater than 10m.

Field Sampling

The 100 sites with historically open land cover were surveyed in the summer of 2006 and the 75 sites with historically wooded land cover were surveyed in the summer of 2007. Sites were disqualified if the edge area between the road and forest boundary was greater than 10m. Sites with large amounts of disturbance (e.g. cutting, dumping, trails) were also not sampled, and each disqualified site was replaced with another randomly selected site from the same ecoregion and historical land cover type.

Sites were surveyed by walking though the 25 × 100m wooded plot and along the roadside edge of the plot, and any occurrence of *A. petiolata* in either was recorded. Environmental variables recorded at each site included soil moisture and tree dominance. Soil moisture was assessed by assigning each site to one of three categories (xeric, mesic, or hydric) based on observation of soil quality, site hydrology, and vegetation. Tree dominance was used as a crude measure of forest community composition, and was assessed by noting the most abundant species in the canopy, and assigning each a dominance value. Dominance values were equal to 6 - D, where D is the total number of highly abundant tree species at the site. For example, a site with one dominant tree species would receive a dominance value of 5, two dominant species at a site would each get a value of 4, and so forth. Thus, sites could have up to five dominant tree species. Seven species or species groups made up all dominant trees in the study: *Quercus spp*., *Pinus strobus*, *Acer rubrum*, *Acer saccharum*, *Betula spp*., *Fraxinus americana,* and *Tsuga canadensis*.

Additional Environmental Data

Additional site attributes were obtained from GIS datalayers, including geological data, climatic data, and measures of surrounding fragmentation and development. Bedrock type (metamorphic, basin sedimentary, granite, mafic, carbonate) and surficial geology (floodplain alluvium, fine-grained deposits, till and bedrock, sand and gravel,) were found using digitized USGS maps (MassGIS 1999, 2004). Climatic data for the sites was obtained through a GIS-based regression model of New England average annual rainfall and temperature, with temperature measured in growing degree days (Ollinger 1995; Hall et al. 2002). Site-specific solar radiation data (insolation, in $W \cdot h/m^2$) was obtained based on a digital elevation model with the Solar Analyst GIS extension (HEMI 2000). Latitude was also incorporated as both a spatial and climatic factor, with UTM northings (Zone 18T) obtained from the GIS maps used to initially identify sampling sites. For measures of fragmentation and development, maps of forest edge density and road density were created. Road and forest edge density (measured in m / km^2) were mapped (separately) using state road and land cover datalayers (MassGIS 2002b, c) and ArcView 3.2 (ESRI 1996). The average road and forest edge density within a 500m radius of the centerpoint of each plot was calculated. A scale of 500m was chosen to reflect fragmentation, disturbance and potential avenues of dispersal within an area that extends well beyond each plot, while still being site specific.

Data Analyses

Analyses were conducted separately to (1) establish how the environmental variables vary by ecoregion and by historical land cover, (2) determine how *A. petiolata* occurrence varies by ecoregion and historical land cover, (3) determine which, if any, environmental variables predict *A. petiolata* occurrence, and (4) investigate whether environmental variables explain regional and historical variation in *A. petiolata* occurrence. Prior to analysis, numerical environmental variables with non-normal distributions were log transformed to meet normality assumptions. Annual precipitation and temperature were found to be highly correlated ($R^2 = 0.86$), so temperature was dropped as an environmental variable to avoid multicollinearity. Environmental variables included in analyses were forest edge density, log road density, latitude, insolation, precipitation, soil moisture, surficial geology, bedrock geology, and canopy tree dominance.

Ecoregional and land use history differences in environmental variables

To determine the significant ecoregional and land use history differences in environmental factors, a general linear model (GLM) multivariate analysis of variance (MANOVA) was used with ecoregion, historical land cover, and the ecoregion-historical land cover interaction as predictors, and the environmental factors as response variables. For the purposes of this analysis, categorical factors were ordered and treated as continuous variables. Ordering was done by moisture level for soil moisture, particle size for surficial geology, and acidity for bedrock. The least square means of the environmental response variables for each of the ecoregion by historical land cover categories were obtained, and significant differences were tested using post hoc Tukey-Kramer hsd tests. This analysis was done with the GLM procedure in SAS/STAT 9.1 (SAS Institute 2003).

Due to the non-normality of several environmental variables whose distribution could not be corrected by transformation, the results of the MANOVA were verified, to the degree possible, with non-parametric tests. Kruskal-Wallis one-way analyses of variance (SAS NPAR1WAY procedure) were used to determine the effects that ecoregion and historical land cover have (separately) on each of the environmental variables according to the variables empirical distribution function.

A. petiolata occurrence by ecoregion and historical land cover

The effects of ecoregion, historical land cover, and ecoregion in combination historical land cover on *A. petiolata* occurrence were tested using Pearson’s chi-squared tests (SAS CATMOD procedure).

Relationships between A. petiolata occurrence and environmental variables

To determine the effects of environmental factors on *A. petiolata* presence and absence, occurrence was modeled as a function of the factors using a multiple logistic regression based on maximum likelihood estimation. The SAS CATMOD procedure that was used allows the input of a mixture of categorical and continuous predictor variables, so the categorical environmental factors were treated as such. The procedure is also robust to non-normally distributed variables, so non-parametric tests were deemed unnecessary. Bonferroni corrections for multiple tests (Rice 1989) were not used because while some spurious relationships could be found, most conclusions should be sound (Moran 2003)

Relationships between ecoregion and historical land cover, environmental variables, and A. petiolata occurrence

To investigate the relationship between ecoregion, historical land cover, and environmental factors in predicting *A. petiolata* occurrence, the multiple logistic regression model was modified to include the regional and historical factors as predictors, in addition to environmental factors. Ecoregion and historical land used were added to the model in a stepwise fashion such that the effects of each individually, and then in combination, could be determined. The model was also run as a GLM ANOVA to obtain the adjusted least square mean occurrence levels by ecoregion and historical land cover, with significant predictors selectively removed. This allowed the effects of individual environmental predictors on ecoregional and historical land cover differences in occurrence to be seen. Finally, the multiple logistic regression model was run separately for each ecoregion and historical land cover to examine any differences in environmental predictors within each category. Due to over-parameterization and limited sample size several of the environmental variables (*Pinus strobus*, *Acer rubrum*, *Betula spp*., and *Tsuga canadensis* dominance, bedrock, and surficial geology), were removed from the model, allowing the maximum likelihood computations to converge. All statistical tests were performed using SAS/STAT 9.1 (SAS 2003).

Results

Ecoregional & Land Use History Comparison

Sites in different ecoregions and with different historical land cover were found to have clear overall environmental differences. The MANOVA showed that the environmental variables differed significantly overall by ecoregion (Wilk's $\Lambda = 0.120$, $F = 76.77$, $p < 0.0001$), by historical land cover (Wilk's $\Lambda = 0.676$, $F = 5.01$, $p < 0.0001$), and by the ecoregion-historical land cover interaction (Wilk's $\Lambda = 0.816$, $F = 2.36$, $p = < 0.0043$). Nearly half the environmental variables differed significantly by ecoregion, four of fifteen differed significantly by historical land cover, and two showed interaction effects (see Table 2.1). These significant differences were largely in agreement with non-parametric Kruskal-Wallis one-way ANOVAs.

	Ecoregion				Historical Land Cover				Ecoregion × Historical Land Cover	
Environmental Factors	***F***	***P***	**X^2**	***P***	***F***	***P***	**X^2**	***P***	***F***	***P***
Anthropogenic										
Forest Edge Density	1.63	0.2037	1.62	0.2027	5.14	0.0246	3.94	0.0471	0.70	0.4043
Road Edge Density*	2.69	0.1026	6.23	0.0125	0.42	0.5174	2.07	0.1504	1.10	0.2968
Geophysical										
Latitude	9.69	0.0022	14.43	0.0001	1.30	0.2562	0.21	0.6446	2.26	0.1348
Insolation	31.89	< 0.0001	45.70	< 0.0001	1.08	0.3001	0.73	0.3918	0.01	0.9039
Precipitation	692.36	< 0.0001	126.13	< 0.0001	0.63	0.4286	1.24	0.2650	2.79	0.0966
Soil Moisture	1.97	0.1620	0.16	0.6926	0.00	1.0000	3.16	0.0756	1.45	0.2303
Surficial Geology	0.54	0.4615	0.48	0.4888	0.06	0.8060	0.27	0.6066	4.90	0.0281
Bedrock	0.91	0.3422	1.03	0.3110	0.00	1.0000	0.00	0.9612	0.51	0.4760
Tree Dominance										
Acer rubrum	22.18	< 0.0001	19.56	< 0.0001	2.46	0.1183	1.49	0.2218	1.75	0.1879
Acer saccharum	28.03	< 0.0001	30.47	< 0.0001	16.59	< 0.0001	20.07	< 0.0001	0.54	0.4645
Betula spp.	0.00	0.9619	0.15	0.6942	0.02	0.8862	0.85	0.3552	2.80	0.0963
Fraxinus americana	62.47	< 0.0001	56.05	< 0.0001	30.03	< 0.0001	24.37	< 0.0001	18.67	< 0.0001
Pinus strobus	0.95	0.3300	0.43	0.5127	1.45	0.2309	1.39	0.2388	0.14	0.7076
Quercus spp.	59.07	< 0.0001	47.67	< 0.0001	15.54	< 0.0001	21.27	< 0.0001	1.52	0.2187
Tsuga canadensis	4.63	0.0328	2.91	0.0882	1.67	0.1984	0.08	0.7780	3.84	0.0516

Table 2.1: *F* ratios (from GLM MANOVA results), *H* test statistics (from Kruskal-Wallis one-way ANOVA results), and significance values for environmental variables at sites in different ecoregions and with different historical land covers. *F* ratios are based on type III sum of squares.

The anthropogenic fragmentation and disturbance factors showed some significant environmental differences across ecoregion and historical land cover (see Figure 2.3). While Tukey-Kramer post hoc comparisons indicated no significant differences between individual ecoregion by historical land cover classes, analysis of variance demonstrated that historically open sites were surrounded by significantly greater forest edge densities ($P = 0.0236$). This result was confirmed by Kruskal-Wallis one-way ANOVA ($P = 0.0471$), which also indicated that road density was greater in the vicinity of Connecticut Valley sites than Berkshire Valley sites ($P =$

0.0125). This was one of the few effects for which there was disagreement between the parametric and non-parametric tests, leaving the actual significance of this result ambiguous.

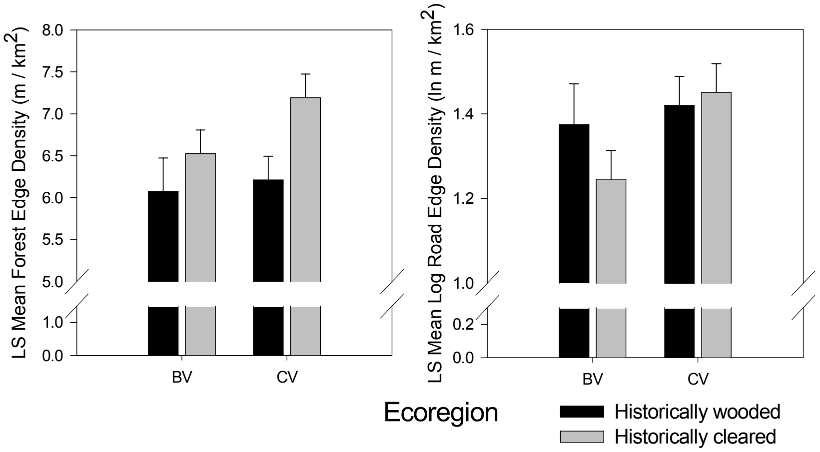

Figure 2.3: Ecoregional and historical land cover comparisons of least square mean forest edge density and log road edge density (± SE). Though no significant differences exist between bars, the MANOVA F ratio indicates a significant historical land cover effect for forest edge density ($P = 0.0246$), and Kruskal-Wallis one-way ANOVA indicates a significant ecoregional effect for road edge density ($P = 0.0125$).

All three climatic variables differed significantly by ecoregion, but not by historical land cover or ecoregion-historical land cover interaction (see Figure 2.4). Sites in the Berkshire Valley were significantly further south, by an average of about 9 km, than sites in the Connecticut Valley ($P = 0.0022$). Berkshire Valley sites also received significantly greater amounts of solar radiation ($P < 0.0001$) and precipitation ($P < 0.0001$). All these results were confirmed by the Kruskal-Wallis one-way ANOVA.

Surficial geology had an ecoregion-historical land cover interaction effect ($P = 0.0281$), but the individual effects of ecoregion and historical land cover were insignificant. In the Berkshire Valley, historically wooded sites had greater amounts of sand and gravel, while sites that were cleared tended to have more floodplain alluvium (see Figure 2.5). In the Connecticut Valley the opposite was true - sites that were historically left wooded were more likely to have fine-grained or alluvial sediments, while historically cleared sites were found more often on sand and gravel deposits.

The remaining two geophysical factors, soil moisture and bedrock, did not differ significantly by ecoregion and/or historical land cover.

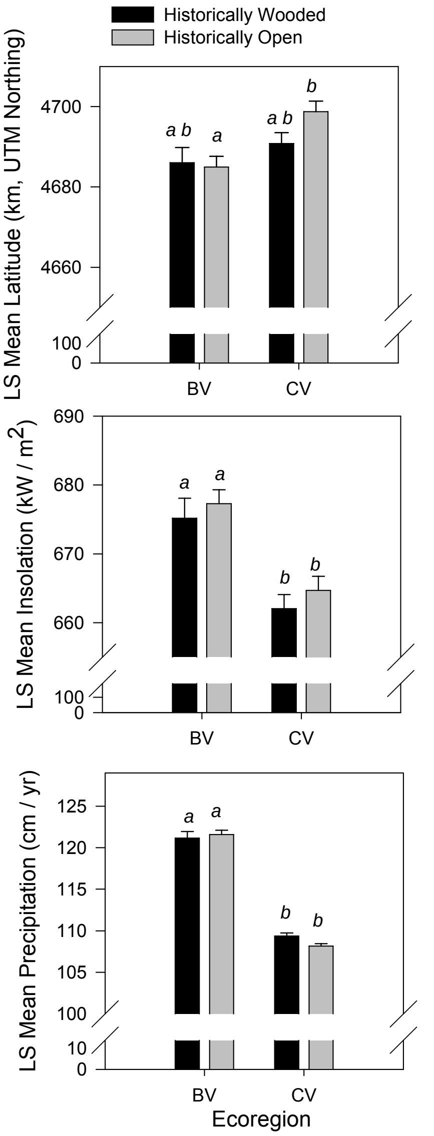

Figure 2.4 Ecoregional and historical land cover comparisons of least square means (+1 SE) for climatic factors. Multivariate analysis of variance indicates significant ecoregional effects on latitude ($P = 0.0022$), insolation ($P < 0.0001$), and precipitation ($P < 0.0001$). Different letters above bars indicate significant differences between categories.

In canopy composition, there were ecoregional differences among at least four of the seven most common species, and historical difference among three (see Figure 2.6). *Acer rubrum* was far more dominant in Connecticut Valley sites ($P < 0.0001$). *Acer saccahrum* and *Fraxinus americana* were both significantly more dominant in the Berkshire Valley ($P < 0.0001$ for both species) and in historically cleared areas ($P < 0.0001$ for both species). However, in *F. americana*'s case, there was also an interaction effect ($P < 0.0001$), as the historical effect was large in the Berkshire Valley and insignificant in the Connecticut Valley. *Quercus spp.* were the opposite of *F. americana* and *A. saccharum* - more dominant in the Connecticut Valley ($P < 0.0001$), and in historically wooded sites ($P < 0.0001$). *Tsuga canadensis* was more prevalent in the Berkshire Valley ($P = 0.0328$), but the significance of this difference is put into question by the Kruskal-Wallis one-way ANOVA, which reported the effect as insignificant ($P = 0.0882$). In any case, the ecoregional difference was largely due to the high dominance of *T. canadensis* in historically wooded sites in the Berkshire Valley (the interaction effect is nearly significant at $P = 0.0516$).

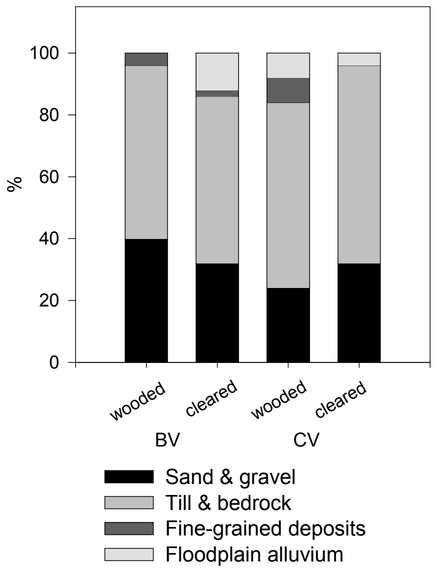

Figure 2.5: Comparison of surficial geology compositions. No significant ecoregional or historical land cover differences were found, but the MANOVA indicated a significant interaction effect ($P = 0.0281$).

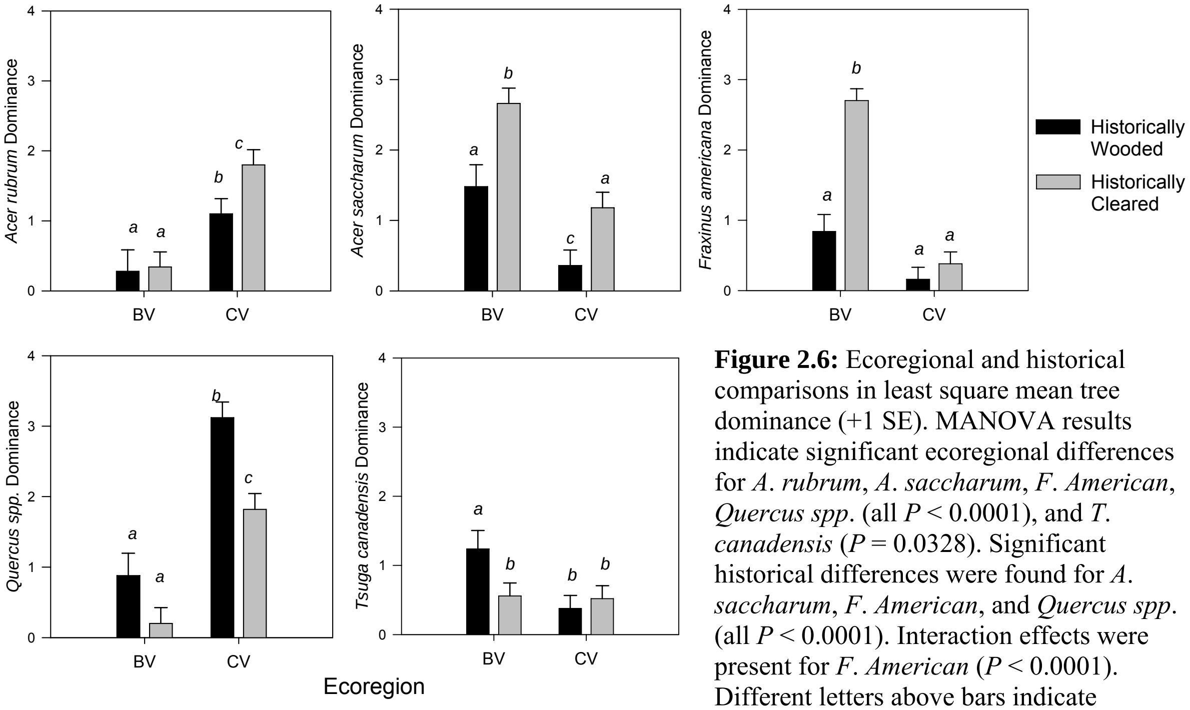

Figure 2.6: Ecoregional and historical comparisons in least square mean tree dominance (+1 SE). MANOVA results indicate significant ecoregional differences for *A. rubrum*, *A. saccharum*, *F. American*, *Quercus spp*. (all $P < 0.0001$), and *T. canadensis* ($P = 0.0328$). Significant historical differences were found for *A. saccharum*, *F. American*, and *Quercus spp*. (all $P < 0.0001$). Interaction effects were present for *F. American* ($P < 0.0001$). Different letters above bars indicate significant differences between categories.

Alliaria Petiolata Occurrence

A. petiolata was found in 58 of the 175 (33.1 %) of the sites surveyed. The vast majority of these (78.0 %) were in the Berkshire Valley where 57.5% of the sites surveyed had garlic mustard (see Figure 2.7). In contrast only 15.0 % of Connecticut Valley sites had *A. petiolata*. A chi-squared test confirmed that ecoregion has a highly significant effect on *A. petiolata* occurrence ($X^2 = 26.92$, $P < 0.0001$). Presence at historically cleared and wooded sites was 39.0% and 25.3% respectively, which was not a significant difference ($X^2 = 0.94$, $P = 0.3316$). The ecoregion-land use history interaction effect was also insignificant ($X^2 = 0.1031$, $P = 0.5851$).

Figure 2.7: Distribution of sites with *A. petiolata*. Circles represent sites with wooded 1830 land cover (● = *A. petiolata* present, ○ = *A. petiolata* absent). Triangles represent sites with open 1830 land cover (▲ = *A. petiolata* present, △ = *A. petiolata* absent).

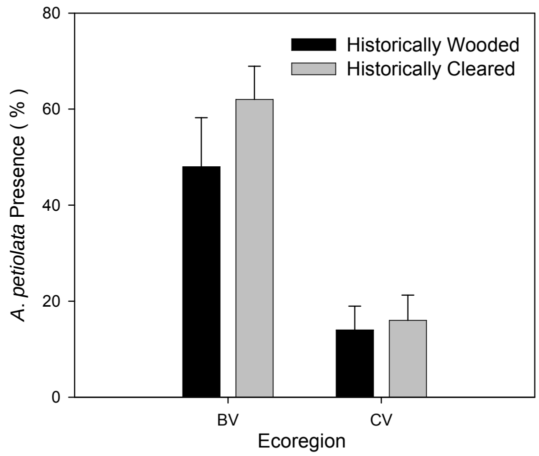

Figure 2.8: *A. petiolata* occurrence by ecoregion and historical land cover. Historical differences are not significant ($P = 0.3316$), nor is there any interaction effect ($P = 0.5815$), but rate of occurrence is presence in the Berkshire Valley is significantly greater than in the Connecticut Valley ($P < 0.0001$).

Of the 15 environmental variables tested in the multiple logistic regression model, two turned out to be significant predictors of *A. petiolata* occurrence. Latitude came out as the strongest predictor of presence ($P < 0.0001$; see Table 2.2), with more southerly sites having a higher rates of occurrence. *Quercus* species dominance was the other significant predictor (P = 0.0063), as *A. petiolata* had lower rates of occurrence at sites that were more dominated by oak.

Predictor	X^2	p	Estimate
Anthropogenic Factors			
Forest Edge Density	0.03	0.8545	-0.0335
Log Road Edge Density	0.92	0.3381	0.7586
Geophysical Factors			
Latitude	29.88	< 0.0001	-1.81×10^{-4}
Insolation	0.13	0.7207	-6.78×10^{-6}
Precipitation	0.86	0.355	-0.0646
Soil Moisture (hydric)	2.11	0.1461	-0.5889
Surficial Geology	2.77	0.4282	-
Bedrock	1.19	0.879	-
Tree Dominance			
Acer rubrum	1.66	0.1969	-0.3033
Acer saccharum	1.3	0.2539	0.2608
Betula spp.	0.04	0.8344	-0.0481
Fraxinus americana	0.79	0.3746	0.2431
Pinus strobus	0.95	0.3306	-0.2199
Quercus spp.	7.47	0.0063	-0.5869
Tsuga canadensis	0.62	0.4316	0.2099

Table 2.2: Multiple logistic regression of environmental variables against *A. petiolata* occurrence. Estimate for soil moisture is between mesic and hydric soils. Estimates for the multi-category bedrock and surficial geology variables are omitted.

Predictor	X^2	p	Estimate
Anthropogenic Factors			
Historical Land Cover	1.50	0.2202	0.5006
Forest Edge Density	0.01	0.9178	-0.0220
Log Road Density	0.15	0.7016	0.3134
Geophysical Factors			
Latitude	23.47	< 0.0001	-1.68×10^{-4}
Insolation	0.00	0.9547	1.26×10^{-6}
Precipitation	6.48	0.0109	-0.4404
Soil Moisture (hydric)	3.96	0.0467	-0.9306
Surficial Geology	3.15	0.3688	-
Bedrock	1.81	0.7711	-
Tree Dominance			
Acer rubrum	2.50	0.1135	-0.4665
Acer saccharum	0.07	0.7926	0.0731
Betula spp.	1.16	0.2809	-0.2925
Fraxinus americana	0.04	0.8424	0.0612
Pinus strobus	2.02	0.1552	-0.4074
Quercus spp.	2.83	0.0925	-0.4287
Tsuga canadensis	0.06	0.8116	-0.0772
Geographical Factors			
Ecoregion	6.48	0.0109	-3.1994

Table 2.3: Multiple logistic regression of environmental variables, ecoregion, and historical land cover against *A. petiolata* occurrence. Estimate for soil moisture is between mesic and hydric soils. Estimates for the multi-category bedrock and surficial geology variables are omitted.

Historical land cover was not a significant predictor when included in the model (P = 0.2939), nor did it alter the magnitude of other predictors in any significant way. When ecoregion was added to the model, however, it again turned out to be a significant predictor (P = 0.0109), and the *Quercus* effect became insignificant (P = 0.0925; see Table 2.3). Latitude remained highly significant ($P < 0.0001$; see Figure 2.9). Precipitation also became significant when ecoregion was taken into account (P = 0.0109), as sites receiving greater amounts of precipitation were more likely to have *A. petiolata* populations (see Figure 2.10). Taking both ecoregion and historical land cover into account in the model, as opposed to just ecoregion, made little difference except in the case of soil moisture. Soil moisture was not a significant predictor when ecoregion alone is included in the model (P = 0.0620), but becomes significant ($P = 0.0467$) when historical land cover is taken into account, with *A. petiolata* appearing to favor mesic sites over hydric sites (See Figure 2.11).

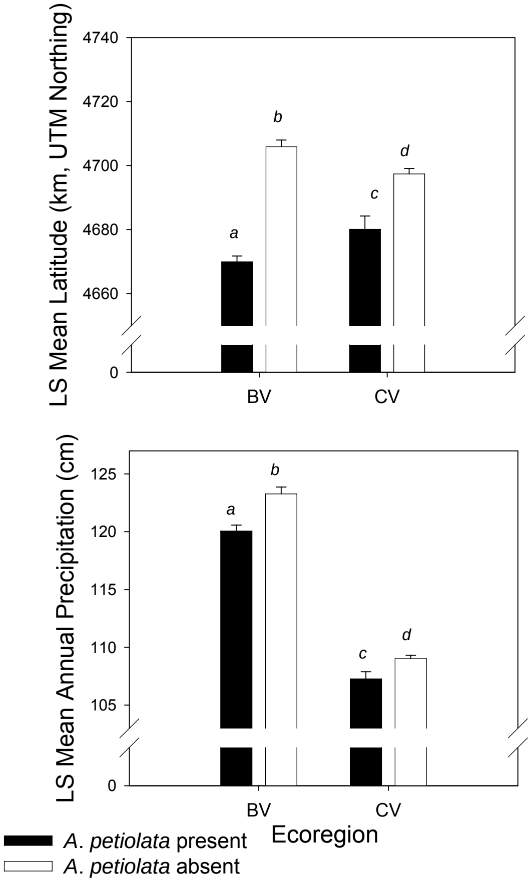

Figure 2.10: Differences in least square mean latitude and precipitation (+1 SE) between sites with and without *A. petiolata*, broken down by ecoregion. Multiple logistic regression models found that both latitude and precipitation were significant predictors of *A. petiolata* presence ($P < 0.0001$ and $P = 0.0109$, respectively). Different letters above bars indicate significant differences between categories.

Ecoregion remains a significant, strong predictor throughout all iterations of the model, however, the least square mean differences in *A. petiolata* occurrence between the Connecticut and Berkshire Valleys do change as different factors are added and removed from the model. By noting whether individual factors increase or decrease the adjusted ecoregional difference, we can tell whether or not these factors work with or against the ecoregional effect. This is illustrated in Figure 2.12, which shows how taking into account or omitting different factors moves the ecoregional difference in different directions. For instance, taking into account the environmental variables increases the ecoregional difference compared to the case when environmental factors are ignored. Omitting *Quercus spp*. dominance or latitude increases the adjusted ecoregional difference, so the inclusion of these factors helps to explain the ecoregional difference. The omission of precipitation as a factor, on the other hand, decreases the adjusted ecoregional difference, meaning that the precipitation effect works in the opposite direction of the ecoregional effect.

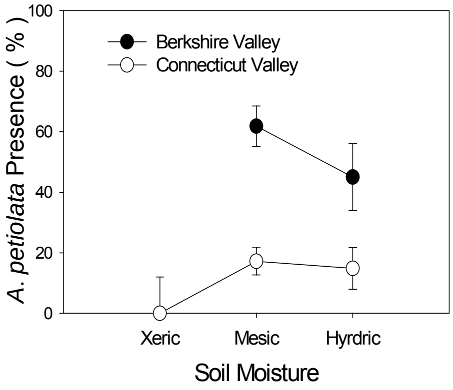

Figure 2.11: *A. petiolata* occurrence (±1 SE) as a function of soil moisture. Soil moisture (mesic v. hydric), was found to be a significant factor in predicting *A. petiolata* presence (P = 0.0467), based on multiple logistic regression. Xeric soils were not found in the Berkshire Valley.

The addition of historical land cover and the omission of soil moisture do little to change the ecoregional difference, therefore do little to explain it. (Historical land cover was added to the model before omitting soil moisture because soil moisture was only a significant predictor of *A. petiolata* occurrence when historical land use is taken into account).

The modified logistic regression used to analyze the sites of each ecoregion separately contained nine environmental variables plus historical land cover (see Tables 2.4a & b). In the Berkshire Valley, latitude was the only significant predictor of *A. petiolata* presence (P = 0.0219). In the Connecticut Valley, both latitude and precipitation were significant (P =

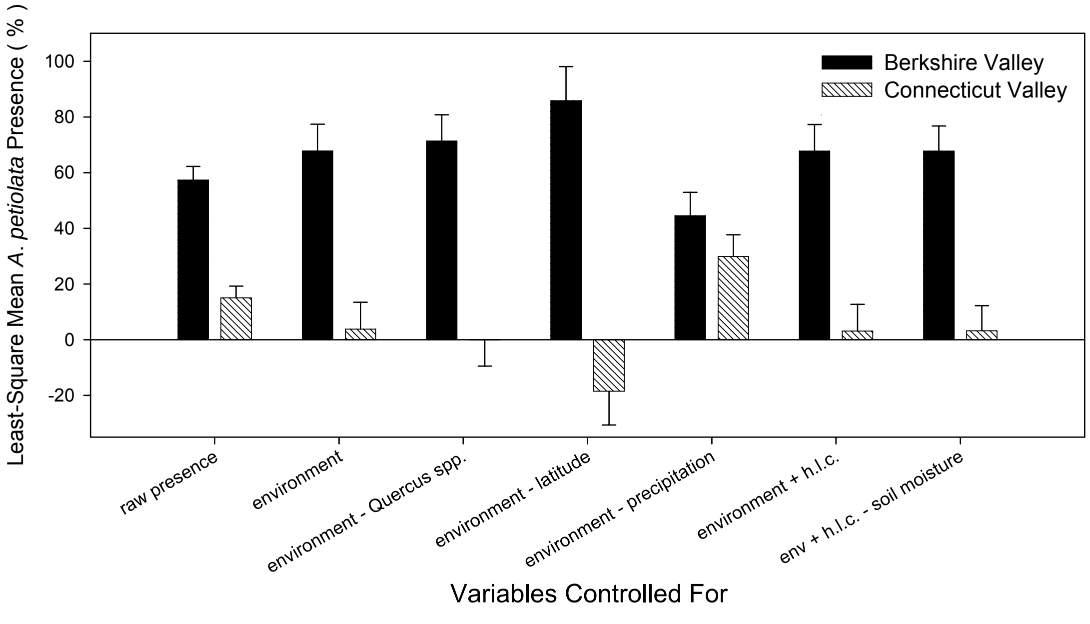

Figure 2.12: Least square mean *A. petiolata* occurrence comparisons by ecoregion, adjusted for different sets of factors taken into account in multiple logistics regression. Changes in ecoregional difference indicate whether significant factors act to explain the observed ecoregional effect. Environment (env) = all environmental factors. h.l.c. = historical land cover.

0.0006 and *P* = 0.0155 respectively). All significant effects acted in the same direction as they did in the overall logistic regression.

(a)

Predictor	X^2	p	Estimate
Anthropogenic Factors			
Historical Land Cover	0.15	0.6989	0.6036
Forest Edge Density	0.36	0.5462	-0.3705
Road Density*	0.86	0.3544	-3.2911
Geophysical Factors			
Latitude	5.25	0.0219	-4.47×10^{-4}
Insolation	0.00	0.9736	-3.05×10^{-6}
Precipitation	2.32	0.1277	-0.9698
Soil Moisture	0.18	0.6749	-0.7359
Tree Dominance			
Acer rubrum	0.18	0.6749	2.5697
Fraxinus americana	1.74	0.1866	1.4172
Quercus spp.	0.83	0.3621	1.1693

(b)

Predictor	X^2	p	Estimate
Anthropogenic Factors			
Historical Land Cover	0.54	0.4638	0.3086
Forest Edge Density	0.61	0.4334	-0.1878
Road Density*	1.06	0.3039	0.85
Geophysical Factors			
Latitude	11.64	0.0006	-1.23×10^{-4}
Insolation	0.09	0.7692	7.56×10^{-6}
Precipitation	6	0.0155	-0.5405
Soil Moisture	1.97	0.1607	-0.7237
Tree Dominance			
Acer rubrum	2.45	0.1175	-0.4653
Fraxinus americana	0.56	0.4547	0.264
Quercus spp.	2.03	0.1539	-0.3443

Tables 2.4: Modified multiple logistic regression models run separately for **(a)** the Berkshire Valley, and **(b)** the Connecticut Valley.

Conclusions

The field survey of *A. petiolata* distribution in western Massachusetts has demonstrated that there a large differences in occurrence between ecoregions, with *A. petiolata* being significantly more common in the Berkshire Valley than in the Connecticut Valley. Historical land cover does not appear to affect *A. petiolata* presence. This does not mean that land use history plays no role in *A. petiolata* distribution, but it appears unlikely that pre-introduction land cover is an important influence.

There are several important ecoregional and historical land cover differences in environmental variables. Some of the strongest ecoregional differences were in climate, with sites sampled in the Berkshire Valley being further south and receiving more solar radiation and more rain than sites in the Connecticut Valley. A strong negative correlation between temperature and precipitation indicates that the Berkshire Valley sites should also have colder average annual temperatures. The climatic differences found for the sites used in this study are in agreement with Hall et al.'s characterization of Massachusetts ecoregions (Hall et al. 2002).

There are also ecoregional differences in the forest compositions of sites, with *Acer saccacharum*, *Fraxinus americana*, and *Tsuga canadensis* being more prevalent in the Berkshire Valley, and with *Acer rubrum* and *Quercus spp*. being more prevalent in the Connecticut Valley. These differences coincide with the differences found by Westfeld et al. in the composition of the Northern Hardwood zone, which extends into the northern Berkshire Valley, and the Central Hardwood zone, which extends into the southern Connecticut Valley (Westveld et al. 1956).

Environmental variation between sites with different land use history consists largely of differences in tree abundance. *Quercus spp*. was more dominant in historically wooded sites while *Acer saccacharum* and *Fraxinus americana* were more dominant in historically cleared sites. The area around historically cleared sites also had higher forest edge density.

Environmental predictors of *A. petiolata* occurrence are climate and water related. Not surprisingly, *A. petiolata* was not found at xeric sites, and seems to prefer mesic soils over hydric soils. This preference, along with the negative relation between occurrence and precipitation, suggest that oversaturation may be more of a limitation for *A. petiolata* than drought in Massachusetts' climate. Climatic models show that *A. petiolata* requires a minimum of 50 centimeters of annual precipitation (Welk et al. 2002), but the evidence from this study indicates that in the range of 105 to 130 centimeters, increased precipitation is detrimental. Though the absence of xeric soils in the Berkshire Valley helps to explain some of the ecoregional difference in *A. petiolata* occurrence, precipitation worked strongly against the ecoregional difference. *A. petiolata* was more common in the Berkshire Valley in spite of the fact that there was more precipitation there.

Latitude was one of the most significant predictors of occurrence, though its effects were small. *A. petiolata* was more common in lower latitude sites, and this tendency held within each individual ecoregion as well as when the regions were pooled. Since the Berkshire Valley's sites were further south, on average, this effect helps to explain some of the ecoregional difference in occurrence.

The latitudinal effect could be due to a climatic gradient that is captured better by position on a north-south axis than by annual precipitation. Moving northward in Massachusetts brings higher elevations, steeper slopes, cooler temperatures, and increases in precipitation (Hall et al. 2002). These climatic changes are much more pronounced when moving east to west, however (Hall et al. 2002), and precipitation, tightly correlated with temperature, was taken into account. Furthermore, southern New England is well within *A. petiolata*'s climate envelope based on temperature and minimum rainfall (Welk et al. 2002). An alternative explanation for the latitudinal effect is that *A. petiolata* was first introduced to more southern localities in the regions of study, and the effects can still be seen today because the populations have not had as much time to fill in the more northern parts of the regions. We will come back to this in our discussion in Chapter IV.

Though there are many significant ecoregional differences in tree dominance, only the prevalence of *Quercus spp*. helped to explain the ecoregional discrepancy in *A. petiolata* occurrence. *Quercus spp*. dominance was not, however, a significant factor once ecoregion was taken into account as a predictor, which could mean that the ecoregional effect is masking a *Quercus spp*. effect on *A. petiolata*. Alternatively, *A. petiolata* and *Quercus spp*. could both be responding to a different ecoregion-associated effect. While this study does not give a clear picture of the connection between *A. petiolata* and *Quercus spp*., it does show that both respond strongly to ecoregion.

From this regional occurrence field survey, we can conclude that *A. petiolata* presence in western Massachusetts is influenced by soil moisture, precipitation, and latitude. The ecological, historical, and geological factors examined do not appear be important limiting factors in *A. petiolata*'s regional distribution. There also does not appear to be a dearth of dispersal corridors and forest edge habitats. The clearest pattern to emerge from this study is that there is drastic ecoregional difference in occurrence, with *A. petiolata* being far more common in the Berkshire Valley than in the Connecticut Valley, and that this difference is only partly explained by underlying environmental variables.

Chapter III - Regional, Historical, and Environmental Variation in *Alliaria petiolata* Performance

Introduction

In the northeastern United States, *Alliaria petiolata* is most common along roads, forest edges, and in riparian zones, but it has also demonstrated an ability to colonize and proliferate within intact forest communities, which is unusual for an invasive plant (Nuzzo 1993; Von Holle et al. 2003). An important component of exploring *A. petiolata*'s distribution and invasion ecology is to investigate its ability to enter different habitats. This capacity may be influenced by historical, regional, environmental, or demographic factors. The purpose of the study presented in this chapter is to examine the performance of established *A. petiolata* populations on a regional scale and determine what factors control its ability to colonize the forest understory.

Field experiment have demonstrated that forest edges are more invasible to *A. petiolata* than forest interiors (Meekins and McCarthy 2001). Though *A. petiolata* exhibits considerable resilience in responses to the varying light conditions of understory and edge habitats (Byers and Quinn 1998; Myers et al. 2005), germination, survival, and reproductive effort tends to be higher on the edge (Meekins and McCarthy 2001). It is therefore likely that invasion of a forested area begins with the establishment of a source population on the edge, followed by colonization of the interior. The factors that restrict *A. petiolata*'s initial establishment at a forest edge site may be similar to or different than those which restrict its occurrence in the forest interior. Furthermore, the factors that influence an invasive plant's occurrence in a habitat, such as the understory, can differ from those that influence its persistence and abundance (Turnbull et al. 2000; DeGasperis and Motzkin 2007). Here we will look separately at the factors that determine *A. petiolata*'s establishment and abundance in the forest understory.

Regional population dynamics and opportunities created by historical landscape disturbances could influence *A. petiolata*'s forest understory colonization behavior so ecoregional and historical land use variation will remain an important focus. The environmental variables examined in the occurrence survey will also be taken into account here. However, ecological resistance to invasion can sometimes be overcome by high propagule pressure (Von Holle and Simberloff 2005), and abundance can be limited by seed availability (Turnbull et al. 2000), so in addition to considering environmental variables, the size of the edge source population is taken into account as well.

By looking at regional and historical variation in *A. petiolata* understory occurrence and abundance while taking into account variation in environment and source population, we can build an understanding of the factors influencing *A. petiolata*'s edge to understory habitat shift in the forests of western Massachusetts. We will also be able to see if edge establishment, understory establishment, and understory abundance are fundamentally different processes.

Methods

To assess the influence of historical, regional, and environmental factors on the performance of *A. petiolata* in forests and forest edges, wooded, roadside sites with established *A. petiolata* populations were selected from semi-random field surveys. Sites were located across the Berkshire and Connecticut Valleys and in areas with both wooded and open historical land cover. Data was collected on the forest understory establishment and abundance of *A. petiolata*, as well as on site-specific environmental factors relating to anthropogenic, geophysical, and ecological phenomenon.

Study Sites

Study sites consisted of 67 plots with established *A. petiolata* populations, 58 of which were found in the randomized occurrence survey (see Chapter II), and nine of which were additional sites where *A. petiolata* was found in previous, unrelated field surveys. The ecoregion and historical land cover breakdown was unbalanced, as follows: Berkshire Valley – 31 open, 13 wooded, Connecticut Valley – 14 open, 9 wooded.

The additional sites were added to increase sample size, particularly in the Connecticut Valley where only 15 sites with *A. petiolata* were found in the occurrence survey. All supplemental sites met the same criteria as sites selected in the occurrence survey (known historical land cover, roadside forest edge, minimal size, and minimal distance from other sites; see Chapter II, p. 12-13). There were no significant differences in rates of understory establishment or abundance between additional sites and those from the random survey.

The understory colonization part of this study used all 67 sites, but the abundance analysis was confined to the 48 plots in which *A. petiolata* had established in the forest understory (as opposed to being confined to the edge, see Figure 3.1). The ecoregion and historical land cover breakdown for the 48 sites used in the abundance analysis was as follows: Berkshire Valley – 25 open, 9 wooded, Connecticut Valley – 9 open, 5 wooded.

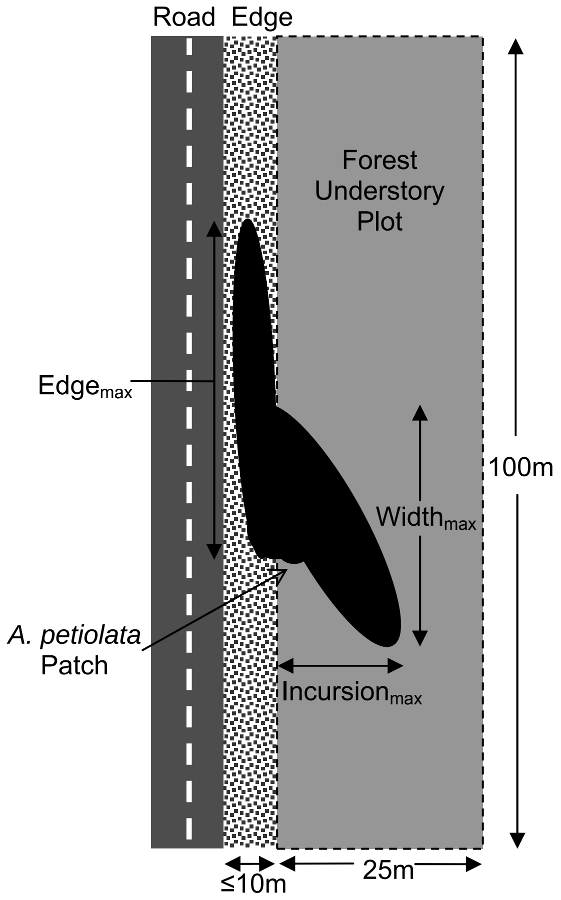

Figure 3.1: Design of survey sampling plots. A plot consists of a 25 × 100m tract of woodland, with one long boundary along a roadside edge, and at least 25m of woods on all other sides. The edge area between the woodland boundary and the road was no greater than 10m.

Field Sampling and Data Collection

All sites were sampled in the summers of 2006 and 2007 in the manner described in Chapter II: Methods (p. 14-15), but in addition to measuring environmental variables and noting the occurrence of *A. petiolata* at each site, the size of *A. petiolata* populations was measured and the occurrence of the plant along the edge and in the forest understory was recorded separately. The edge was considered to be the area between the road and the 100 meter-long forested plot boundary (where the boundary was formed by large-diameter tree trunks). The understory was considered to be the 25 × 100 meter forest plot (see Figure 3.1).

A. petiolata population size was measured in several ways. For edge populations, size was measured as the linear distance of edge with *A. petiolata* growing along it. In the understory, the dimensions of the largest patch of continuous *A. petiolata* were measured (maximum width and maximum incursion depth, with incursion depth being the deepest point of penetration measured perpendicular to the edge, see Figure 3.1). *A. petiolata* cover in the largest patch was estimated using a modified Braun-Blaunquet scale (0%, < 1%, 1-3%, 3-5%, 5-15%, 15-25%, 25-50%, 50-75%, > 75%). The largest patch was the focus of measurements based on the idea that the size and density of the largest sub-population can be is representative of the optimal performance of an *A. petiolata* population at the site.

Four metrics of *A. petiolata* understory abundance were used based on the population measurements: incursion and patch cover (measured directly), and patch area and plot cover (derived). Patch area was calculated as follows:

$$\text{Area}_{\text{patch}} = \text{Width}_{\text{max}} \times \text{Incursion}_{\text{max}}$$

Approximate cover percentages for the entire plot were also calculated as follows:

$$\%\ \text{Cover}_{\text{plot}} = \text{Area}_{\text{patch}} \times \%\ \text{Cover}_{\text{patch}} / \text{Area}_{\text{plot}}$$

Where $\text{Area}_{\text{plot}}$ is 2500m^2. Patch cover values were the mid-points of the ranges in the Braun-Blaunquet scale. Incursion was log transformed and area, patch cover, and plot cover were all square root transformed to bring distributions closer to normality. Each of the four abundance metrics gives a slightly different picture of *A. petiolata*'s population dynamics in an understory plot, including density (patch cover and plot cover), ubiquity of invasion (patch area and plot cover), and the population's ability to survive in the forest understory habitat (incursion).

The site-specific environmental data collected in the field and with GIS records in the occurrence study was also collected and used in this study. For all sites, forest edge density, road density, latitude, insolation, precipitation, soil moisture, surficial geology, bedrock type, and tree dominance data was used. Edge population size was used as an estimate of propagule pressure.

Data Analyses

Analyses were performed separately for (1) *A. petiolata* occurrence in the forest understory, and (2) abundance in the understory. This allowed for the possibility that different mechanisms may be responsible for the initial colonization of the understory and for performance in the understory once a population is established. Both analyses follow the general approach used in the occurrence study of Chapter II, with the effects of ecoregion and historical land cover, and environmental factors being tested first separately, and then in combination to see how they may affect one another's predictive ability. Environmental variables included in analyses were forest edge density, log road density, latitude, insolation, precipitation, soil moisture, surficial geology, bedrock geology, canopy tree dominance, and *A. petiolata* edge population size.

A. petiolata understory occurrence

The effects of ecoregion, historical land cover, and ecoregion in combination historical land cover on *A. petiolata* understory occurrence were each tested using a Pearson's chi-squared test (SAS CATMOD procedure). All 67 study sites with *A. petiolata* populations were included in this analysis.

To determine the effects of environmental factors on understory occurrence, presence in the understory was modeled as a function of the 15 environmental variables, plus the edge population size, in a multiple logistic regression based on maximum likelihood estimation (SAS CATMOD procedure). Edge population size was included because a large edge population could provide the propagule pressure necessary for an understory population to establish.

To investigate the relationship between ecoregion, historical land cover, and environmental factors in predicting *A. petiolata* understory occurrence, the regional and historical factors were added as predictors in stepwise fashion to the multiple logistic regression model. The model was also run as a GLM ANOVA to obtain adjusted, least square mean understory occurrence levels for significant categorical predictors. All statistical tests were performed using SAS/STAT 9.1 (SAS 2003).

A. petiolata understory abundance

A. petiolata understory abundance was analyzed based on the set of 48 sites that had populations in the forest understory. To see if understory abundance differed between ecoregions or areas of different historical land cover, these predictors and their interaction were tested for differences in all four abundance metrics (incursion, patch area, patch cover, site cover). A GLM MANOVA (SAS GLM procedure) was used to take into account interactions among the dependent abundance variables, and to test for an overall effect of the historical and regional predictors. Differences in least square mean abundance levels for individual ecoregion by historical land cover categories were tested with Tukey-Kramer post hoc hsd tests. Due to abundance variables with distributions that departed slightly from normality even after transformation, non-parametric tests were used to verify the results of the MANOVA. Kruskal-Wallis one-way analyses of variance (SAS NPAR1WAY procedure) were used to determine the effects that ecoregion and historical land cover have (separately) on each of the abundance metrics.

The effects of environmental factors on *A. petiolata* understory abundance were tested in a GLM multiple regression/MANOVA, using the SAS GLM procedure, which can deal with both numerical and categorical predictor variables. The model was run with ecoregion, historical land cover, and other significant factors included and excluded in stepwise fashion in order to determine how historical, regional, and environmental effects interact in predicting abundance. All four abundance metrics were used. Significant categorical factors were verified with Kruskal-Wallis one-way analyses of variance. MANCOVA models dividing the sites by ecoregion and/or historical land cover were not used due to limited sample sizes.

Results

Understory Colonization

Of the 67 sites surveyed, 48 (71.6 %) had *A. petiolata* populations present in the understory, while the rest had populations only along the edge (nine sites had populations in the understory only). While a higher proportion of sites in the Berkshire Valley and in historically wooded areas had *A. petiolata* in the understory (See Figure 3.2), there was no significant ecoregional effect (X^2 = 1.53 P = 0.2157), historical land cover effect (X^2 = 0.72 P = 0.3949), or interaction effect (X^2 = 1.53 P = 02157).

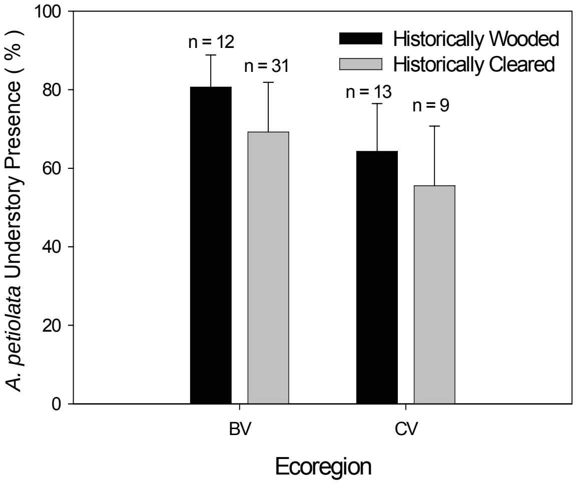

Figure 3.2: *A. petiolata* presence (+1 SE) in the forest understory (at sites with *A. petiolata*) by ecoregion and historical land cover. Ecoregional and historical land cover differences, and the ecoregion-historical land cover interaction are all insignificant (P = 0.2157, P = 0.3949, and P = 0.8273 respectively).

Sixteen environmental variables were tested in the multiple logistic regression model and seven turned out to be significant predictors of *A. petiolata* presence in the understory (see Table 3.1a). Neither of the anthropogenic factors were significant, but among the geophysical factors, sites with higher annual precipitation were more likely to have understory populations (P = 0.0251), as were sites with more hydric soils (P = 0.0216; see Figure 3.3). Decreased dominance in four of the seven tree species was associated with higher likelihood of *A. petiolata* presence in the understory (*Acer saccharum* P = 0.0100, *Pinus strobus* P = 0.0260, *Quercus spp.* P = 0.0263, *Tsuga canadensis* P = 0.0088; see Figure 3.4). *A. petiolata* edge population size has a significant positive influence on understory population presence (see Figure 3.5).

Predictor	X^2	p	Estimate
Anthropogenic Factors			
Forest Edge Density	0.68	0.4091	0.286
Log Road Edge Density	0.51	0.4758	-0.887
Geophysical Factors			
Latitude	0.35	0.5540	3.0×10^{-5}
Insolation	3.07	0.0797	1.2×10^{-4}
Precipitation	5.02	0.0251	0.603
Soil Moisture (hydric)	5.28	0.0216	2.291
Surficial Geology	0.80	0.3708	-
Bedrock	5.71	0.0575	-
Biological Factors			
Acer rubrum	3.53	0.0602	-1.178
Acer saccharum	6.63	0.0100	-1.814
Betula spp.	0.08	0.7748	-0.148
Fraxinus americana	0.83	0.3618	-0.480
Pinus strobus	4.95	0.0260	-1.473
Quercus spp.	4.94	0.0263	-1.458
Tsuga canadensis	6.86	0.0088	-2.587
A. petiolata Edge Population	6.36	0.0116	0.078

(a)

Predictor	X^2	p	Estimate
Anthropogenic Factors			
Historical Land Use	0.57	0.450	-0.740
Forest Edge Density	0.90	0.3422	0.348
Log Road Density	0.68	0.410	-1.144
Geophysical Factors			
Latitude	0.76	0.3836	5.1×10^{-5}
Insolation	2.66	0.1031	1.2×10^{-4}
Precipitation	2.87	0.090	0.588
Soil Moisture (hydric)	5.31	0.0212	2.619
Surficial Geology	0.91	0.340	-
Bedrock	5.77	0.056	-
Biological Factors			
Acer rubrum	2.19	0.1389	-0.967
Acer saccharum	6.80	0.0091	-1.842
Betula spp.	0.00	0.9557	-0.033
Fraxinus americana	0.07	0.7978	-0.183
Pinus strobus	4.74	0.030	-1.474
Quercus spp.	4.84	0.0277	-1.620
Tsuga canadensis	7.02	0.0081	-2.650
A. petiolata Edge Population	6.93	0.0085	0.080
Geographical Factors			
Ecoregion (BV)	0.02	0.8884	0.245

(b)

Tables 3.1: Multiple logistic regression of *A. petiolata* understory occurrence against **(a)** environmental variables and **(b)** environmental variables, ecoregion, and historical land cover. Estimate for soil moisture is between mesic and hydric soils. Estimates for the multi-category bedrock and surficial geology variables are omitted.

When ecoregion and historical land cover are added to the logistic regression model, neither turn out to be significant predictors of *A. petiolata* understory occurrence (ecoregion *P* = 0.8884, historical land cover *P* = 0.4495). Precipitation ceases to be a significant predictor (*P* = 0.0904) when ecoregion is taken into account. All other factors, including *Acer saccharum*, *Pinus strobus*, *Quercus spp.*, and *Tsuga canadensis* dominance, as well as *A. petiolata* edge population size, remained significant even after ecoregion and historical land cover were taken into account (see Table 3.1a).

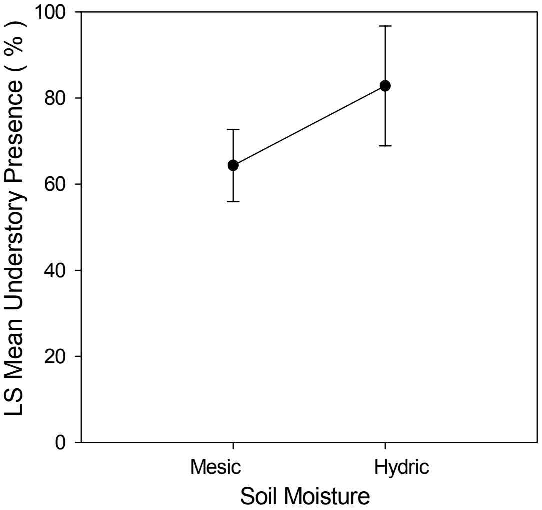

Figure 3.3: Least square mean understory presence (±1 SE) across mesic and hydric soil moistures. The difference was found to be significant in the multiple logistic regression model (*P* = 0.0212*)*.

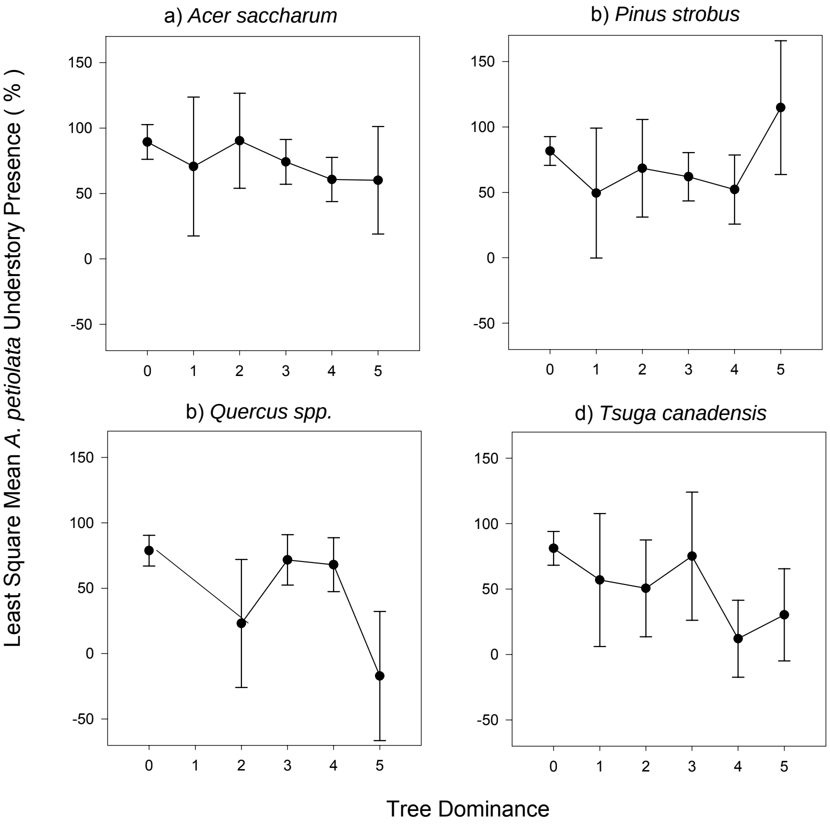

Figure 3.4: Changes in least square mean *A. petiolata* understory presence (±1 SE) over increases in tree abundance. In a multiple logistic regression model of *A. petiolata* understory occurrence, increases in each of the four species' abundance levels had a negative impact on understory occurrence. **(a)** *Acer saccharum*, $P = 0.0091$; **(b)** *Pinus strobus*, $P = 0.0295$; **(c)** *Quercus spp.*, $P = 0.0277$; **(d)** *Tsuga canadensis*, $P = 0.0081$.

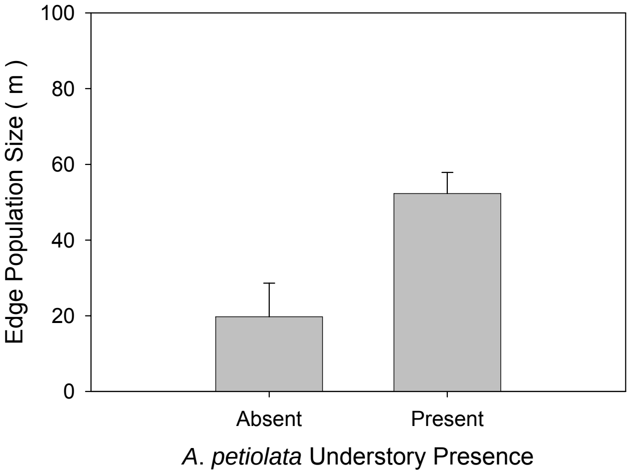

Figure 3.5: Mean edge population size (+1 SE) for sites with and without *A. petiolata* understory populations. Edge population size was a significant predictor of understory occurrence in a multiple logistic regression model ($P = 0.0085$).

Understory Abundance Analysis

The 48 sights in which there were understory *A. petiolata* populations varied widely in abundance from those with just a few low-density square meters to those in which nearly the entire plot was covered with a dense population. The ecoregion-historical land cover multivariate analysis of variance found no significant overall effects of ecoregion ($\Lambda = 0.96$ $F = 0.41$ $P = 0.797$), historical land cover ($\Lambda = 0.80$ $F = 2.49$ $P = 0.058$), or ecoregion-historical land cover interaction ($\Lambda = 0.98$ $F = 0.22$ $P = 0.924$) on abundance (see Table 3.2). Historical land cover, however, had a nearly significant overall effect and abundance was consistently higher in historically cleared sites for all the measures except incursion (see Figure 3.6). The historical land cover effect was significant for the individual abundance measures of patch cover ($P = 0.039$) and plot cover ($P = 0.024$) based on analysis of variance, but this was not confirmed by Kruskasl-Wallis one-way analysis of variance (patch cover $P = 0.082$, plot cover $P = 0.105$), throwing the significance of these result into question.

	Ecoregion				**Historical Land Cover**				**Ecoregion × Historical Land Cover**	
Abundance Metric	***F***	***p***	X^2	***p***	***F***	***p***	X^2	***p***	***F***	***p***
Incursion†	0.51	0.478	2.188	0.139	0.03	0.863	2.63	0.105	0.07	0.788
Patch Area‡	0.48	0.490	0.816	0.367	2.00	0.164	2.42	0.120	0.08	0.776
Patch Cover‡	0.50	0.484	0.528	0.468	4.52	0.039	3.02	0.082	0.23	0.636
Plot Cover‡	0.72	0.400	0.544	0.461	5.50	0.024	2.63	0.105	0.11	0.738
Overall Abundance Effect	0.41	0.797	-	-	2.49	0.058	-	-	0.22	0.924

Table 3.2: *F* ratios (from GLM MANOVA results), *H* test statistics (from Kruskal-Wallis one-way ANOVA results), and significance values for ecoregion, historical land cover, and the ecoregion-historical land cover interaction. † Incursion was natural log transformed. ‡ Patch area, plot, and cover were square root transformed.

Multivariate analysis of variance with environmental variables revealed some of the significant environmental predictors of *A. petiolata* abundance. Adding historical land cover and ecoregion had negligible effect on the model, and these factors are included in the results shown in Tables 3.3 (a) and (b).

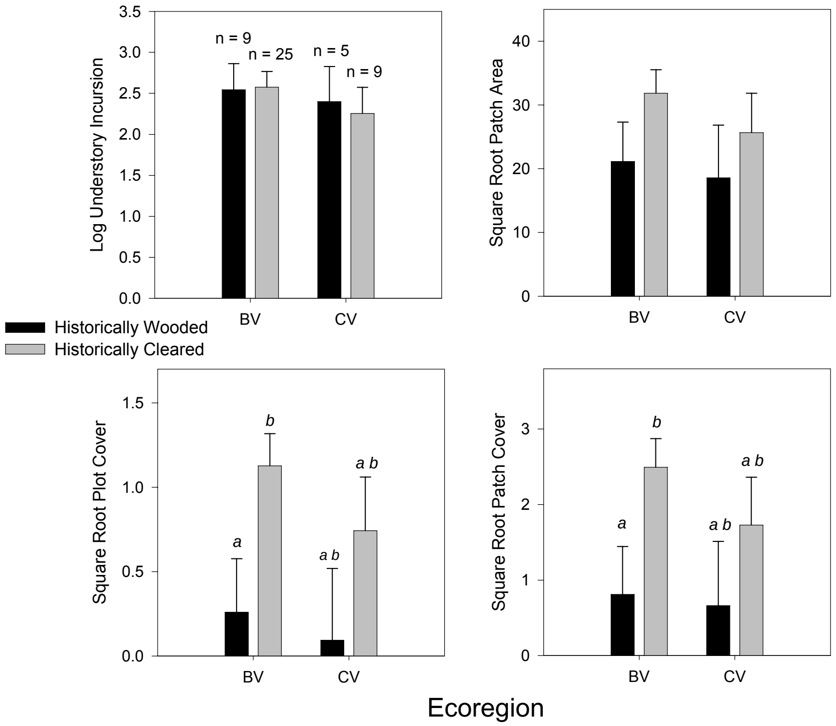

Figure 3.6: The four different measures of *A. petiolata* understory abundance (+1 SE) by ecoregion and historical land cover. MANOVA results found no overall effect of ecoregion and/or historical land cover on abundance, but ANOVA results indicate a significant historical effect on plot cover and patch cover. Different letters above bars indicate significant differences between categories.

Significant overall effects were found for latitude ($\Lambda = 0.57$ $F = 4.00$ $P = 0.0145$), and edge population size ($\Lambda = 0.41$ $F = 7.43$ $P = 0.0007$; see Table 3.3a). Latitude, however, was not a significant factor in predicting any of the individual measures of abundance. Edge population size, on the other hand, had a strong positive effect on all measures of abundance (incursion $P = 0.0236$, patch area $P < 0.0001$, patch cover $P = 0.0013$, plot cover $P = 0.0033$). No other significant effects were found. The fit for the model was good with $R^2 = 0.573$ for incursion, $R^2 = 0.764$ for patch area, $R^2 = 0.713$ for patch cover, and $R^2 = 0.718$.

The MANOVA model was re-run without edge population because the strength of this effect could be masking other predictors (see Table 3.4b). Latitude remained a significant overall predictor of *A. petiolata* abundance ($\Lambda = 0.64$ $F = 3.15$ $P = 0.0344$), but again had no significance when it comes to predicting individual abundance metrics.

(a)

Predictor	Incursion†		Patch Area‡		Patch Cover‡		Plot Cover‡		Overall Abundance Effect
	F	Estimate	F	Estimate	F	Estimate	F	Estimate	
Anthropogenic Factors									
Historical Land Cover (wooded)	0.08	0.135	0.32	-3.27	2.93	-1.319	2.58	-0.614	1.19
Forest Edge Density	0.28	0.077	0.45	1.20	0.01	0.001	0.03	-0.005	0.45
Log Road Edge Density	1.34	-0.472	0.47	-3.85	0.07	0.204	0.02	0.067	0.70
Geophysical Factors									
Latitude	0.89	1.31×10^{-5}	1.08	2.29×10^{-4}	1.14	-2.34×10^{-5}	2.07	-1.57×10^{-5}	4.00**
Insolation	0.05	1.30×10^{-6}	0.05	3.77×10^{-5}	0.14	7.50×10^{-6}	0.19	4.47×10^{-6}	0.07
Precipitation	0.91	-0.058	0.00	0.071	0.51	-0.075	0.21	-0.019	0.85
Soil Moisture (hydric)	1.48	-0.321	0.03	0.909	0.96	-0.449	0.97	-0.207	1.39
Surficial Geology	0.35	-	0.58	-	2.14	-	2.3	-	0.86
Bedrock	1.23	-	1.73	-	1.08	-	0.95	-	1.29
Tree Dominance									
Acer rubrum	0.00	0.004	0.37	1.740	1.92	-0.405	1.50	-0.177	2.68*
Acer saccharum	0.01	-0.021	0.56	-1.494	0.00	-0.006	0.03	-0.026	0.54
Betula spp.	0.18	0.035	0.78	-2.097	0.07	0.029	0.01	-0.034	1.56
Fraxinus americana	0.42	0.081	0.58	1.569	0.54	0.164	0.66	0.093	0.19
Pinus strobus	0.07	0.028	0.00	0.084	0.43	0.118	0.49	0.063	0.44
Quercus spp.	0.30	-0.089	0.29	-1.164	0.18	0.085	0.11	0.032	0.53
Tsuga canadensis	3.23	0.234	0.25	0.927	1.83	0.308	1.17	0.119	1.81
A . petiolata Edge Population	5.85**	0.010	25.05****	0.283	12.6***	0.024	10.65***	0.011	7.43****
Geographical Factors									
Ecoregion (CV)	0.69	-0.732	0.24	-6.987	0.3	-0.824	0.08	-0.175	0.36

(b)

Predictor	Incursion†		Patch Area‡		Patch Cover‡		Plot Cover‡		Overall Abundance Effect
	F	Estimate	F	Estimate	F	Estimate	F	Estimate	
Anthropogenic Factors									
Historical Land Cover (wooded)	0.65	0.004	0.65	-7.13	3.07*	-1.647	2.84	-0.766	1.33
Forest Edge Density	0.04	0.064	0.04	0.82	0.11	-0.031	0.13	-0.020	0.27
Log Road Edge Density	0.65	-0.569	0.65	-6.73	0.00	-0.041	0.01	-0.046	0.79
Geophysical Factors									
Latitude	0.02	4.62×10^{-6}	0.02	-2.13×10^{-5}	2.75	-4.46×10^{-5}	3.86‡	-2.56×10^{-5}	3.15**
Insolation	1.98	1.45×10^{-5}	1.98	4.25×10^{-4}	1.81	4.04×10^{-5}	1.83	1.97×10^{-5}	0.45
Precipitation	0.74	-0.096	0.74	-1.034	1.68	-0.169	1.1	-0.063	0.95
Soil Moisture (hydric)	1.90	-0.58	1.90	-6.61	3.58*	-1.09	3.46*	-0.50	1.46
Surficial Geology	1.60	-	1.60	-	3.39**	-	3.7**	-	1.06
Bedrock	0.79	-	0.79	-	0.79	-	0.73	-	1.06
Tree Dominance									
Acer rubrum	0.19	0.007	0.19	1.851	1.31	-0.395	1.09	-0.172	2.50
Acer saccharum	0.01	0.040	0.01	0.298	0.29	0.146	0.11	0.044	0.39
Betula spp.	0.40	0.014	0.40	-2.692	0.04	-0.022	0.01	-0.057	1.40
Fraxinus americana	0.00	0.024	0.00	-0.113	0.03	0.022	0.07	0.026	0.19
Pinus strobus	0.08	0.006	0.08	-0.562	0.10	0.063	0.14	0.038	0.49
Quercus spp.	1.08	-0.166	1.08	-3.444	0.03	-0.109	0.05	-0.058	0.76
Tsuga canadensis	0.15	0.223	0.15	0.590	1.30	0.279	0.89	0.106	1.86
Geographical Factors									
Ecoregion (CV)	0.16	-0.70	0.16	-5.92	0.24	-0.73	0.08	-0.13	0.36

Table 3.3: *F* ratios and estimates from GLM multivariate analysis of variance for incursion, patch area, patch cover, and plot cover *A*. *petiolata* abundance metrics. *F* ratios are based on type III sum of squares. **(a)** Model with all factors included. **(b)** Model with edge population size omitted to uncover other effects. Estimates for multi-category surficial geology and bedrock variables are omitted. * $P < 0.10$ ** $P < 0.05$ ***$P < 0.01$ **** $P < 0.001$ † Incursion was natural log transformed. ‡ Patch area, plot, and cover were square root transformed.

Surficial geology was not significant overall ($P = 0.4104$), but did predict patch cover ($P = 0.0336$) and plot cover ($P = 0.0248$). Kruskal-Wallis one-way analysis of variance found no significance for surficial geology in predicting incursion ($X^2 = 4.58$ $P = 0.206$) or patch cover ($X^2 = 7.46$ $P = 0.059$), but did find a significant effect on patch area ($X^2 = 8.27$ $P = 0.041$) and plot cover ($X^2 = 8.22$ $P = 0.042$). The effect of surficial geology was that abundances tended to be lower on sand and gravel soils than on flood plain alluvium (see Figure 3.7). None of the other environmental variables appeared to effect *A*. *petiolata* understory abundance.

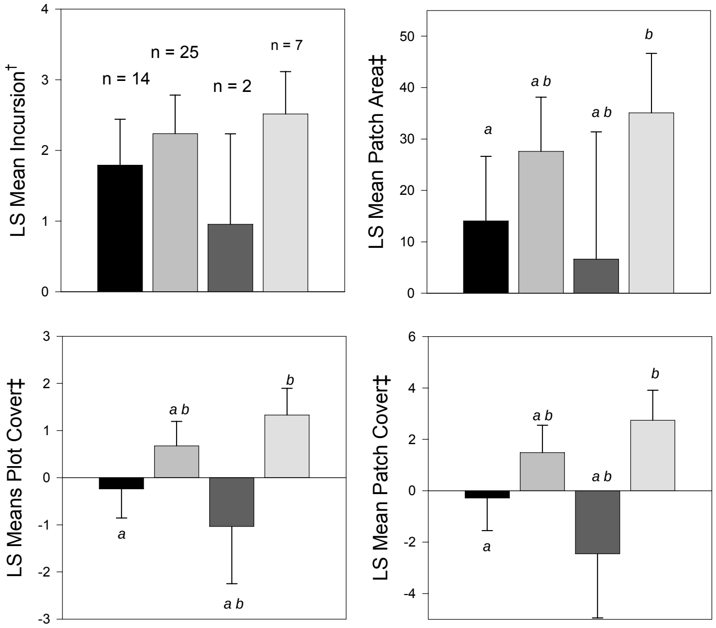

Figure 3.7: Least square mean *A*. *petiolata* understory abundance levels (+1 SE) by surficial geology. Surficial geology was a significant predictor of plot cover ($P = 0.0336$) and patch cover ($P = 0.0248$) in multivariate analysis of variance, though the effect, thought the effect was masked when *A*. *petiolata* edge population size was taken into account. Different letters above bars indicate significant differences between categories. † Incursion was natural log transformed. ‡ Patch area, plot, and cover were square root transformed.

Conclusions

The results of this regional survey of *A*. *petiolata* performance indicate that there is no significant ecoregional or historical land cover effect on variation in forest understory abundance or occurrence. The increased abundance seen in historically cleared areas did not hold up when environmental variables were taken into account. Though this could be due to historical influences on environmental factors (vice versa), the significance of environmental variables that appear to influence understory abundance (surficial geology, maybe latitude), does not change when historical land cover is taken into account.

The results of the survey support the model of forest invasion by which *A. petiolata* first establishes on the edge, and then moves into the understory. *A. petiolata* was found on the edge of most sites where it was present, and at several of the sites where edge populations were absent (but understory populations present), active mowing and maintenance may have been responsible for the absence. In contrast, nearly one fifth of all sites surveyed lacked understory populations, and many others had very small populations. This is further supported by the fact that edge population size was the most consistent predictor of *A. petiolata* understory colonization. Both understory occurrence and some measures of abundance increased as edge population size increased. This relation is most likely due to the increased propagule pressure which is associated with a large source population. Because this result holds true even with other environmental variables take into account, it suggests that *A. petiolata* is an invasive plant for which propagule pressure can overcome ecological resistance, as described by Van Holle and Simberloff (Von Holle and Simberloff 2005).

Edge population size was of particular interest as a predictor of understory abundance because it was significant across all four abundance metrics, and was one of the few significant predictors. This means that population density, ubiquity of invasion, and ability to thrive in the understory habitat are all related to the source population size more than any of the other ecological, geophysical, or anthropogenic factors measured. The only other factors affecting understory abundance are latitude and surficial geology. Latitude has a significant overall effect, but does not significantly change any of the individual measures of abundance, which may mean that it changes the relationship between the different metrics, but not their actual values. *A. petiolata* appears to do well on alluvial surface geology in comparison to soils with more sand and gravel. This may be associated with greater water retention (though there is no significant soil moisture effect), or nutrient retention. The nutrient retention explanation probably make more sense because *A. petiolata* is described as a nitrophile (Nuzzo 2000) and could presumably better compete on nutrient rich soils. However, the surficial geology effect is masked by the edge population size effect, so without controlled experimentation uncertainty remains.

With respect to environmental factors, it appears that different processes are at work when it comes to *A. petiolata* understory occurrence, understory abundance, and site occurrence (Chapter II). Surficial geology and maybe latitude influence understory abundance. Increased soil moisture, and potentially precipitation, is positively associated with understory presence. This contrasts with the effects found in the occurrence survey of Chapter II, which indicated that *A. petiolata* is restricted by too much water. A possible explanation for this is that hydric soil may be associated with seasonal flooding that causes disturbance in the forest understory that *A. petiolata* can take advantage of. On the edge, however, roadside runoff and a lack of thirsty, deep-rooted trees to compete with may make increased water unnecessary or even harmful, as hydric-adapted edge species could out-compete *A. petiolata* or keep it from establishing at a site in the first place.

Tree dominance is also significant in predicting understory occurrence, but not abundance or site occurrence. Increased dominance is associated with decreased *A. petiolata* presence in the understory for four tree species (*Acer saccharum*, *Pinus strobus*, *Quercus spp.*, and *Tsuga canadensis*). Because all these trees have negative associations with *A. petiolata*, their effects may have more to do with diversity than characteristics of the species themselves. Low abundance levels mean there are many dominant tree species, while high levels mean just a few. High tree diversity may be indicative of a nutrient rich site, or a site at which the formerly dominant trees were selectively logged, leaving a persistent disturbance. Either of these situations may have provided *A. petiolata* an opportunity establish itself in the understory.

A word of caution is warranted with the results of this understory colonization survey, which should not be taken as definitively as the results of the occurrence survey. The design was unbalanced with respect to key variables and sample sizes were small, particularly in the Connecticut Valley and for the abundance analysis. Furthermore, the abundance measure distributions departed from normality and were not entirely correctible through transformation. Nonetheless, there are some clear conclusions that can be drawn, and the information gained represents a good start in understanding the understory colonization behavior of *A. petiolata*.

From this field survey of forest edge *A. petiolata* populations, we can conclude that the most important factor in colonizing the forest understory is a large edge population size. Hydrological and forest community related factors may place limitations on initial establishment in the forest understory. Once established, however, a large source population on the edge can overcome ecological barriers and allow *A. petiolata* to thrive in the understory, potentially but not necessarily aided by favorable soil conditions. Other anthropogenic, geophysical, and ecological factors do not appear to be significant predictors of understory colonization, and neither do regional factors, or 1830 land cover.

Chapter IV - Discussion

Summary of Findings

We began with the large question of what historical, geographic, and ecological factors control non-native plant invasion patterns at the regional scale. This question was approached by looking at *A. petiolata* occurrence and performance in the forest edges of two ecoregions in western Massachusetts, an area with a history of broad-scale anthropogenic landscape disturbance.

In Chapter II, the occurrence survey indicated that *A. petiolata* is far more prevelent in the Berkshire Valley than in the Connecticut Valley. We also found there to be no discernable effect of pre-introduction land use history. Water-related environmental factors (soil moisture and precipitation) appeared to be negatively associated with *A. petiolata* presence, suggesting a possible oversaturation effect. *A. petiolata* had higher occurrence levels in more southern sites, and this latitudinal effect may be associated with climate, but is more likely a consequence of invasion history. Anthropogenic fragmentation, geology, and tree dominance did not appear to be important. Despite finding several significant environmental effects on *A. petiolata* occurrence, environmental factors could not fully explain the ecoregional difference.

In Chapter III, the performance survey found no discernable regional or historical effect on *A. petiolata*'s ability to colonize the understory either in terms of understory occurrence or abundance. Different environmental factors appear to influence the processes of understory establishment and understory abundance. Understory occurrence is negatively related to the dominance of many common tree species, implying that more diverse stands have higher rates of *A. petiolata* occurrence. Increased water availability, particularly due to hydric soils, also appears to facilitate understory establishment. In contrast, environmental factors were not found to have significant influences on understory abundance, though alluvial deposits may have some positive influence. The most important factor in colonizing the forest understory is the size of the source population on the edge, which is strongly correlated with both understory occurrence and abundance, all else being equal.

Several important general conclusions can be drawn from the findings of the two studies. First, is that geography matters in the regional-scale occurrence of invasive plants independent of the biotic, geophysical, or anthropogenic environment. Even when all the environmental differences between the Berkshire and Connecticut Valley are taken into account, considerable difference exists between the ecoregions in the prevalence of *A. petiolata*. There is also a latitudinal effect in occurrence that appears to be independent from latitudinal variation in environment.

Second, pre-introduction historical land use does not effect *A. petiolata* occurrence or performance at the regional scale. Land use history may still play a role in *A. petiolata* distribution or abundance at smaller scales or when later land use patterns are taken into account, but land cover around the time of the peak in New England agriculture does appear to be associated with *A. petiolata* distribution today.

Finally, different spatial, temporal, and environmental factors have different levels of influence over different aspects of *A. petiolata* invasion. Regional-scale occurrence was most influenced by spatial and water-related factors. Forest understory occurrence was influenced by population dynamics, biotic community, and water-related factors, but the hydrological effects were in the opposite direction of those influencing regional distribution. Abundance in the understory was primarily influence by population dynamics. While many of the specific environmental effects found in this field survey would be better examined in controlled experiments, these three findings stand on solid ground and should inform future work on plant invasions at the regional scale and on *A. petiolata*'s invasion patterns in particular.

Ecological and Evolutionary Implications

The findings from this study bring up several important questions about ecology of *A. petiolata*, some which have been already been explored, and others for which further research is warranted. The importance of soil moisture has been noted before by others (Cavers et al. 1979; Anderson and Kelley 1995; Byers and Quinn 1998; Nuzzo 2000; Meekins and McCarthy 2001), and minimal levels of rainfall have been modeled (Welk et al. 2002), but nowhere has too much water been reported as a limiting factor. In this sense, the results of the performance study, which suggested increased soil moisture facilitates understory colonization, make more sense than the results of the occurrence survey. However, *A. petiolata* is not known as a wetland species, so it would seem that there must be a ceiling to the level of moisture that can be tolerated. This is a hypothesis that needs testing.

A. petiolata's status as a multi-habitat species with wide ecological amplitude has been established (Nuzzo 1993; Byers and Quinn 1998; Meekins and McCarthy 2001), and many have looked at the plant's responses to different light regimes (Dhillion and Anderson 1999; Meekins and McCarthy 2000, 2001; Myers et al. 2005), but research into other factors that facilitate or inhibit understory colonization has been more limited (Meekins and McCarthy 2001; Stinson et al. 2007). We have seen that different environmental factors can be important for understory colonization compared to regional-scale distribution. Soils are one such factor that should be further investigated. Based on findings from the studies presented here and other work on invasive plants in New England, it is likely that soil attributes play a role in *A. petiolata* abundance (DeGasperis and Motzkin 2007; Von Holle and Motzkin 2007).

The importance of a large edge population for understory colonization indicates that population dynamics are important in understanding the edge to understory habitat shift. The understory colonization survey has shown that different factors limit understory establishment and abundance, and this may indicate a source-sink dynamic. Source-sink dynamics have been researched in other multi-habitat invasive plants (Thomson 2007) and it would be useful to explore this possibility in *A. petiolata*. Research on the demography of edge and understory populations is ongoing (K. Stinson, unpublished), and promises to be an informative line of inquiry in learning about *A. petiolata* invasion patterns.

A multi-habitat reciprocal transplant experiment demonstrated that *A. petiolata* was able to respond to changing environmental conditions through phenotypic plasticity (Byers and Quinn 1987). However, molecular research has shown that considerable genetic variation exists in North American *A. petiolata* populations and that there is considerable population differentiation within the introduced range (Meekins et al. 2001; Durka et al. 2005). Furthermore, common garden experiments have shown North American *A. petiolata* to have reduced competitive ability compared to its Eurasian conspecifics (Bossdorf et al. 2004). Evolution of invasive plants to new habitats has been demonstrated (Maron et al. 2004), so this is something to watch for in *A. petiolata*, which could be a good model study system for researching the evolutionary and population genetics of an invasive plant (Weinig et al. 2007).

The findings of the understory colonization survey also suggest that community composition or diversity may be important, particularly in the initial establishment phase. There has been an ongoing debate in invasive species literature about whether diversity makes a community more or less invasible (Levine and D'Antonio 1999; Naeem et al. 2000). The study in Chapter III only took into account tree species, and in a rather crude way, so it would be interesting to see whether diversity does play a role in *A. petiolata* invasion. Work has been done on the effect of *A. petiolata* on the understory community (Stinson et al. 2007), but the effects of community compositions on *A. petiolata* are unknown.

Historical and Geographical Implications

The unexplained predominance of *A. petiolata* in the Berkshire Valley and at more southern sites suggests that we look beyond environmental factors to explain this variation. Though we were unable to find a land use history effect, it may be that the history of *A. petiolata* invasion is responsible for its current distribution in western Massachusetts. Nuzzo compiled herbaria records of North American *A. petiolata* that gives a rough picture of the history and geography of the invasion (see Figure 4.1). Some of the earliest samples were collected from New York and southern Connecticut, and by the 1930s the plant was found both in eastern Massachusetts and throughout the Hudson Valley. The earliest record of *A. petiolata* in western Massachusetts is from 1960 (Mehrhoff et al. 2003). It may not be possible to know exactly how and when *A. petiolata* arrived in the Connecticut and Berkshire Valleys (it could spread naturally or be transported by humans) but we can make some educated guesses based on the findings of Chapter II.

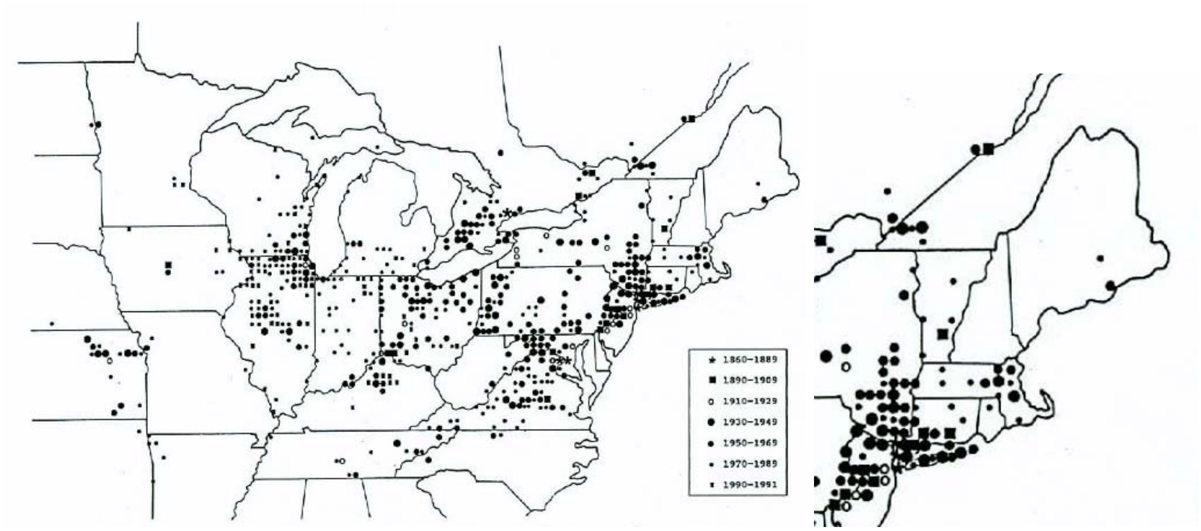

Figure 4.1: *A. petiolata* distribution over time in eastern North America, based on first herbaria record of occurrence in 15' quadrats (Nuzzo 1993).

The predominance of *A. petiolata* in more southern sites and the fact that the earliest introductions were mostly south of the area of study suggests that *A. petiolata* invaded from south to north. This especially makes sense in the Connecticut Valley because the city of Springfield is in the southern portion of this region and was one of the area's early human population centers, as well as its biggest. This would have made human transport to this area more likely, and anthropogenic disturbance could have facilitated the invasion.

The early and widespread expansion of *A. petiolata* up the Hudson Valley in the 1930-40s could be the explanation for the prevalence of *A. petiolata* in the Berkshire Valley. The Hudson Valley is only about 25 km east of the Berkshire Valley, so it may be that propagule pressure from this area is responsible for the ecoregional difference. The Connecticut Valley is not in the vicinity of any early, dense *A. petiolata* populations that were recorded.

These ideas are speculation and rely on herbaria records that are often incomplete and inconsistent. The best way to trace the history of *A. petiolata* spread through the Northeast would be with a molecular biogeography study like that done by Durka et al., but at the regional rather than continental scale (Durka et al. 2005). Reconstructing an invasion requires consistent, spatially explicit data over time. While we may only be able to get at this indirectly for the past, data collected now can help us in the future. This study has created a preliminary picture of *A. petiolata*'s current distribution (which could be repeated in the future), and efforts like Mehrhoff's Invasive Plant Atlas of New England will help us follow the unfolding of the *A. petiolata* invasion over time (Mehrhoff et al. 2003). Such approaches that take into account the spatial and temporal, as well as environmental patterns of invasion will be very useful for expanding our knowledge of invasion biology.

Applications

There is also a more applied side to this approach. Land managers and conservationists need to be kept informed of the exotic plants that are in their area, and knowledge of when, where, and how fast invasions are occurring is the first step for prevention. Information on how land use history affects species distributions can also aid in landscape restoration. More detailed experiments on the environmental influences of invasion discussed here and elsewhere are necessary, but so too are predictive models of where invasions are likely to occur. Classification and regression trees and time-series maps may be especially helpful (McDonald and Urban 2006; Endress et al. 2007; Mack et al. 2007). From the findings presented here, it is clear that the most useful approaches to understanding and dealing with invasions will take into account spatial, temporal, and environmental patterns.

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