Regional and Environmental Influences on Understory Vegetation in the New England Forest

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Abstract

I identified the strongest variables influencing species composition in the understory of four regions of New England. Vegetation sampling took place in Martha's Vineyard, MA (n=20), Petersham, MA (n=9), the Blue Hills region of NH (n=70), and the region of Levi Pond, VT (n=18). Although these four regions occupy the same general area of New England, the species assemblages generated by two-way cluster analysis indicate that there is considerable variation in the understory species composition among regions. Using non-metric multidimensional scaling I found that soil organic matter (%), nitrogen (%), C/N ratio, extractable calcium, sulfur, potassium, magnesium, iron, manganese, aluminum, zinc and sodium could all explain species composition in the understory, however, region was the underlying and most powerful of these variables. The influence that regional differences exert on the understory species composition is a result of the combined effects of climate, forest structure, overstory composition, soils, and disturbance history in each region.

1. Introduction

The New England forest represents a beautiful and marvelously intricate network of flora and fauna. Understory vegetation comprises an important part of this network and is too often overlooked by both those who appreciate the forest for its aesthetic value and by the ecologist and researchers who study these forest ecosystems. Understanding the species and patterns that occur in the understory requires more than mere identification and classification and begs the larger question, why are these species here? What underlying variables in the forest allow species to persist where they do? And why are we able to observe the same types of species in different geographic regions? In short, what are the driving forces behind understory species composition in the New England forest?

These questions resounded with me as I collected field data through the Wildland and Woodland long term research project at the Harvard Forest. Because vegetation sampling took place in four different regions of the New England forest I was able to observe compositional shifts in species moving from region to region. My curiosity was also piqued when my field partner and stumbled upon species that were characteristic of one region showing up unexpectedly in another region. Based on our field observations we hypothesized that some of the environmental factors influencing species composition in each region could be attributed to the disturbance history, the microtopography, soil variables, slope and aspect, and overstory composition in each plot and in each region.

Many of the factors mentioned above have in fact been found to influence the understory species composition in studies conducted across eastern North America and extending into some of the mid-western states. Specifically some of these studies have found that human influences, both historic and present, may determine both the species richness and the composition in the understory (D’Amato et al. 2008; Bellemare et al., 2002; Whitney and Foster, 1988; Ford et al. 2000; Ellum et al., 2010; Holle and Motzkin, 2007). Stand age can influence understory composition (Ford et al., 2000; Davison and Forman, 1982) in addition to microtopography (Beatty, 1984; Beatty, 2003), soils (Gerhardt and Foster, 2002; Hutchinson, 1999; Maguire and Forman, 1983; Brakenhielm and Quinghong, 1995; Tilman, 1987, D'Amato et al., 2008; Holle and Motzkin, 2007; Small and McCarthy, 2005), landform (Gerhardt and foster, 2002), slope-aspect (Siccama et al., 1970; Small and McCarthy, 2005; Huebner et al., 1995), tree basal area (Hutchinson et al., 1999; Ford et al., 2000; Fountain, 1980) and overstory composition (Beatty, 1984; Ellum, 2010; Berger and Puettmann, 2000; Rogers, 1981).

Unfortunately, many of these studies have conflicting or inconsistent results from one another. While some of these contradictions can be explained by the use of different experimental designs and geographic locations, the use of different data analysis methods may also be responsible for inconsistencies. Most studies utilize ordination or another form of multi-variable analysis. These analyses encompassed a broad spectrum of methods and techniques most of which may result in a slightly different outcome for the same dataset (McCune and Medford, 1999).

In an attempt to answer my initial question; what are the driving forces behind understory species composition in the New England forest? I applied the Wildland and Woodlands dataset to the some of the environmental variables that were found to be significant in the previously mentioned studies. In this analysis I hoped to determine not only the most influential factors on understory composition in the Wildands and Woodlands dataset, but also see how my own results would compare with some of the results that are contradictory within the literature.

Before it was possible to explore the dataset in terms of understory species and the influences of the environmental variables, it was first necessary to understand ordination and classification techniques utilized in community ecology. Since these techniques are widely used in community ecology but only limitedly understood, an outline and explanation of the most common ordination and classification techniques can be found in section 2.1 of the background section. This section is followed by an exploration of the many factors that have been attributed with understory species composition and richness by other studies and a summary of their results.

2. Background

2.1 Ordination and Classification Techniques

Multivariate methods have been used by community ecologists as early as 1950, however the methodology and programming behind these techniques has undergone a drastic evolution since the time when they were first introduced (Gauch, 1982). Ordination and classification are presently two important multivariate methods used in community ecology. These two methods allow ecologists to identify species assemblages and identify the environmental and anthropogenic factors that influence these assemblages. Although ordination and classification are deeply intertwined, classification will be explained first and ordination outlined in the section to follow.

Classification

Classification, also referred to as clustering, puts samples into classes and is most useful when assigning names, mapping, or defining natural community types (Palmer, 2009). Classification begins with the entire population and then divides groups into progressively smaller and smaller groups. This technique may be hierarchal or nonhierarchical, but of the two, hierarchical classification is more commonly used in community ecology because this technique portrays results as a dendrogram or linkage diagram for easy interpretation (Kent and Coker, 1992).

TWINSPAN, a two-way indicator species analysis, is among the most widely used classification technique. In TWINSPAN all the samples in the dataset are characterized initially via reciprocal averaging (an ordination technique that will be discussed in the sections to follow)(Gauch, 1982). The results of this ordination are then divided into two clusters and this step is repeated until each cluster has a chosen minimum number of members (Gauch, 1982). Clusters are defined based on species “preference” for a community type through the use of “pseudospecies” (Dufrene and Legendre, 1997). The pseudospeices concept essentially takes one species and then creates several “versions” of this species depending on the percent cover (Kent and Coker, 1997) . An example given in Kent and Coker (1997) using the species *Agrostis capillaris.* This single species is converted into five pseudo species using TWINSPAN by incorporating the percent cover of *A. capillaries* as part of the species identification. For example the species *A. capillaries*is may be represented in TWINSPAN as:

A. *apillaries* 1: percent cover up to 2%
A. *apillaries* 2: percent cover 3-5%
A. *apillaries* 3: percent cover 6-10%
A. *apillaries* 4: percent cover 11-20%
A. *apillaries* 5: percent cover over 20%
(Kent and Coker, 1997)

Depending on the relative abundance of this species, TWINSPAN will identify the presence or absence of the species for the five species classes listed. For example, if *A. capillaris* is present in the dataset with a percent cover of 2, TWINSPAN will record a presence for *A. capillaris* 1 and absence in the remaining four classes because only *A. capillaris* 1 describes the species in the dataset (Kent and Coker, 1997). An important aspect of the pseudospecies concept is that it is a cumulative technique, so if *A. capillaris* was identified in the dataset with 60% cover, then all five pseudospecies classes would be counted because theoretically, *A. capillaris* is present at 2% cover, 3-5% cover, 6-10% cover etc. (Kent and Coker, 1997). In this way, the indicator power of a species for a certain community or vegetation assemblage is dependent on the pseudospecies relative abundance (Palmer, 2009).

While TWINSPAN has been widely used since its debut in 1979, this program has recently been subject to criticism from community ecologists. One source of criticism is the use of "pseudospecies" and the dependence of these pseudospecies on their relative abundance in the dataset. Because the relative abundance of a species is dependent on the absolute abundance of other species in the quadrat, if all species are not sampled in the same way, the sampling method can introduce biased frequency values for species (Dufrene and Legendre, 1997). More importantly, TWINSPAN is dependent on a strong gradient in the natural community and as a result is unable to identify an underlying secondary gradient (Dufrene and Legendre, 1997). Another flaw in this method is that the points of division between clusters may be arbitrary, separating samples that actually have very similar species composition (Dufrene and Legendre, 1997). Finally, TWINSPAN depends on CA or DCA ordination for the initial separation of samples, however there is a certain degree of error associated with these two ordination methods (Dufrene and Legendre, 1997). Both of these ordination techniques and their sources of error will be described later in this section.

A two-way cluster may be used as an alternative to TWINSPAN with ecological community datasets. This method is preferred by some ecologists who believe that two-way cluster analysis produces a “better representation of species assemblages” (McCune and Medford, 1999). This method can also be tailored to any dataset or desired outcome by adjusting the distance measures and linkage methods. The distance method determines how “cases” or species are plotted (McCune and Medford, 1999). Two of the most common methods are the Euclidean distance and Sorenson (Bray-Curtis) distance.

The Euclidean distance is a relatively simple metric which works by plotting the cases or species in the dataset based on their dissimilarity. The distance value us then derived by calculating the distance between these species (Garson, 2010). This method is one of the most popular and common distance measures, however it has been criticized for its tendency to overemphasize outliers and its lack of sensitivity in heterogeneous datasets (McCune and Medford, 1999). Heterogeneous datasets have a high level of variability within data and many underlying gradients or variables at work (Otypkova and Chytry, 2006). Instead, McCune and Medford (1999) recommend using the Sorenson (Bray-Curtis) distance measure for ecological community data. Sorenson distance is a result of percent dissimilarity between cases or a proportional coefficient (McCune and Medford, 1999). This method is preferred especially in heterogeneous datasets where the Euclidean distance may be unreliable. A third distance measure that bay be utilized is the Jaccard distance measure, however this method is most applicable in binary datasets (Garson, 2010).

In addition to selecting a distance measure, an appropriate linkage method is also necessitated for reliable cluster results. The oldest and most conventional linkage method is the nearest-neighbor method (Lance and Williams, 1967). Although this method is considered by some to be obsolete, it is a relatively simple method in which the distance between two groups or clusters is the distance between their closest elements (Lance and Williams, 1967). Furthest-neighbor linkage utilizes the same methodology as the nearest-neighbor only instead of measuring the distance between the two closest elements, this method measures between the two most remote elements in each group (Lance and Williams, 1967). The centroid method represents a merging of the two prior methods; in centroid linkage the distance is measured between the means or centroids of variables (Garson, 2010). Median clustering is another method used; this method is similar to the centroid method but it does not weight distances depending on the size of the cluster and as a result small clusters may be lost in datasets where the cluster sizes range markedly (Garson, 2010).

Group average calculates distance based on the average distance between all inter-cluster pairs (Garson, 2010). This is a useful method because it generates distance not just from the nearest or farthest clusters, as in the nearest-neighbor and furthest-neighbor methods, but for all clusters in the dataset (Garson, 2010). Ward's method is the most unique of all linkage methods because it uses an ANOVA-type approach to maximize the distance between groups and minimize the differences within groups generating tighter clusters (Garson, 2010). Ward's method is recommended by McCune and Medford (1999) as a general-purpose linkage method because compared with other methods, Ward's method "minimizes distortions" in the dataset (McCune and Medford, 1999).

At the same time that it is important to select a distance and linkage method that best caters to the dataset and question being asked, there are constraints on these choices. Some distance measures are incompatible with certain linkage methods. While it is possible to combine two incompatible methods, the results of this cluster analysis may be difficult to interpret and therefore careful consideration should be taken to ensure that the most appropriate and compatible methods are selected for cluster analysis.

Ordination

Ordination, like classification, can be used to identify natural communities, however, rather than just clustering similar samples, this technique arranges classes along a continuous gradient. In most cases, arranging samples along a gradient is more representative of the "continuous nature of natural communities" (Palmer, 2009). Ordination can be categorized into two basic types; classical (unconstrained/indirect) and canonical (constrained/direct) ordination (Roberts 2009). The difference between these two types is that classical ordination is based only the variability in species data; environmental factors at play may be extrapolated by the user after the ordination, but these factors are not included with species data analysis. Canonical ordination on the other hand analyzes environmental data alongside the species data (Roberts 2009). Some of the most common classical ordination techniques are outlined in the table below (Table 1). While the ordination technique employed in each study will ultimately rely on the data set and desired outcome, some of these ordination techniques are more powerful and effective than others.

Table 1: A brief comparison of classical or unconstrained ordination techniques (Kent and Coker, 1992).

Classical Method	Author; Date	Distance measured preserved	Relationship of ordination axes with original variables	Criterion for drawing ordination axes
Bray and Curtis (Polar ordination; PO)	Bray and Curtis; 1957			
Principal Component Analysis (PCA)	Gittins Orlóci; 1966	Euclidean distance	Linear	Find axis that maximizes the total variance
Correspondence Analysis (CA)	Benzércri Hill; 1969, 1973	Chi-square distance	Unimodal (Gaussian)	Find axis that maximizes dispersion of species scores
Nonmetric Multidimensional Scaling (NMDS)	Fasham, Prentice; 1977	Any chose distance dissimilarity matrix	Depends on measure chosen	The number of dimensions for the new space is chosen a priori.
Detrended correspondence analysis (DCA)	Hill and Gauch; 1979			

The Bray Curtis (PO) method was one of the first classical ordination methods created, however, this “crude” approach is rarely used today (Anderson, 1971). One of the main reasons that PO has become less widespread in the ecological arena is its inherent tendency to over emphasize outliers (Anderson, 1971). Outliers, samples with a low similarity to other samples, are often present in community data as a result of, disturbed, heterogeneous, or atypical sites (Gauch 1982). While outliers are inherent to most ecological data sets, these samples may result in less “satisfactory” results since they can skew results and make other compositional assemblages less apparent in the final result.

One reason that PO ordination is so susceptible to overemphasis of outliers is because this technique arranges samples between two endpoints or “poles” (Palmer, 2009). These endpoints are assumed to be at the opposite ends of ecological gradients, meaning that endpoints have the greatest ecological distance between them (Palmer, 2009). Since outlier data represents dissimilarity with the other data, these samples are more likely to be identified as endpoints even though they may not represent the two ecological “poles” of the area sampled.

PCA is an ordination technique devised in 1966 to avoid the inherent flaws associated with PO. Distinct from PO, PCA relies on eigenanalysis-based methods rather than a distance-based approach to distinguishing samples (Palmer, 2009). While the math behind this method goes beyond the scope of this thesis, the eignenvalues essentially portray samples on many axes so that variation in samples is expressed as distance between axes (Plamer 2009). While PCA was widely used in community ecology from 1966 through the early 1990’s, this technique has largely been replaced as a result of distortion or “horseshoe” effect (Gauch 1982). Where beta diversity is moderate to high in the dataset, PCA will produce a distorted horseshoe shape where the extremes are incurved at the ends making interpretation difficult (Palmer, 2009).

CA and DCA are two additional classical ordination techniques that also use eigenanalysis-based approaches to ordinate data (Palmer, 2009). These two techniques are distinct from PCA in that they rely on a unimodal model whereas PCA depends on a linear model (Palmer, 2009). While CA ordination eliminates the “horseshoe effect” that is inherent to PCA, this technique is still flawed. CA may still distort datasets with higher beta diversity through the “arch” effect, a less severe version of the “horseshoe effect” (Palmer, 2009). Additionally, this technique may compress the axis extremes so that the distance between samples on the axis may not actually represent the difference in species composition (Palmer, 2009).

DCA corrects the “arch effect” in CA by detrending the data either by polynomials or by segments. This technique also reduces compression that can occur at the axes extremes using nonlinear scaling (Palmer 2009). Since its creation, DCA has become more widely used than CA and the other classical methods described earlier (Kent and Coker, 1992). However, like all ordination technique, DCA is not flawless; some ecologists have argued that detrending of segments in DCA can affect the outcome of the ordination. Because the number of segments is defined by the user, the results of a DCA ordination may differ substantially depending on the number of segments used (Dufrene and Legendre 1997).

Nonmetric multidimensional scaling is another classical ordination technique that may be utilized. Like PO, NMDS depends on distance-based approaches for ordination; however, in NMDS samples are spaced according to “stress” or the difference in rank order between ordination difference and ecological difference (Urban et al., 2002). One reason that this technique has become more popular in recent years is because NMDS does not make any assumptions about underlying gradients and is not as susceptible to “noise” (Urban et al., 2002). Noise describes variation in species composition that cannot be explained by environmental variation (Gauch, 1982). For example, two environmentally identical samples will probably not have identical species composition; in this case, the species variation is considered “noise” since it has no obvious ecological explanation. Another interesting feature of NMDS ordination is that although this method is considered “classical” environmental data can be analyzed in this ordination. However, distinct from canonical ordination, environmental gradients are added after species have already been ordinated; this means that environmental factors may reflect species composition but these variables are not ordinated alongside the species data.

At present, NMDS and DCA are the two most popular classical ordination techniques (Palmer 2009). While both techniques have advantages and disadvantages, the decision to use one technique over the other relies largely on the dataset and area sampled. DCA is more reflective of vegetation changes along a gradient whereas NMDS is more a type of “species composition representation” because gradients are not as apparent (De’ath, 1999). Finally users should be wary of utilizing either of these techniques without a solid understanding of the methods behind each technique since the results are sensitive to the number of dimensions specified by the user in NMDS or the number of segments selected in DCA (Palmer, 2009).

The previously mentioned ordination techniques are all relevant in the identification of species clusters and natural community types; however when species are assumed to be directly related to environmental factors, direct gradient analysis or canonical ordination must be employed. There are two primary canonical ordination techniques that are used; canonical correspondence analysis and redundancy analysis (Tables 2). While there are other several other canonical ordination methods that may be used in community ecology currently, most are recent and not yet widespread enough to be discussed in this thesis.

Table 2: A brief comparison of canonical ordination techniques (Anderson and Willis, 2003).

Canonical Method	Distance measured preserved
Canonical Correspondence Analysis	Chi-Squared
Redundancy Analysis	Euclidean distance

CCA is essentially a combination of CA with multiple regression; CA ordinates samples according to species and sample scores and multiple regression the limits the sample scores to a linear combination of the environmental variables (Palmer 2009). Depending on the strength of the relationship between the environmental variable and the species composition, CCA will create an environmental axis with the species oriented according to their response to that variable (Palmer, 2009). The influence of an environmental variable on species composition is measured by inertia (Palmer, 2009). In CCA, inertia is simply a quantitative means of identifying the dispersion of species along the environmental axis (Palmer, 2009). CCA is currently one of the most useful and widely used ordination techniques, but like all the ordination methods described, this technique is not flawless.

Fortunately, the issues that arise in CCA have more to do with the environmental variables selected than the actual ordination methods. For example, CCA can attempt to relate the environmental variables with samples but it cannot account for underlying gradients (which may be immeasurable or unquantifiable) that may really be affecting species composition. Users should also be wary of including too many variables in analysis; the number of variables should not reach the number of samples (Palmer, 2009). In the same way that any multiple regression analysis or model can result in a deceivingly high “variance explained value” when too many variables are included in analysis, CCA may result in a deceivingly high inertia value if too many variables are included in analysis (Palmer, 2009).

RDA is a more recent canonical ordination technique that is very similar to CCA. The differences between the two techniques are very subtle and user preference will depend largely on the user's dataset and desired results. Since RDA is linear (whereas CCA is multiple regression), RDA focuses less on species composition than CCA and therefore, RDA is more apt to distinguish gradients where all species are positively correlated than CCA (Palmer, 2009).

The advantages and applicability of these two canonical techniques in different datasets is explored in Roberts, 2009. This study provides an excellent comparison between CCA and RDA when applied four different vegetation studies in community ecology. Roberts (2009) identifies the advantages and limitations of each technique depending on the dataset to which it is applied.

2.2 Environmental and Anthropogenic Factors Influencing Understory Species Richness and Composition

As mentioned in the introduction, there are several variables that have been measured in terms of how they factor into the unique species assemblages and species richness in the understory. These factors include; human influences, both historic and present, stand age, microtopography, soils, landform, slope-aspect, tree basal area and density, and overstory composition.

Disturbance History

Human influences on the landscape are an important aspect of any ecological study since humans have had a profound impact on the North American forest structure and composition since the early 19th century up to present day. The disturbance history and forest age is often related to both species composition and species richness in the understory. D'Amato et al. (2008) found that old-growth forests support a significantly greater herbaceous and shrub species richness and abundance than disturbed sites in *Tsuga canadensis* stands in western Massachusetts.

Old-growth and secondary-growth forests may also support different understory species compositions. D'Amato et al. (2008) found that certain understory species such as *Aralia nudicaulis, Dryopteris intermedia,* and *Viburnum alnifolium* can be used as significant indicators of old-growth *Tsuga canadensis* stands. Whitney and Foster (1988) also found that certain understory species were only found in undisturbed, intact forests. *Aralia nudicaulis, Chimaphila umbellata, Epigaea repens,* and *Medeola virginiana* showed a strong affinity for primary growth forest (Whitney and Foster, 1988). Other species including *Lycopodium clavatum, Lycopodium obscurum, Polytrichum commune, Pteridium aquilinum,* and *Rubus flagellaris* have a stronger affinity for secondary growth forest (Whitney and Foster, 1988).

Gerhardt and Foster (2002) found similar results by classifying land use as either undisturbed woods or historic pasturelands and comparing land use with species composition in CCA. They found that undisturbed woods had a higher occurrence of shade tolerant species such as *Clintonia borealis*, *Trillium undulatum* and *Coptis trifolia*, while historic pasturelands supported more shade-intolerant species. Looking strictly at rich mesic forest species, Bellemare et al. (2002) was able to distinguish which forest species are restricted to primary growth stands and which are able to establish in both primary and secondary growth stands using DCA ordination. *Cardamine diphylla, Cardamine x diphylla, Tiarella cordifolia, Asarum canadense* and *Claytonia caroliniana* occur almost exclusively in primary forest. However, other rich mesic forest species such as *Arisaema triphyllum, Caulophyllum thalictroides, Polystichum acrostichoides,* and *Aster divaricatus* are able to colonize secondary forest as well.

Ellum et al. (2010) also found that anthropogenic disturbances can dictate understory species composition. Recently disturbed or open-sites had a high occurrence of shade intolerant species including the weedy species *Parthenocissus quinquefolia*. In contrast, undisturbed forest had higher relative importance values for shade tolerant species such as *Arisaema triphyllum* and the endangered *Polygonatum biflorum* (Ellum et al., 2010).

The association of weedy species with disturbed or cleared forests may be related to their life cycle pattern. Weedy species typically colonize rapidly post-disturbance by immediately increasing seed and ramet production in order to take advantage of newly formed light gaps and open substrate by (Ellum, 2009). This life cycle pattern puts native plant species at a disadvantage because unlike invasive or weedy species, native herbs invest more energy in vegetative growth than reproductive structures and dispersal; as a result these species are not as competitive for substrate and light in recently disturbed regions as their weedy counterparts (Ellum, 2009).

Non-native invasive species share many of the same general dispersal methods as weedy species and as a result, are often associated with heavily disturbed sites. Holle and Motzkin (2007) were able to directly link the presence of non-native species with the presence of historic disturbance by humans. Previously cultivated sites and those with a history of soil disturbance have a higher occurrence of non-native plant species than undisturbed sites (Holle and Motzkin, 2007).

Stand Age

The age of a forest can also be broken down into smaller age classes than just old-growth vs. secondary-growth. Ford et al. (2000) sampled vegetation in hardwood stands in Northern Georgia aged at 15, 25, 50 and $\geq$ 85 years. They were able to determine that while species richness and diversity did not have a significant dependence on stand age, there is a slightly non-significant trend of increased species of richness and diversity with stand age (Ford et al., 2000). Alternately, Davison and Forman (1982) found that herb diversity in a mature oak forest was negatively related with stand age.

Composition may also shift with the stand age (Ford et al., 2000). Certain species were more abundant in older age classes including *Tiarella cordifolia* and *Disporum lanuginosum* while other species were more common in younger forest types including *Lysimachia quadrifolia* and *Potentilla canadensis*.

Microtopography

Microtopography, or heterogeneity of terrain, is typically the result pits and mounds that form when forest trees are uprooted and left to decay (Beatty, 1984). As a result, microtopography is lacking from previously cleared or historic agricultural lands where trees have been cut and removed. The microtopography of a site is also dependant on the degree of historic land use. Historic plowing or tilling overturns the soil destroying any microtopography and exposing fresh substrate, however old pastures may still retain some degree of microtopographic heterogeneity (Beatty, 2003).

The importance of pit-and-mound topography in the understory is related to the microsites and microhabitats that result from uneven terrain. These microsites and microhabitats have unique chemical and physical characteristics in pits versus on mounds. Through niche differentiation, certain understory species may be more able to colonize and establish on pit-and-mound topography than tracts of land where this feature is absent (Beatty, 2003).

Pit-and-mound topography is also associated with higher species diversity because dominant species are able to establish on the highly competitive mounds while other more tolerant species are able to persist in the more deleterious pit conditions without the risk of being out-competed by dominant species (Beatty, 2003).

Soil

Soil is one of the most important factors driving species richness and composition in the understory. The effects of soils on understory vegetation may be the result of soil texture, nutrient content, moisture and pH.

Soil texture can be described in terms of its clay, silt and sand content. These three groups reflect particle size; sands are the largest with particles 0.50-0.25mm in diameter, silts are smaller at 0.05-0.002mm and clay represents the smallest particle size at less than 0.002mm (Oostings, 1956). The large particle size of sandy soils facilitates the flow of fluids and a result, soil nutrients and cations move through sandy soils quickly (Singer and Munns, 1987). In contrast, clay soils are more likely to retain water and nutrients (Singer and Munns, 1987). As a result, depending on the ratio of these three textures in the soil different species may be able to establish and persist in the understory. Gerhardt and Foster (2002) used the proportion of sand by volume in canonical correspondence analysis to confirm that soil texture was related to the understory composition.

Soil moisture may also have pronounced effects on the species composition in the understory however the results are conflicting. Hutchinson (1999) used canonical correspondence analysis to conclude that understory species composition is strongly correlated to soil moisture. Shrubs and saplings were found at more than 25% frequency on xeric or dry plots (Hutchinson, 1999). However, as the soil moisture content increases, forbs are the species with the highest frequency (Hutchinson, 1999). As expected, the most common species were strongly associated with intermediate soil moisture levels (Hutchinson, 1999). In contrast, Maguire and Forman (1983) found that soil moisture was not related to species composition in the understory. These conflicting results reflect the sample sizes and range of soil moisture levels sampled in these two studies. Whereas Hutchinson (1999) observed 315 species on sites ranging from xeric to mesic, Maguire and Forman (1983) recorded only 22 herbaceous species and 11 shrub and seedling species. McGuire and Forman (1983) also observed much less variation in soil moisture with percentages ranging only from 43.6-54.1. The combination of lower species richness, in addition to less variation in soil moisture could explain why Maguire and Forman (1983) did not find that moisture had and effect on understory vegetation whereas Hutchinson (1999) did.

The amount of nitrogen, an important soil macro-nutrient, in the soil is yet another factor that contributes to species richness and composition in the understory. This macronutrient is vital to plant growth and development (Table 3). Nitrogen can be measured in terms of the nitrogen deposition, nitrogen mineralization, combustible nitrogen and nitrogen release.

Table 3: Summary of soil macronutrients and the role they play in plant growth and development (Aber and Melillo, 2001).

Element (Macronutrient)	Uses	Taken Up As
Carbon (C) **Hydrogen (H)** **Oxygen (O)**	Carbohydrates and derivatives basic building blocks for nearly all plant products	CO_2 H_2O
Nitrogen (N)	Amino acids, proteins, enzymes, nucleic acids, chlorophyll	NO_3^- NH^+_4
Phosphorus (P)	Sugar phosphates (ATP, ADP), nucleic acids, phospholipids	$H_2PO^-_4$
Potassium (K)	Not structural, enzyme co-factor catalyzes protein formation; stomata, charge balance across membranes	K^+
Sulfur (S)	Amino acids, proteins, enzymes	SO^-_4
Magnesium (Mg)	Chlorophyll, enzyme cofactor	Mg^{2+}
Calcium (Ca)	Crucial to membrane function; binds wood fibers together; stabilizes waste products in vacuoles	Ca^{2+}

Brakenhielm and Qinghong (1995) examined species richness and diversity in response to the rate of nitrogen deposition in the soil. They found that nitrogen deposition in a spruce-mixed conifer stand was weakly negatively correlated with species richness and positively correlated with species diversity. Tilman (1987) also found that by increasing nitrogen levels in the soil along a gradient, species richness significantly decreased in response. While both these studies reached the same conclusion, they took place in drastically different settings; Tilman (1987) sampled in abandoned agricultural fields where as Brakenhielm and Quinhong (1995) sampled in a more natural forested setting. Their conclusion can be explained by the fact that nitrogen poor sites support a lower plant biomass, and consequently lower cover, allowing a greater number of species to establish; in contrast, nitrogen rich sites support a higher plant cover and as a result have lower species richness but a higher diversity value (Aber and Mellillo, 2001).

The soil nitrogen level is also related to understory species composition. Tilman (1987) found that different understory plants responded to changes in soil nitrogen deposition differently. Early successional annuals and short-lived perennials had a greater abundance in low nitrogen plots compared with long-lived herbaceous and woody species whose abundance was greater in high nitrogen plots (Tilman, 1987). Hutchinson et al. (1999) measured nitrogen mineralization rate in the soil and found that of all the understory species surveyed, forbs increased in frequency the most with increasing nitrogen mineralization rate.

Some of the other important macronutrients in the soil are outlined in Table 3. These nutrients provide important products for plant growth via base exchange and have the potential to influence understory richness and composition (Oostings, 1956). Macronutrients are relevant to the study of non-native invasive flora. Holle and Motzkin (2007) found that non-native species richness has a stronger positive relation to soil calcium levels than their native counterparts (Holle and Motzkin, 2007).

More generally, the overall soil fertility has been tested for its relation to species richness in the understory. Hutchinson et al. (1999) used extractable NH_4^+, P and NO_3^- as measures of soil fertility and found a positive correlation between understory richness and soil fertility. In a more controlled experiment, Tilman (1987) added nitrogen along a gradient to test for an association with species richness. In contrast to the results from Hutchinson et al. (1999), Tilman (1987) found a negative correlation between the amount of nitrogen added and the species richness. These conflicting results are likely due to differences in the ecosystems sampled and the form of nitrogen being tested.

Tilman (1987) takes place in abandoned fields in the oak savannah whereas Hutchinson et al (1999) sampled in second-growth oak forest in eastern North America. Additionally, Hutchinson et al (1999) measured the concentration of NH_4^+ in the soil and nitrogen mineralization rate, whereas, Tilman (1987) measured commercial nitrogen fertilizer (NH_4NO_3).

The ratio of carbon to nitrogen is another aspect of the soil that can influence the species composition and richness in the understory. Understory species that are associated with nutrient-rich, mesic soils typically occur in sites with low C/N ratio (Bellemare et al., 2002) Small and McCarthy, 2005 also found that the understory species composition in the eastern oak forest where they sampled was strongly related to the ratio of C/N ratio in the soil. C/N ratio can also predict understory species richness; higher herb richness may be found at lower C/N soil plots and lower herb richness may be found at sites with high C/N ratio in the soil (Small and McCarthy, 2005).

Soil pH has been found in some studies to affect understory composition, however there is some debate over the relative influence of this variable on understory species. Hutchinson et al. (1999) used CCA to determine that the soil pH did have an effect on species composition in the understory. This observation can be explained by the fact that increased acidity, or a lower pH may alter the chemical processes in the soil (Oostings, 1956). Typically, acidic soils also have higher aluminum and iron content and lower calcium levels; thus by altering the concentration of soil cations, pH may indiretly dictate which species are able to persist in the understory (Oostings, 1956). In contrast to the results determined by Hutchinson et al. (1999), Maguire and Forman (1983) did not find that soil pH was related to the understory species composition in the mature Hemlock-hardwood forest they tested. This contrast could be the result of the different forest types sampled or the different analysis methods. Hutchinson et al. (1999) analyzed the species distribution with respect to pH using CCA, however Maguire and Forman (1983) used multivariate analysis to test the relation of soil pH to already established herb patches. The use of multivariate analysis is not as powerful as CCA and may limit the ability of Maguire and Foreman (1983) to find a relationship between pH and species composition. Another important distinction between these two studies is that Maguire and Forman (1983) used soil cut-off points in their analysis eliminating soil pH values lower than 3.95 or higher than 4.05. By limiting the range of pH values they may have limited their ability to detect the response of understory species to pH.

Landform

Just as soils can influence understory species richness, landform as well can affect the understory vegetation. Gerhardt and Foster (2002) describe landform as the combination of geomorphology, landscape position, soil drainage, topography and soil profiles. Based on these variables, six landform categories were created for plots in a *transition Hardwood-White Pine-Eastern Hemlock forest* in central New England. These categories include: well-drained glacial outwash, marginal moraine, bedrock ridge, stream drainage, basin, and poorly drained glacial outwash. They found that understory the most species-rich communities are more commonly found on poorly drained basins and species-poor communities often occur on well-drained glacial outwash.

Slope and aspect

Both slope and aspect may influence species richness in the understory. Siccama et al. (1970) found that there is a negative marginally non-significant relationship between species diversity and aspect moving from an easterly aspect to westerly aspect. Small and McCarthy (2005) found that NE (345.5-104.5°) and INT (105-165°) had higher mean species richness per plot than SW (165.5-284.5°) plots. While the aspect categories used in these two are not the same, both studies suggest a general trend of higher species richness or diversity at eastern aspects and lower richness/diversity at western aspects. Position on the forest slope can also affect the species richness of the understory. Plots identified as "low slope" supported greater herb richness than "upper slope" plots (Small and McCarthy, 2005).

Slope and aspect can also be classified together and tested for their combined effect on understory richness and composition. Using a numeric categorical scheme Huebner et al. (1995) created groups by combining the slope (gentle, moderate or steep) with a range of aspects representing either a northern or southern aspect. Using these categories Huebner et al. (1995) was able to conclude that slope-aspect is correlated with the species richness; bottomland sites (flat, no aspect) were the richest sites; steep north facing slopes were the next most rich and south facing slopes (both moderate and steep) supported the lowest species richness of all slope-aspect categories (Huebner et al., 1995). This shadows the results of Gerhardt and Foster (2002) that flat or bottomland sites support the greatest understory species richness.

Tree Basal Area

Basal area as well may influence species richness in the understory though the effects of this variable on the understory species richness are conflicting. Hutchinson et al (1999) found that species richness is negatively correlated with tree basal area. Ford et al., (2000) found the same trend of decreasing understory richness with increased basal area. However, he did find that species evenness increased with increased basal area. In contrast, Fountain (1980) did not find that tree basal area was significantly related to the diversity of herbaceous species.

Overstory Composition

Just as the basal area may dictate species composition and richness in the understory, the tree species that comprise this basal area can also have important influences on the understory species richness and composition. *Fagus grandifolia* is one canopy species that is associated with decreased species richness in the herb layer (Rogers, 1981; Kooijman and Cammeraat, 2010). This trend can be attributed to the inhospitable environment that may be found beneath the *F. grandifolia* overstory. *F. grandifolia* has a very low transmittance percentage and therefore light is limited in the understory (Barbier et al. 2008). This species also produces one of the most acidic topsoils of all hardwood species (Barbier et al. 2008; Kooijman and Cammeraat, 2010).

Berger and Puettmann (2000) found that aspen (*Populus spp.)*, hardwood and conifer dominated overstories all illustrated different trends in the relationship between the basal area and the understory species diversity. They found that the proportion of aspen basal area was positively correlated with herbaceous diversity; hardwood basal area was negatively related and conifer basal area was not significantly related (Berger and Puettmann, 2000).

Ellum et al. (2010) found that as the basal area of *Tsuga (*hemlock) increases, the species richness significantly declines. Species richness also follows a decreasing trend among forest types from hardwood≥regenerating forest, hardwood-pine and pine ≥ mixed ≥ hardwood- hemlock> hemlock-hemlock (Ellum et al., 2010).

The species that comprise the forest overstory may factor into the understory composition as well. Generally, broad-leafed and coniferous dominated canopies support different understory species and species assemblages (Whitney and Foster, 1988). *Vaccinium angustifolium* has a stronger affinity for coniferous forest types while *Aster acuminatus* has a stronger association with broad-leafed forest types (Whitney and Foster, 1988).

The presence and abundance of *Tsuga canadensis* can also have a strong effect on understory composition (Beatty, 1984). Using DCA ordination, Beatty (1984) found a clear separation between different species based on their location in either “hemlock frequent”, “hemlock occasional”, or “hemlock absent” plots. Based on this separation, Beatty (1984) found that certain understory species were more apt to grow under a *Tsuga* canopy while other species were only found in a hardwood dominated overstory.

3. Materials and Methods

3.1. Study Area

Over the course of two summers, 118 permanent plots were established and sampled in Martha’s Vineyard, MA, Petersham, MA, the Blue Hills region of NH, and the Levi Pond region of VT (Fig. 1). The four regions surveyed occupy the broader region of New England and have similar climatic conditions in terms of average monthly temperatures and annual precipitation (Table 4).

Figure 1: Regions surveyed; plots in Levi Pond, Petersham and Martha's Vineyard were sampled during the summer of 2009. Blue Hill plots were sampled during the summer of 2008.

Martha's Vineyard

One of the four regions where vegetation sampling was conducted is Martha's Vineyard, an island off the coast of Massachusetts. This region experiences weather patterns typical of New England but with notably higher average temperatures than the other three regions sampled; for a full regional description refer to Table 1. The plots were located mostly on Haven very fine sandy loam or Eastchop loamy sand; however a few plots fell on Chilmark sandy loam soil type (NRCS, 2010; Fig. 2).

Nearly the entire island of Martha's Vineyard was at one point cleared for agriculture or development and as a result, the forest surveyed in this region is best described as secondary growth. In addition to human disturbance, Martha's Vineyard is also subject to intense natural disturbances including the decline of *Q. velutina (*black oak) and *Q. alba (*white oak), two important tree species on the island. Since 2004 the island has been plagued by the presence of the fall cankerworm, a native insect pest that is largely responsible for the oak deaths on the island (Polly Hill Arboretum, 2009).

South Petersham

Field sampling in southern Petersham was conducted on sites within the township of Petersham and owned by the Harvard Forest, the Massachusetts Audubon Society or the Trustees of Reservations. The Harvard Forest plays an especially important role in this study because it is through this research station that the Wildland and Woodland project was originally designed and carried out. Since 1907 the Harvard Forest has been conducting both short and long term ecological research projects on the 3000 acres of land it owns in Petersham, MA. (http://harvardforest.fas.harvard.edu/index.html).

This region can be described as having a cool, moist and temperate climate; precipitation is distributed evenly throughout the year but annual precipitation is notably higher than the other three regions sampled (Table 4) The acidic soils that characterize this region are moderately well-drained sandy loam glacial till with some alluvial and colluvial deposits (Zen et al., 1983; Scanu, 1988). The plots in Petersham were distributed on Charlton-Chatfield-Hollis association, Charlton-Paxton association, Hinckley loamy sand, Lyman-Tunbridge-Berkshire association, Peru-Marlow association, and Woodbridge-Paxton association soils (NRCS, 2010; Fig. 3).

The dominant tree species in this region encompass all successional stages from early sucessional species such as *Pinus strobus (*eastern white pine) to mid and late sucessional species (Thompson and Sorenson, 2000*)*. The high abundance of early sucessional trees in this region can be attributed to this area's long history of human disturbance. Cultivation in this region has been traced back as early as 1160 AD and humans continue to develop and harvest the forested lands of Petersham today (Tritsch, 2005). Although all plots were located on conservation land, trails run throughout the area surveyed and nearly all sites exhibited signs of historic human disturbance including nearby stone walls and multi-stemmed hardwoods (Wessels, 1997).

Blue Hills

Vegetation sampling also took place in Strafford, New Hampshire. Like Petersham, precipitation in this region is evenly distributed throughout the year (see Table 4 for a full regional description). The majority of plots in Blue Hills were located on Gloucester sandy loam, Hollis-Charlton sandy loam and Hollis-Gloucester sandy loam (extremely-very rocky). However, some plots were sampled in Acton sandy loam, Champlain loamy sand, Deerfield loamy sand, Hinckely loamy sand, loamy sand, Hollis-Charlton sandy loams, Leicester sandy loam, Medomak mucky silt loam, Paxton sandy loam, Ridgebury sandy loam, Rumney sandy loam, and Windsor loamy sand (NRCS, 2010; Fig. 4).

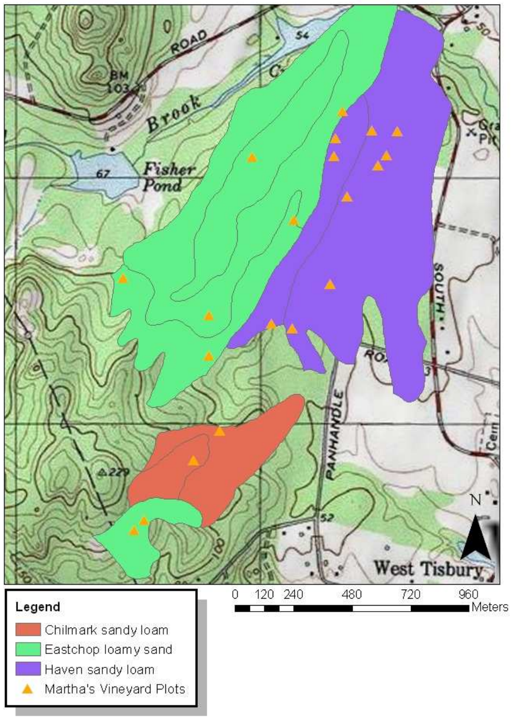
The area surveyed is protected from development by the Blue Hills Foundation & George Lovejoy Jr. However, this area is still subject to some small scale timber harvesting from the New England Forestry Foundation through their forestry easement (New England Forestry Foundation, 2010).

Levi Pond

Sampling was also conducted with the Levi Pond Wildlife Management Area, located in the town of Groton, VT. This region experiences weather patterns typical of New England and like Petersham and Blue Hills, precipitation in this region is evenly distributed throughout the year (see Table 4 for a full regional description). Nearly all the plots in Groton occurred on Tunbridge-Monadnock soils; however some plots were located on Tunbridge-Dixfield, Dixfield sandy loam, and Colonel-Cabot association soils (NRCS, 2010; Fig. 5). While the Vermont Fish and Wildlife does manage this region for small-scale timber harvesting, hunting and walking/hiking trails, the areas sampled showed little evidence of recent human disturbance (Vermont Fish and Wildlife, 2008).

Table 4: Comparison of the physical and environmental features in Martha’s Vineyard, MA; Petersham, MA; Blue Hills NH; and Levi Pond, VT

Region	**Martha’s Vineyard MA**	**Petersham MA**	**Blue Hills NH**	**Levi Pond VT**
County	Dukes	Worcester	Strafford	Caledonia
Number of Plots	20	9	70	18
Geographic Location	41.4°N; 70.6°W	42.5°N; 72.0°W	43.2°N; 71.1°W	44.2°N; 72.3°W
Land Ownership/ Management	Polly Hill Arboretum and the Nature Conservancy	Harvard Forest, Massachusetts Audubon Society, Trustees of Reservations	Blue Hills Foundation & George M. Lovejoy, Jr.	State of Vermont; managed by the Vermont Fish and Wildlife Department
Microtopography	Even/mostly flat	Pit-and-mound	Pit-and-mound	Pit-and-mound
Slope	0%- 29%	3% -25%	0%-57%	0%-30%
Elevation	60-190 m	220-410 m	600-1000 m	450-600 m
Average Temperature	23.4°C- $^{-}$1.1°C (NCDC/NOAA, 2008)	22.6°C- $^{-}$2.3°C (NCDC/NOAA, 2008)	28.2 °C- $^{-}$11.1°C (NCDC/NOAA, 2008)	26.8°C- $^{-}$11.1°C (NCDC/NOAA, 2008)
Annual Precipitation	115.7 cm (NCDC/NOAA, 2008)	160.6 cm (NCDC/NOAA, 2008)	147.2 cm (NCDC/NOAA, 2008)	103.1 cm (NCDC/NOAA, 2008)
Soils	well-drained loamy sand (http://nesoil.com/images/eldridge.htm)	sandy loam (Zen et al., 1983; Scanu, 1988)	well-drained sandy loam (NRCS, 2010)	well-drained loam (NRCS, 2010)
Surficial Geology	Silty laustrine deposits; clay or mud/silt (http://nesoil.com/images/eldridge.htm)	Granite, gneiss and schist (Zen et al., 1983; Scanu, 1988)	Basal till, quartzite, pelitic schist, metasedimentary rock and granite (NRCS, 2010)	Limestone and phyllite (NRCS, 2010)
Dominant Tree Species	- *Fagus grandifolia* - *Quercus alba* - *Quercus velutina*	- *Pinus strobus* - *Acer rubrum* - *Quercus rubra* - *Betula lenta* - *Tsuga canadensis*	- *Acer rubrum* - *Pinus strobus* - *Pinus resinosa* - *Quercus rubra* - *Fagus grandifolia* - *Tsuga canadensis*	- *Acer saccharum* - *Acer rubrum* - *Fagus grandifolia*
Dominant Forest Type	Oak-Woodland (The Nature Conservancy, 2010)	Hardwood-White Pine-Hemlock (Braun, 1950)	Beech-Oak and Mixed Pine (The Nature Conservancy, 2010)	Mixed Hardwood Coniferous Forest (Vermont Fish and Wildlife, 2008)



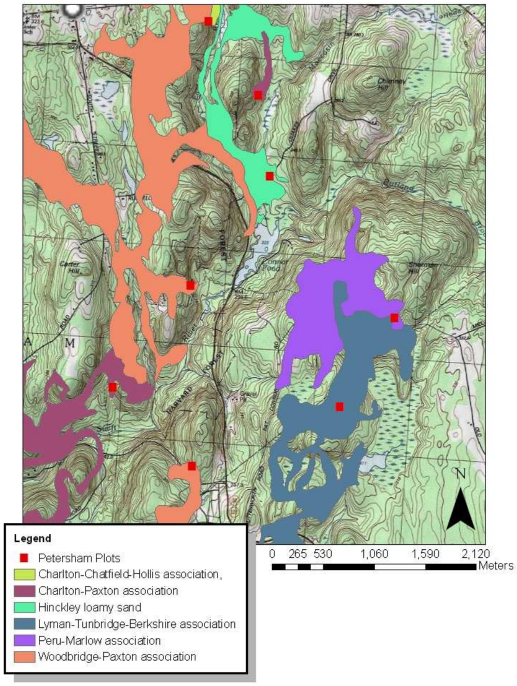
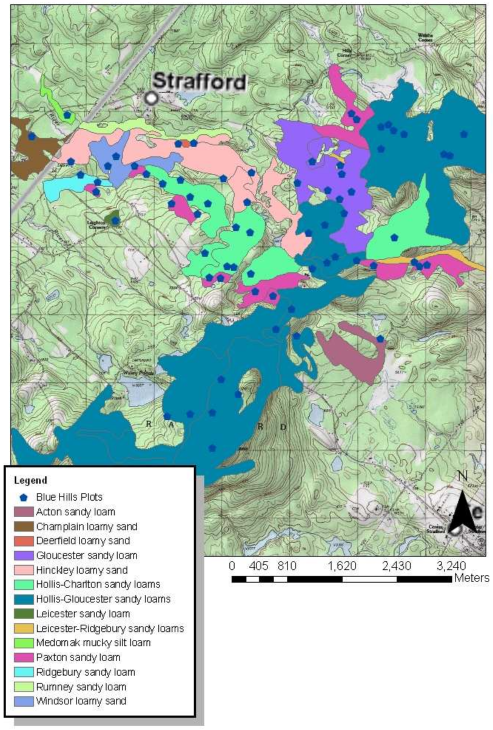


Figure 2: Soil types in Martha’s Vineyard, MA. Points designate plots where sampling occurred.

Figure 3: Soil types in Martha’s Petersham, MA. Points designate plots where sampling occurred.



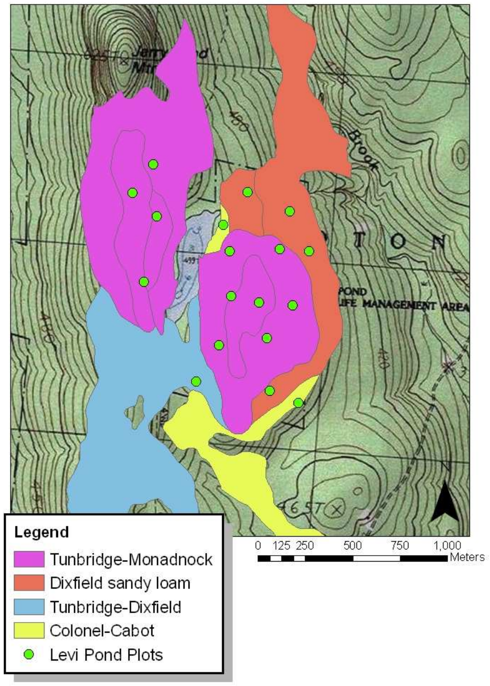


Figure 4: Soil types in the Blue Hills region of NH. Points designate plots where sampling occurred.

Figure 5: Soil types in the Levi Pond region of VT. Points designate plots where sampling occurred.

3.2 Plot set-up and location

During the summers of 2008 and 2009 plots were established and sampled in the Martha's Vineyard, MA (n=20), Petersham, MA (n=9), the Blue Hills region of NH (n=70) and the Levi Pond region of VT (n=18). Plots were randomly generated using ArcGIS with the exception of two plots in the Levi Pond region which were deliberately placed in hemlock stands. Plots that fell within wetlands or rocky summits were excluded. Any plots that intersected with trails, rivers or streams or were less than 20 meters from a road were relocated to 20 meters away from the obstruction and remarked.

Plots were located using a hand held Garmin E-Trex H and a compass. The GIS-generated points were marked with a steel post and labeled. The plot boundaries were measured out 20 meters to west and 20 meters to the south from the initial GIS-generated point and connected to form a 400meter^2 plot. Three more posts were hammered into the ground to mark the north, east and west points of the plot. At each corner a photograph was taken from the post looking into the plot.

Eight soil samples were collected from randomly selected locations around the plot to account for heterogeneity in the soil; samples were collected with a 10 cm soil core. Large decaying leaves, twigs and stones were removed from each sample and the eight samples were combined in one bag. From the highest point of the plot the landscape position was classified as either basin, low-slope, mid-slope, upper-slope, hilltop or flat upland. Slope in degrees and aspect were both quantified using a compass. For all four regions, compasses were set at 17° west of north declination.

3.3 Disturbance history

Visible cultural features were noted both within the plot and the area approximately 50 meters around the plot. These features included proximity to roads, trails, cemeteries, foundations and stone walls.

Any evidence of disturbance or disease within the plot or the 10-20 meters around the plot was recorded. Disturbances included the presence of many dead trees, woody debris, pits and mounds, fire scars, tree wounds, herbivory, multi-stemmed hardwoods or tree stumps. Diseases such as beech bark disease, hemlock woolly adelgid, ash decline and the fall cankerworm were also noted.

3.4 Vegetation sampling

A census was taken for all vascular herbs, fern and fern allies, shrubs (shorter than 1.4m), and seedlings found within each 20 x 20 meter plot. Species were identified in the field using Cobb et al. (2005), Petrides (1972) and Newcomb (1989). Species not identified in the field were collected and brought back to the lab. Grass, sedge and rush species were identified only to genus. Cover class was estimated using a six point Braun-Blanquet cover scale for all understory species (less than 1.4 meters tall) and rocks (P ＜1%, 1= 1-5%, 2=5-25%, 3=25-50%, 4=50-75% and 5=75-100%)(Braun-Blanquet, 1965). All woody species (including shrubs and trees) taller than 1.4 meters were identified and measured for the diameter at breast height (DBH). Multiple stemmed trees were measured by individual stems but grouped together. Standing deadwood was identified to species when possible and measured. Cut stumps were identified by species or as either hardwood or softwood and their diameter was measured.

3.5 Soil Analysis

Soil samples were sent to Brookside Laboratories, New Knoxville, OH, USA for all analyses. Samples were air-dried and ground to pass through a 2-mm sieve; combustible organic matter (%) was determined following the methods in Schulte and Hopkins (1996). The total exchange capacity (meq/100g) was determined using summation methods follow Ross, 1995. pH was measured as the 1:1 ratio in water (McLean, 1982). Soil texture or the percentage of sand, silt and clay in the soil was determined using the hydrometer method. Bray II P was measured following Bray and Kurtz, 1945. The Mehlick III methods was used to determine extractable S, Ca, Mg, Na, B, Fe, Mn, Cu, Zn, Al, and P (Melich,1984). Extractable Zn, Mn, Fe, and Cu were determined using methods the DTPA method from Linsay and Norvell (1978). Total combustible carbon and nitrogen were calculated using methods from Nelson and Sommers (1996). Electrical conductivity-soluble salts, cations and minor nutrients were determined according to Soil, Plant, and Water Reference Methods for the Western Regions (2003).

3.6 Data Analysis

Data was entered and organized in Microsoft excel. All woody stems ($\geq$ 1.4m tall) were distinguished as either trees (DBH $\geq$ 5.0 cm) or saplings (DBH $<$ 5.0 cm). Density was calculated for saplings and trees as the number of stems per hectare. Tree and sapling relative abundance is determined as the sum of stems per species divided by the total number of stems for all species in a plot. We determined the basal area for each tree and sapling using the following equation:

$$\frac{(3.1415*(DBHcm/2))^2}{1000}$$

Relative basal area quantifies the contribution that each species makes to the stand structure relative to other species in each plot. The basal area for each individual tree or sapling was converted to relative basal area by summing the total basal area of each species per plot and multiplying this value by:

$$\frac{10000ha}{400m^2}$$

Relative importance values for canopy trees and tree saplings were calculated by averaging relative basal area and the relative abundance for each species by plot. Frequency for trees, saplings and understory species is the percentage of the total number of plots in which that species was sighted; frequency was calculated individually for Martha's Vineyard, Petersham, Blue Hills, and Levi Pond; and for all four regions combined.

Forest type categories were created based on the relative basal area of each tree species taller than 1.4 meters in each plot. By sequentially adding the basal area of the tree species with the highest relative basal area in each plot until I reached a sum of 0.80 for the cumulative basal area per plot I generated forest type designations. These specific categories were broadened into more general natural communities that could be used to describe several plots. The "northern hardwood" designation may include the following hardwood species; *Acer rubrum, Quercus rubra, Betula alleghaniensis, Betula papyrifera,* or *Betula lenta* . The "rich northern hardwood" forest type is distinguished from "northern hardwoods" by the presence of *Acer saccharum* and/or *Fraxinus americana.* Forest types with "pine" in the designation may include both *Pinus resinous* and *Pinus strobus*. The 12 forest type categories created include: Hemlock-Beech, Hemlock-Northern Hardwoods, Hemlock-Pine, Northern Hardwoods, Oak, Oak-Beech, Pine, Pine-Fir, Red Spruce, Rich Northern Hardwoods, Spruce-Fir, and White Pine-Northern Hardwoods.

Linear regression was used to identify predictors of understory species richness (Minitab solutions 15, 2006). Potential predictors tested included C/N ratio in the soil, total tree basal area, *T. canadensis* basal area, *P. strobus* basal area, *P. resinosa* basal area, and *F. grandifolia* basal area. Because the distribution of these variables was differed by region, all regressions were run for each region independently. Soil variables were compared between regions using the Kruskal-Wallis test. A non-parametric approach was used to account for the violation of both normality (Kolmogorov-Smirnov statistic) and homogeneity of variance (Bartlett's test or Levene's test).

Species area curves were generated in PC-ORD as a way to gauge the adequacy of the sample size in each region in its representation of the regional species richness (McCune and Medford, 1999). This measure was a particular importance in our study because the number of plots surveyed in each region ranged considerably from 70 plots in the Blue Hills region to 9 plots in Petersham.

Two-way cluster analysis was used to produce a hierarchical classification of the data set by row (plot) and by column (species). Two-way cluster analysis was used over TWINSPAN to account for more than one underlying gradient in species composition and to avoid issues that may arise through the use of pseudospecies (McCune and Medford, 1999). This was done in PC-ORD using Sorenson (Bray and Curtis) distance. This distance measure was selected over other metrics such as Euclidean distance because Sorenson distance retains sensitivity in heterogeneous data sets and gives less weight to outliers. This feature is important to the present dataset because as a result of the small sample size in Martha's Vineyard, Petersham and Levi Pond, a majority of species were recorded in fewer than five plots and as a result would be analyzed as outlier data. Additionally, McCune and Medford recommend the use of Sorenson distance over Euclidean distance because they believe it has a "better" application to ecological community data (McCune and Medford, 1999). Group average was the linkage method used; this method was selected based on its compatibility with the Sorenson distance and because unlike other linkage methods, this metric is based on information about all inter-cluster pairs (not just the nearest or furthest clusters as in nearest and furthest neighbor methods) (Garson, 2010). As recommended by McCune and Medford, the matrix was revitalized by columns so that associations among species rather than among plots were emphasized in the final dendrogram (McCune and Medford, 1999).

Non-metric multidimensional scaling (NMDS; McCune and Medford, 1999) was used to identify environmental variables influencing the species composition in all four regions. NMDS was chosen because this ordination technique has fewer assumptions and can accommodate "non-normal, discontinuous" data (McCune and Medford, 1999). Additionally, NMDS is known to be one of the most robust ordination methods and given that data came from four different regions a robust method was necessary to account for this important underlying gradient. The "slow-and-thorough" autopilot mode was used; this mode runs the ordination 250 times with real data and 250 times with randomized data in order to determine the "optimal ordination solution" (McCune and Medford, 1999). The environmental variables entered into ordination included, sand%, silt%, clay%, TEC, pH, organic matter, S (mg/kg), P (mg/kg), Bray II P (mg/kg), Ca (mg/kg), K (mg/kg), Na (mg/kg), Ca (%), Mg (%), K(%), Na (%), other bases (%), H (%), Fe (mg/kg), Mn (mg/kg), Cu (mg/kg), Zn (mg/kg), Al (mg/kg), Carbon (%), Nitrogen (%), C:N ratio, Forest type, slope and aspect. Aspect for each plot was categorized numerically as, 1)North (338°-23°), 2)Northeast (24°-68°), 3)East (69°-113°), 4)Southeast (114°-158°), 5)South (159°-203°), 6)Southwest (204°-248°), 7)West (249°-293°) or 8)Northwest (294°-338°). The Pearson and Kendall correlations (r^2) were used to score the relationship between each factor and the axes.

4. Results

4.1 Vegetation Characteristics

A total of 177 understory species were identified across the 117 plots in the four regions sampled. This value includes seedlings, ferns and fern allies, herbs, grammoids, vines, and shrubs/saplings $\leq$ 1.4m tall. The four regions possessed a total of 44 tree species (DBH $\geq$5.0cm). Herbs constituted the highest portion of understory species richness with 71 species. Shrubs were the next richest group with 46 species; ferns also contributed to understory richness with a total of 19 different ferns identified. Only three different vine species were recorded and six different lycopods. This data set also includes seven grammoid classifications however, due to time and identification constraints most of the grass and sedge species observed were not identified to species but grouped generally by genus (For a full list of species presence of absence by region refer to Appendix II.)

4.2. Natural Community Types

Based on two-way cluster analysis for each region there are several unique species assemblages or associations that can be distinguished within each of the four regions. Species lists for each assemblage were generated based on the results of two-way dendrograms (Table 5). These assemblages are distinct for each region but some assemblages closely resemble to the species typical to another region or another assemblage in a different region. The assemblages for each region are outlined in the table below (Table 5) and the corresponding dendrograms (Fig. 6,7,8,9).

Table 5: Species assemblages in Martha's Vineyard, Petersham, Blue Hills, and Levi Pond. Assemblages were created based on the results of Two-way Cluster Analysis.

Martha's Vineyard		***Petersham***		***Blue Hills***		***Levi Pond***	
MV1	*S. albidum,* *F. grandifolia* *I. opaca* *V. angustifolium* *A. rubrum* *A. nudicaulis* *T. borealis*	***SP1***	*A. rubrum* *Q. rubrum* *T. canadense* *Aster sp.* *P. virginianum*	***BHF1***	*P. rubens* *A. rubrum* *Q. rubra* *T. borealis* *M. canadense* *L. obscurum* *P. strobus* *F. grandifolia* *T. canadensis* *B. alleghensis* *V. angustifolium* *A. nudicaulis* *M. repens* *P. aquilinum* *P. biflorum*	***LP1***	*P. rubens* *P. serotina* *F. americanus* *A. nudicaulis* *Dryopteris spp.* *M. canadense*
MV2	*R viscosum* *V. corybosum* *V. dentatum* *Poa spp.*	***SP2***	*F. grandifolia* *V. acerfolia* *P. aquilinum* *G. procumbens* *H. virginiana*	***BHF2***	*J. communis* *L. tristachyum* *R. hispidus* *E. repens* *A. arborea*	***LP2***	*A. rubrum* *F. grandifolia* *T. borealis* *M. uniflora* *L. obscurum* *C. trifolia*
MV3	*S. rugoso* *T. radicans* *R. alleghensis*	***SP3***	*Q. alba* *V. corybosum* *O. virginiana* *Crataegus sp.* *M. uniflora* *C. acaule*	***BHF3***	*A. pensylvanicum* *V. lantoides* *L. lucidium* *T. undulatum* *D. carthusiana* *C. borealis*	***LP3***	*A. balsamea* *V. lantoides* *C. borealis* *L. clavatum* *L. contemplatum* *R. occidentalis* *A. Arborea* *E. caroliniana*
MV4	*M. canadense* *D. punctilobula* *T. noveboracensis* *G. procumbens* *M. virginiana* *Lactuca sp.* *C. cornuta* *C. umbellata*	***SP4***	*A. saccharum* *A. triphyllum* *A. filix-femina* *P. biflorum* *P. quinquefolia* *T. americana* *D. marginalis* *Viola spp.* *Sorbus spp.* *Rubus spp.* *T. erectum* *A. spicatum* *H. americana* *A. filix-femina*	***BHF4***	*B. lenta* *P. virginianum* *G. procumbens* *B. papyrifera* *Goodyera spp.*	***LP4***	*Q. rubrum* *T. cordifolia* *O. sensibilis* *T. canadensis* *T. noveboracensis* *O. claytonia*

MV5		***SP5***		***BHF5***		***LP5***	
	E. hieracifolia		*A. pensylvanica*		*B. populifolia*		*G. procumbens*
	M. pensylvanica		*P. serotina*		*P. resinosa*		*Habernia spp.*
	E. angustifolium		*M. canadenese*		*A. acuminatus*		*V. lantoides*
	H. radicata		*A. nudicaulis*		*C. umbellata*		*Oxalis sp.*
	G. septenrionale		*M. virginiana*		*P. rugelli*		*G. dryopteris*
	C. glabra				*P. asarfolia*		
MV6		***SP6***		***BHF6***		***LP6***	
	Q. velutina		*P. strobus*		*Viola spp.*		*B. alleghaniensis*
	B. lenta		*T. borealis*		*C. trifolia*		*D. punctilobula*
	Q. alba		*B. lenta*		*O. sensibilis*		*Aster spp.*
	G. baccatta		*V. angustifolia*		*Lycopus spp.*		
	A. arborea				*M. lineare*		
	G. frondosa						
				BHF7		***LP7***	
					P. serotina		*P. strobus*
					V. cassenoides		*P. biflorum*
					M. virginiana		*C. thalictroides*
					Carex spp.		*B. virginianum*
					L. clavatum		*A. rubra*
					C. acaule		*G. robertianum*
							P. acrostichoides
							S. amplexifolius
				BHF8		***LP8***	
					C. canadensis		*A. pensylvanicum*
					C. trifolia		*T. undulatum*
					O. claytonia		*M. virginiana*
					M. uniflora		*Viola spp.*
					H. virginiana		*A. triphyllum*
					Plantago spp.		*Poa spp.*

4.3 Regional and Environmental Influences on Understory Composition

In the NMDS ordination for all species and environmental variables, most of the variation is explained by Axis 1 which accounts for 59.6% of the variability in understory vegetation. This axis represents a gradient from high extractable iron and low extractable sulfur, potassium, aluminum and organic matter to low iron and high extractable sulfur, potassium aluminum and organic matter (Fig. 10). Axis 2 explains 24.1% of the variation. This axis ranges from high carbon-to-nitrogen ratio and extractable magnesium and low extractable manganese and zinc to low carbon-to-nitrogen ratio and extractable magnesium and high extractable manganese and zinc (Fig. 10). Combustible nitrogen, extractable calcium, and extractable sodium also factor into understory species composition (Fig. 10). The explanative power of each of the soil and environmental variables depicted in Figure 10 is indicated by the correlation coefficient listed in Table 6.

Table 6: Pearson and Kendall Correlations with ordination axes for factors influencing species composition in the understory. Variables in bold have significant correlation with either Axis 1 or 2.

Variable	**Correlation Coefficient Axis 1**	**Correlation Coefficient Axis 2**
Sand (%)	.015	.103
Silt (%)	.017	.064
Clay (%)	.000	.154
Total Exchange Capacity	.007	.130
pH	.141	.046
Organic Matter (%)	**.226**	.014
Sulfur (mg/kg)	**.192**	.085
Phosphorous (mg/kg)	.129	.068
Bray II P (mg/kg)	.063	.071
Magnesium (mg/kg)	.055	**.213**
Potassium (mg/kg)	**.179**	.092
Sodium (mg/kg)	**.230**	**.302**
Ca (%)	**.117**	**.182**
Boron (mg/kg)	.000	.000
Iron (mg/kg)	**.207**	.001
Manganese (mg/kg)	.034	**.342**
Copper (mg/kg)	.099	.009
Zinc (mg/kg)	.045	**.318**
Aluminum (mg/kg)	**.394**	.002
Carbon (%)	.130	.024
Nitrogen (%)	**.156**	**.145**
C:N ratio	.030	**.301**
Slope	.052	.017

The four regions are also distinguished by the grouping of plots from each region in NMDS; Martha's Vineyard plots are all clustered to the far right-hand side of the graph and Petersham, Blue Hills and Martha's Vineyard clustered into overlapping groups to the left (Fig. 11). The overlapping circles indicate Petersham plots with understory vegetation that resembles either the Blue Hills region or Levi Pond region.

4.4 Forest Structure

The density and size distribution of trees varies considerably by region. Martha's Vineyard had a visibly lower tree density and basal area than the other three regions on average (Table 7). Although the number and size of live tree stems in Martha's Vineyard is lower than in Petersham, Blue Hills and Levi Pond, this region also has the highest sapling density; only Levi Pond approaches the sapling density recorded at Martha's Vineyard.

Table 7: Average density and basal area for canopy trees (DBH$\geq$5.0cm) and saplings (DBH<5.0cm) in Martha's Vineyard, Petersham, Blue Hills and Levi Pond. Density is the number of stems per hectare.

Region	**Tree Density (Individuals/ha)**	**Tree Basal Area (m^2/ha)**	**Sapling Density (Individuals/ha)**	**Sapling Basal Area (m^2/ha)**
Martha's Vineyard	318.75	9.9	920.0	0.4
Petersham	856.3	46.9	602.5	0.2
Blue Hills	1085.1	33.3	465.2	0.5
Levi Pond	1011.1	40.5	905.3	0.4

This trade-off between canopy and sapling trees is reflected in the size distribution of woody species (taller than 1.4 m) as well (Fig. 12). The tapering curve illustrates a frequency to size trade off where the highest frequency is found in the smaller size classes and the lowest frequency is found in the largest size classes. In Petersham, Blue Hills and Levi Pond this taper stops at around 60 cm DBH, however the Martha's Vineyard curve trails off at about 40cm DBH. This region has a clear absence of trees in the larger size classes; the largest tree in Martha's Vineyard approaches a mere 48 cm DBH compared with 60 cm trees found in the regions of Levi Pond and Petersham.

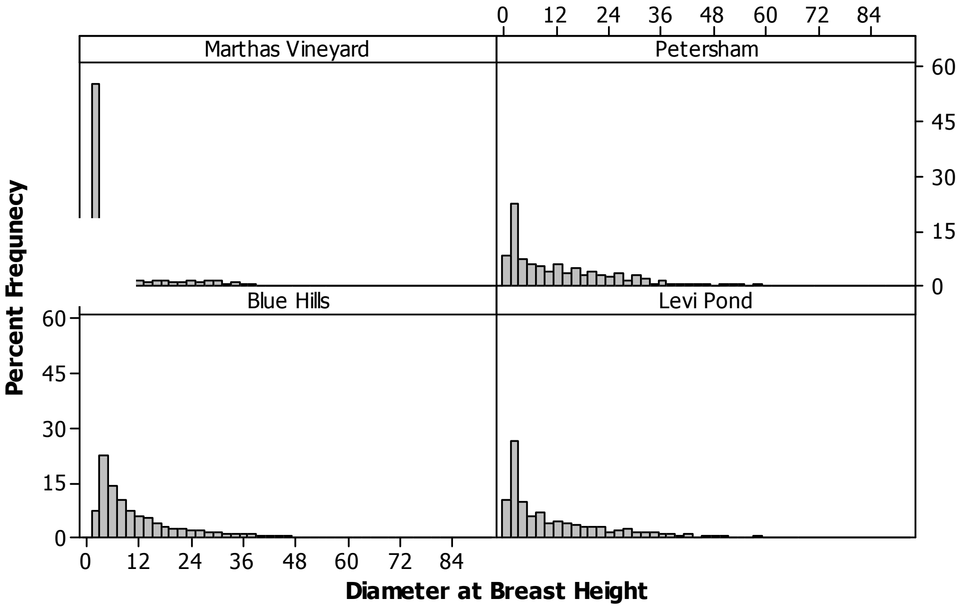


Figure 12: Diameter distribution of all woody stems (taller than 1.4m) in Martha's Vineyard, Petersham, Blue Hills and Levi Pond. The smallest size class has the highest frequency and frequency decreases as diameter increases.

The overall basal area of trees negatively influenced the understory species richness in the understory in the Blue Hills region (Fig. 13c). Basal area did not have a significant effect on the species richness in the understory in Martha's Vineyard, Petersham, Levi Pond (Fig. 13a,b,d).

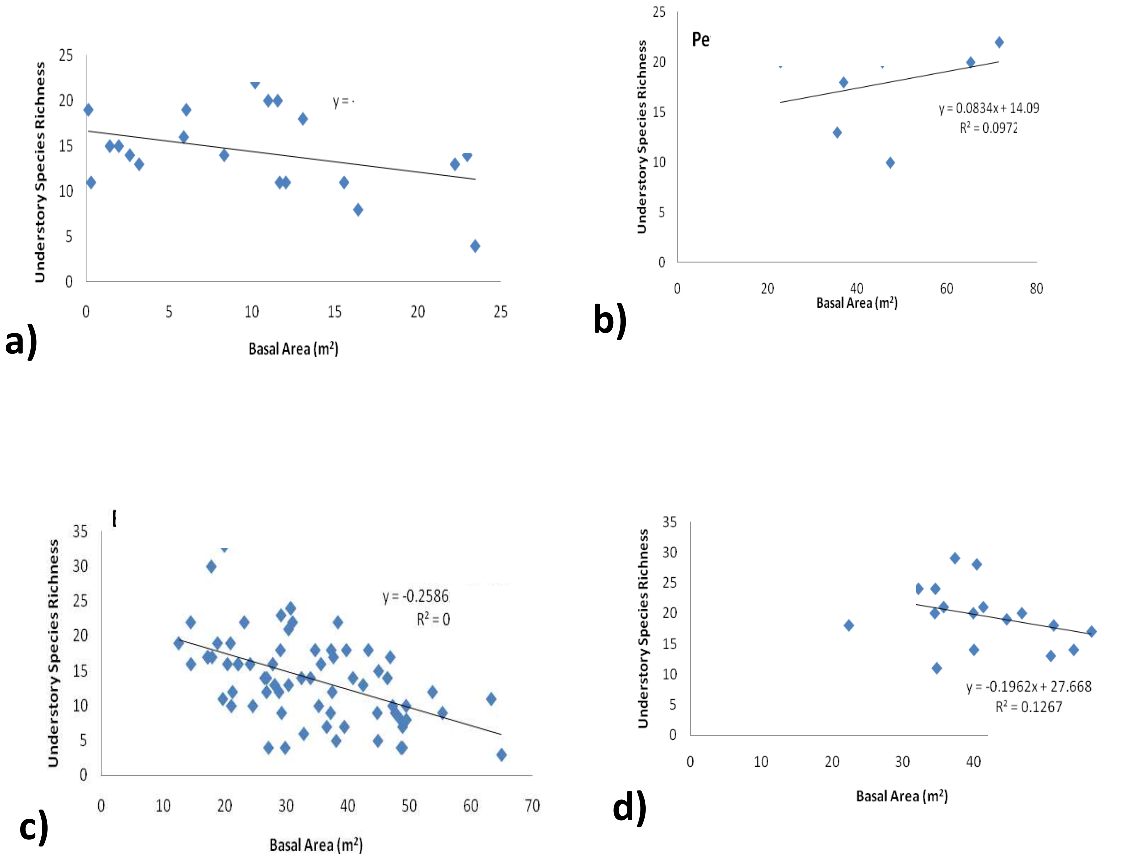


Figure 13 a-d: Correlation of basal area and understory richness in (a) Martha's Vineyard, (b) Petersham, (c) Blue Hills, and (d) Levi Pond. Only (c) Blue Hills has a significant negative relationship between tree basal area and the species richness in the understory (Linear regression; $p \leq 0.05$). However, the trendline in (a) Martha's Vineyard and (d) Levi Pond does indicate a slightly non-significant negative correlation between these two variables. Note that the scale of the Y axis varies by region.

4.5 Overstory Composition by Region

The composition of tree species in each region is a mix of generalist species that are found in all four regions and several species that are unique to one or two regions. Generalist species include *F. grandifolia*, *A. rubrum*, *Q. rubra*, *Prunus serotina* , *P. strobus*, and *T. Canadensis* (Figure 14). While these species are able to establish in three or four of the regions surveyed their frequency is variable within each region.

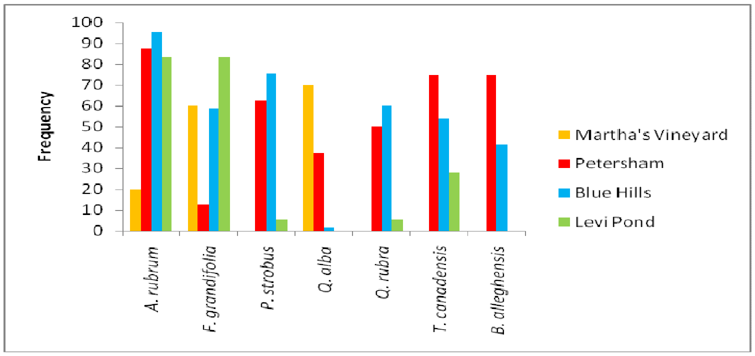


Figure 14: Frequency of most common canopy trees in each of the four regions. *A. rubrum* is very frequent in all regions with the exception of Martha's Vineyard. Refer to Appendix II for a full list of species names and abbreviations.

The four regions can also be distinguished from one another by comparing the relative importance values for individual tree species. Martha's Vineyard represents the most distinct of the four regions with *Q. alba*, *F. grandifolia* and *Q. velutina* comprising the top three most important trees (Fig. 15). Levi Pond also possesses a unique canopy composition with *A. saccharum* and *A. rubrum* filling in as the most important trees in this region. Like Levi Pond, Petersham and Blue Hills both have a high relative importance value for *A. rubrum*. However, in these two regions *P. strobus* and *T. canadensis* replace *A. saccharum* as the most important trees. While Petersham and Blue Hills closely resemble reach other in terms of canopy tree relative importance; the high relative importance of *B. lenta* in Petersham distinguishes between the two regions.

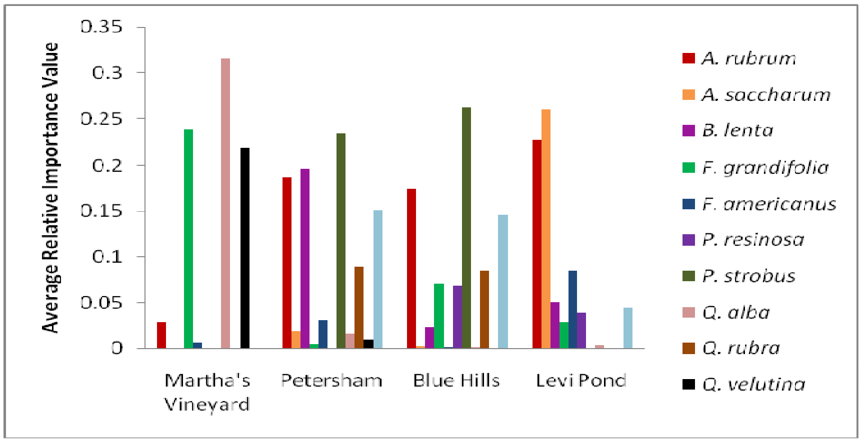


Figure 15: Relative importance of canopy trees for the four regions surveyed. Only species whose cumulative RIV for all four region exceeded 0.1 were listed. Refer to Appendix II for a full list of species names and abbreviations.

In addition to sharing many of the same important tree species, Petersham and Blue Hills also have the most overlap of the four regions in terms of forest type (Fig. 16). For both of these regions, Northern Hardwoods (n=4 in Petersham; n=17 in Blue Hills) is the dominant forest type with Hemlock-Northern-Hardwoods and White Pine-Northern Hardwood falling closely in second. In contrast, Levi Pond is dominated by the Rich Northern Hardwoods forest type (n=12). Martha's Vineyard stands out as unique since the only forest types present here are Oak (n=9) and Oak-Beech (n=11).

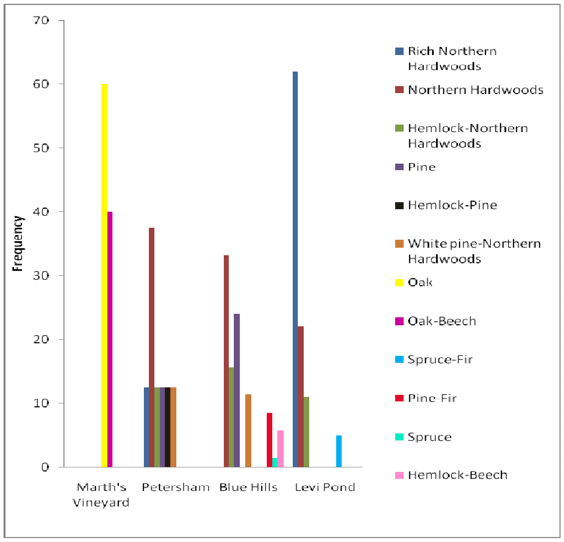


Figure 16: Forest type frequency in Martha's Vineyard, Petersham, Blue Hills, and Levi Pond.

The overstory composition was also a determinant of understory species richness. Blue Hills plots with higher *Tsuga Canadensis* basal area values supported significantly lower species richness than those with lower *T. canadensis* basal area (Fig. 17 b). This trend was not found to be significant in Petersham or Levi Pond (Fig. 17a, c).

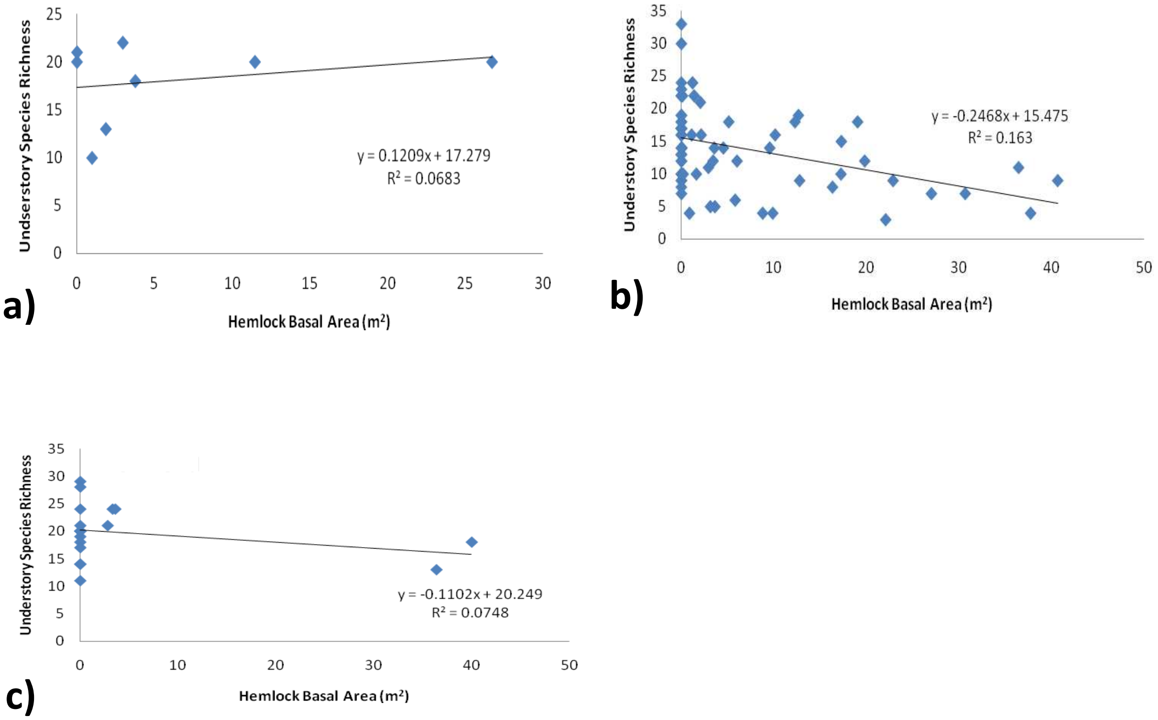


Figure 17a-c: Correlation between *T. canadensis* basal area and understory richness in (a) Petersham, (b) Blue Hills, and (c) Levi Pond. Only (c) Blue Hills has a significant negative relationship between *T. canadensis* basal area and the species richness in the understory (Linear regression; $p \leq 0.05$). The trendline in (d) Levi Pond does indicate a slightly non-significant negative correlation between these two variables. Martha's Vineyard was not included in this analysis because *T. canadensis* was not present in any of the sampled plots in this region. Note that the scale of the Y axis varies by region.

Neither the basal area of pine (*P. strobus* and *P. resinosa)* nor the basal area of beech (*F. grandifolia)* had any influence on species richness. Regression of pine to species richness was not applied to Martha's Vineyard because there is no pine basal area in this region and Petersham did not have sufficient beech basal area to test for a regression between beech basal area and species richness.

4.6 Soils Variables by Region

The soil conditions within Martha's Vineyard, Petersham, Blue Hills and Levi Pond are variable among the four regions. In most cases, there was a substantial amount of variation in soil conditions within the same region on a plot by plot basis; however the variation among regions was even greater. Organic matter was significantly higher in Petersham, Blue Hills and Levi Pond compared with the low organic matter values recorded on Martha’s Vineyard (Fig. 18).

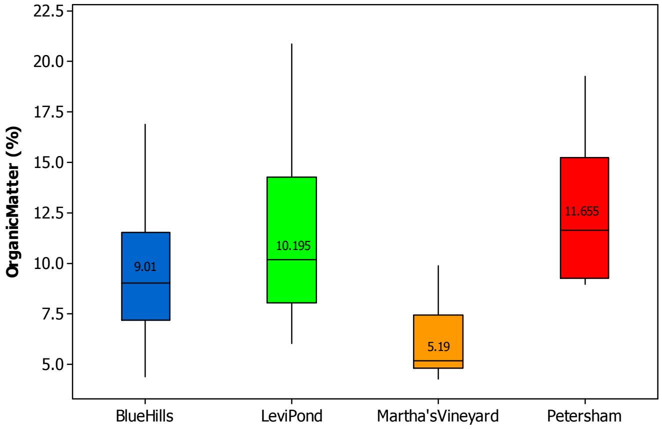


Figure 18: The distribution of percentage of organic matter is different within the four regions sampled. (Kruskal –Wallis; ($p \leq 0.05$). Numbers inside boxes represent the median value for each region; boxes represent the median confidence interval.

The C/N ratio in the soil was also significantly different regions. Martha ’s Vineyard had higher C/N ratio values than Levi Pond and Petersham (Fig. 19).

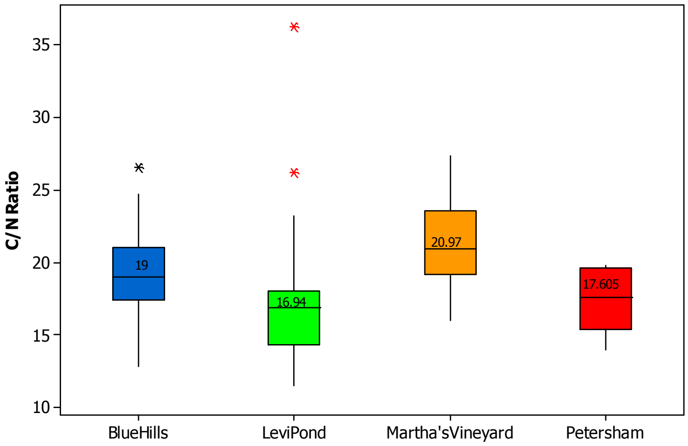


Figure 19: Distribution of the C/N ratio was different among the four regions (Kruskal-Wallis; $p \leq 0.05$). Numbers inside boxes represent the median value for each region; boxes represent the median confidence interval.. * marks outlier data.

The C/N ratio is also a predictor of understory species richness. In Blue Hills C/N ratio had a significant negative relationship with species richness in the understory (Fig. 20c). Regression analysis for the C/N ratio and understory species richness in Martha's Vineyard, Petersham or Levi Pond was not significant (Fig. 20 a, b, d).

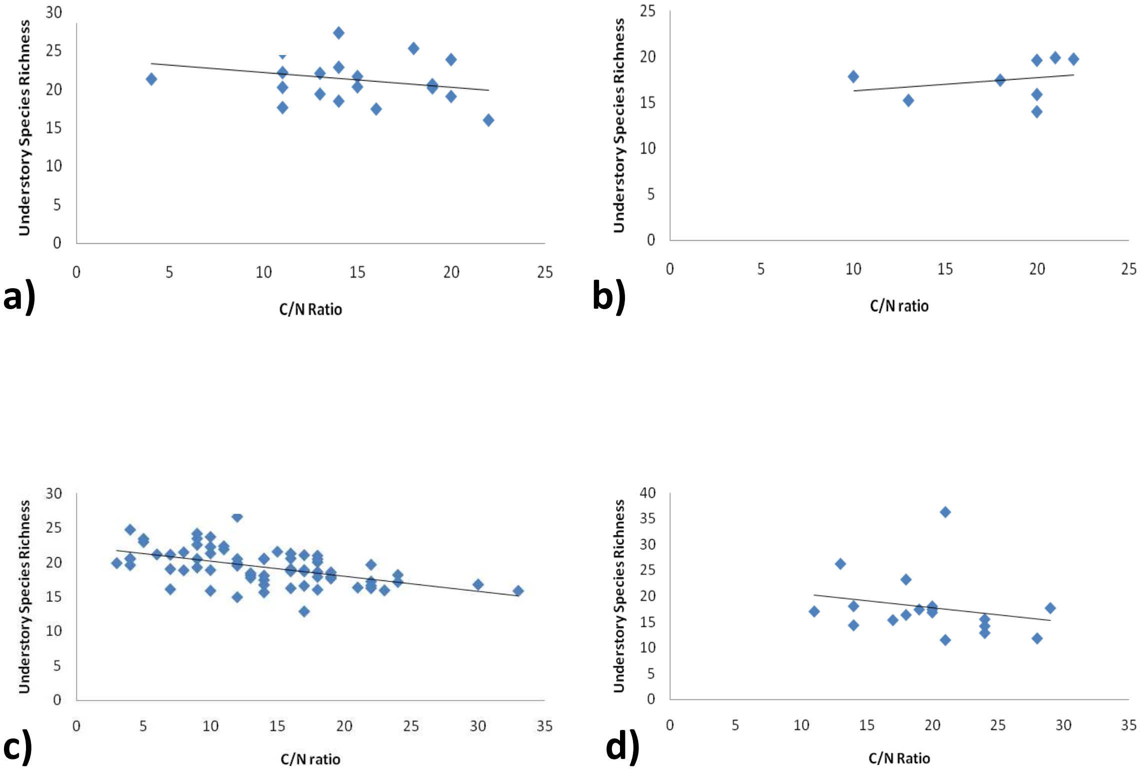
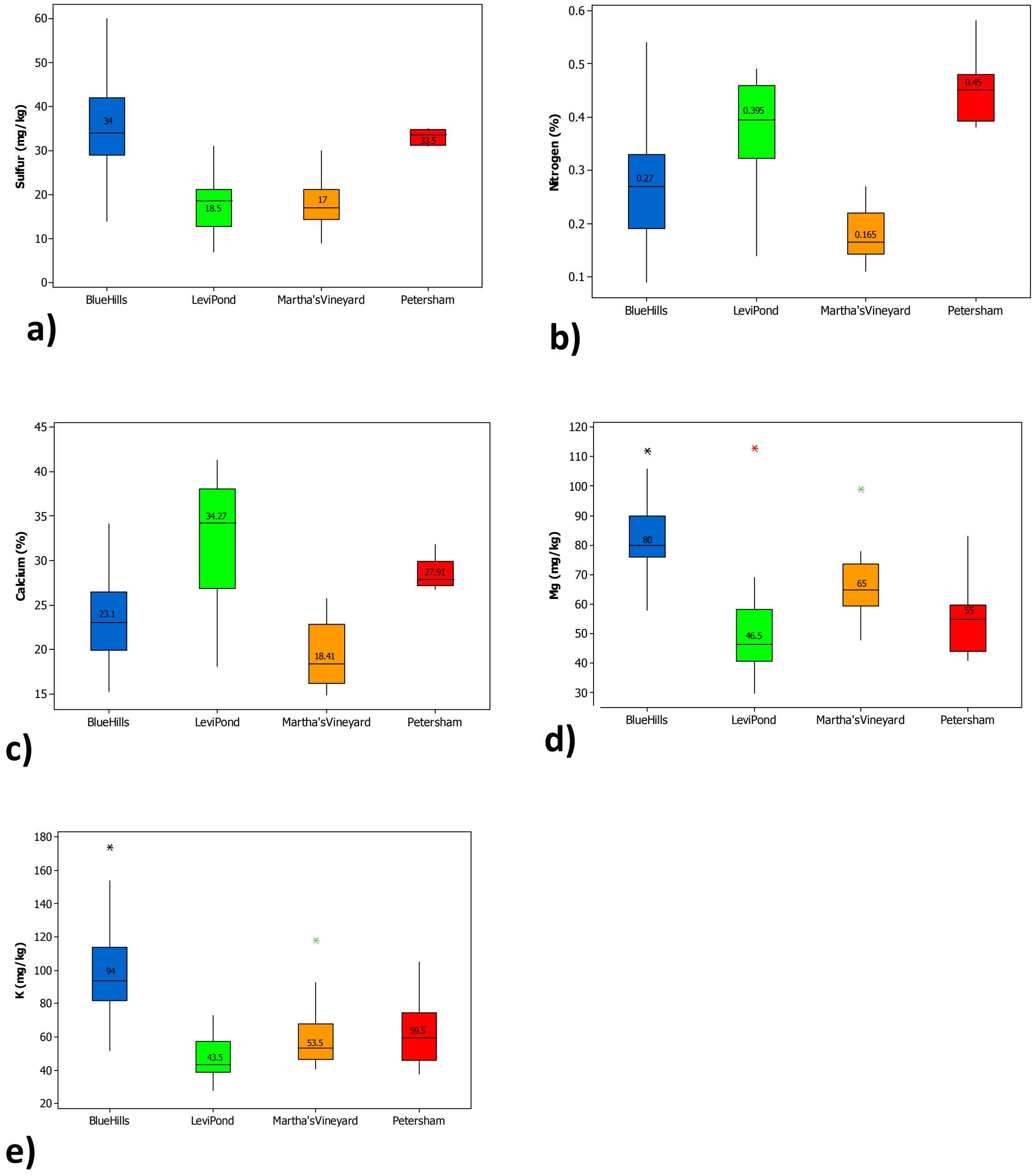


Figure 20 a-d: Correalation between C/N ratio and understory richness in (a) Martha's Vineyard, (b) Petersham, (c) Blue Hills, and (d) Levi Pond. Only (c) Blue Hills has a significant negative relationship between C/N ratio and the species richness in the understory (Linear regression; $p \leq 0.05$). The trendline in (a) Martha's Vineyard and (d) Levi Pond does indicate a slightly non-significant negative correlation between these two variables. Note that the scale of the Y axis varies by region.

The four regions were variable in the extractable macronutrients sulfur (mg/kg), potassium (mg/kg), magnesium (mg/kg), nitrogen (%), and calcium (%). Sulfur concentration was highest in the Blue Hills and Petersham region and lowest in Levi Pond and Martha's Vineyard (Fig. 21a). The percent of extractable nitrogen and calcium were both higher in Levi Pond and Petersham and lower in Blue Hills and Martha's Vineyard (Fig. 21 b,c). Both extractable magnesium and potassium were highest in the Blue Hills region (Fig. 21 d,e)



Figures 21a-e: Distribution varied among the four regions in the amount of extractable macro-nutrients (a)sulfur, (b) nitrogen, (c) calcium, (d) magnesium, (e) potassium. (Kruskal-wallis; $p \leq 0.05$) Numbers inside boxes represent the median value for each region; boxes represent the median confidence interval. Note that Y axis scales are different for each graph. *marks outlier data.

The distribution of extractable soil micronutrients were also different among the regions sampled. Zinc is highest in Levi Pond especially compared with the Blue Hills and Martha’s Vineyard zinc distributions (Fig. 22a). Both Levi Pond and Petersham have higher manganese values than Blue Hills and Martha’s Vineyard (Fig. 22b). Martha’s Vineyard and Petersham both have higher iron on average than Blue Hills and Levi Pond (Fig. 22c).

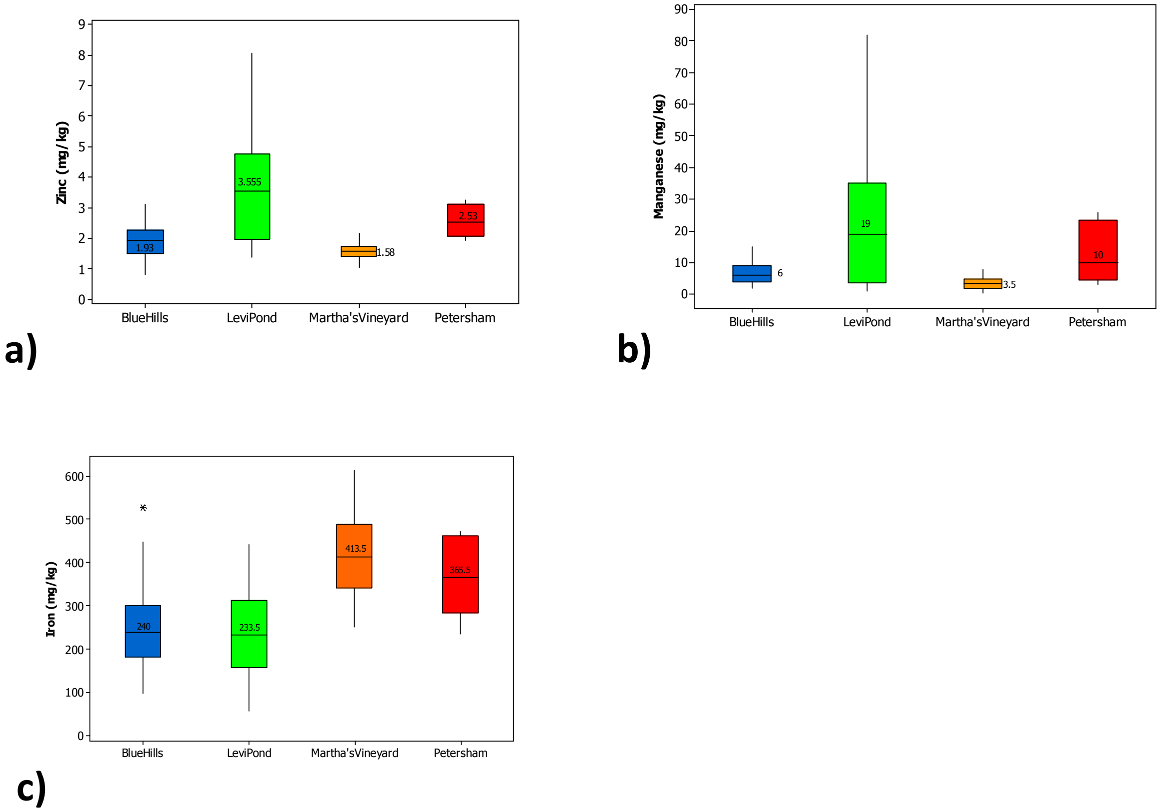


Figure 22a-c: The distribution of the micronutrients (a) zinc, (b) manganese and (c) iron in the soil were also variable among regions (Kruskal Wallis; p$\leq$0.05). Numbers inside boxes represent the median value for each region; boxes represent the median confidence interval. Note that Y axis scales are different for each graph. *marks outlier data.

The amount of aluminum and sodium is also different depending on region. Aluminum is higher in both Blue Hills and Petersham and lowest in Martha’s Vineyard

(Fig. 23). Extractable sodium is notably higher in Blue Hills than in the other three regions (Fig. 24).

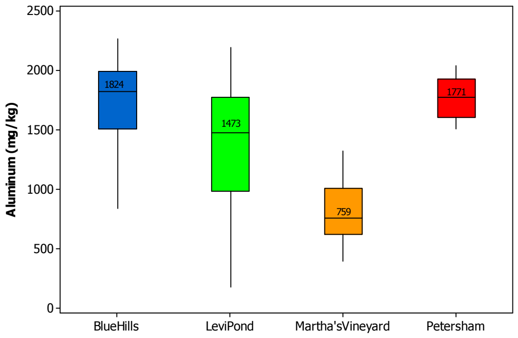


Figure 23: Distribution of aluminum (mg/kg) varied among regions (Kruskal-Wallis; p≤0.05). Numbers inside boxes represent the median value for each region; boxes represent the median confidence interval.

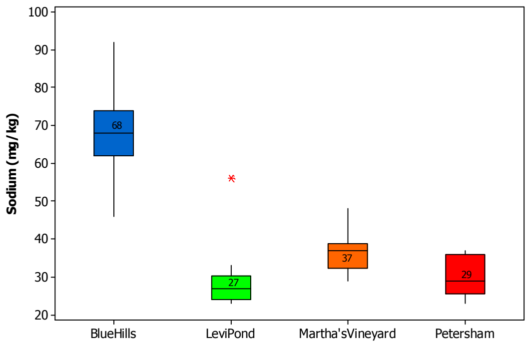


Figure 24: Distribution of sodium (mg/kg) varied among regions (Kruskal-Wallis; p≤0.05). Numbers inside boxes represent the median value for each region; boxes represent the median confidence interval. *marks outlier data.

4.7 Rare and Invasive/Weedy Species

While all four regions did possess non-native, weedy species; a higher number of these species were sighted in Martha's Vineyard and Blue Hills than at Petersham and Levi Pond (Table 8).

Table 8: Weedy or invasive species by region. A random subset of Blue Hills plots were selected for analysis so that differences in sample size would not skew the results (USDA Plant Database).

Species	**Martha's Vineyard n=20**	**Petersham n=9**	**Blue Hills n=20**	**Levi Pond n=18**
Rubus idaeaus			X	
Plantago rugelii			X	
Epigaea repens	X		X	
Hypochoeris radicata	X			
Epilobium angustifolium	X			
Chamerion angustifolium	X			
Geranium robertianum				X
Parthenocissus quinquefolia	X	X		
Rubus fruiticosus			X	
Total	**5**	**1**	**4**	**1**

Rare and endangered plants were also identified in Martha's Vineyard, Blue Hills and Levi Pond (Table 9). Martha's Vineyard recorded the highest number of rare and threatened plants but both Blue Hills and Levi Pond follow closely behind.

Table 9: Rare and threatened species by region. A random subset of Blue Hills plots were selected for analysis so that differences in sample size would not skew the results (USDA Plant Database)

Species	**Martha's Vineyard n=20**	**Petersham n=9**	**Blue Hills n=20**	**Levi Pond n=18**
Cornus florida				X
Polygonatum biflorum			X	
Pyrola asarifolia	X		X	
Galium septenrionale	X			
Sorbus decora				X
Rhododendron viscosum	X			
Total	**3**	**0**	**2**	**2**

5. Discussion

5.1 Region

Region is the overarching and most powerful variable influencing species composition in the New England forest, (Fig. 6; Fig. 7). While there does exist some degree of overlap in terms of composition and environmental features from region to region, even a non-ecologist could distinguish between the sandy and dry shrub-covered plots of Martha's Vineyard and the mesic, fern-rich plots of Levi Pond (Fig. 25). These regional differences in the forested landscape are the result of many different underlying variables, which in turn determine the understory species composition and species richness we observe.

Figure 25: Visual comparison between the Martha's Vineyard and Levi Pond; plots on Martha's Vineyard can be easily distinguished by relatively open canopy and abundance of low growing shrubs. In contrast, the region of Levi Pond can be characterized by a well developed canopy and abundant herb layer in the understory.

Biological distance decay describes the changes in vegetation moving across a regional or spatial gradient. This decrease in species similarity with increasing distance is explained by two primary hypotheses; one is that as the distance increases, environmental similarity diminishes (Nekola and White, 1999). The other hypothesis is that distance limits dispersal and consequently, the movement of species across a landscape (Nekola and White, 1999). Because the present study is focused more on environmental variables and regional gradients than plant phenology and reproduction, only the first hypothesis is explored in detail. Environmental similarity between regions is judged in terms of climate, forest structure, overstory composition, soil characteristics and disturbance history.

5.2 Species assemblages

The most obvious example of biological distance decay is evident in the species assemblages generated by the present study (Table 5). Two-way indicator analysis for Martha's Vineyard (Fig. 6), Petersham (Fig. 7), Blue Hills (Fig. 8), and Levi Pond (Fig.

9) resulted in unique species assemblages which reflect the diminishing similarity in species composition with increasing distance.

At the same time that these unique assemblages exist within each region, our observations negate Nekola and White's (1999) second hypothesis that species differences are a response to limited dispersal. On the contrary, a comparison of species assemblages BHF1 with LP1 and LP2 makes it clear that species such as *P. rubens, A. rubrum, T. borealis, M. canadense F. grandifolia,* and *Aralia nudicaulis* are able to disperse across great distances, including the 230 kilometers between the Blue Hills and Levi Pond region.

The results of two-way cluster analysis also illuminate the some of the similarities that emerge between species assemblages in different regions. For example, species assemblage SP3 vaguely resembles some of the shrubby species found in the sandier soils of Martha's Vineyard (Table 5). This suggests that the SP3 assemblage fell on an atypically dry and sandy area of Petersham where the environmental conditions and underlying variables are similar to those we might find in Martha's Vineyard. The species assemblages BHF6 and SP4 both share many of the species with a preference for the moist, nutrient rich soils that distinguish Levi Pond (Table 5). This overlap in species composition among regions suggests that where underlying variables and environmental conditions converge to create similar conditions in different regions, the same assemblages of species are able to persist.

5.3 Climate

One important gage of environmental similarity is climate. This variable may be described in terms of annual precipitation and average monthly temperatures. Climate has been shown to influence the range and abundance of canopy species (Oswald et al. 2007; Nekola and White, 1999); however few works have focused explicitly on the response of understory species to climate. Oswald et al. (2007) mapped vegetation transitions across southern New England and found that shifts in the major tree species were largely a response to climate (Fig. 26).

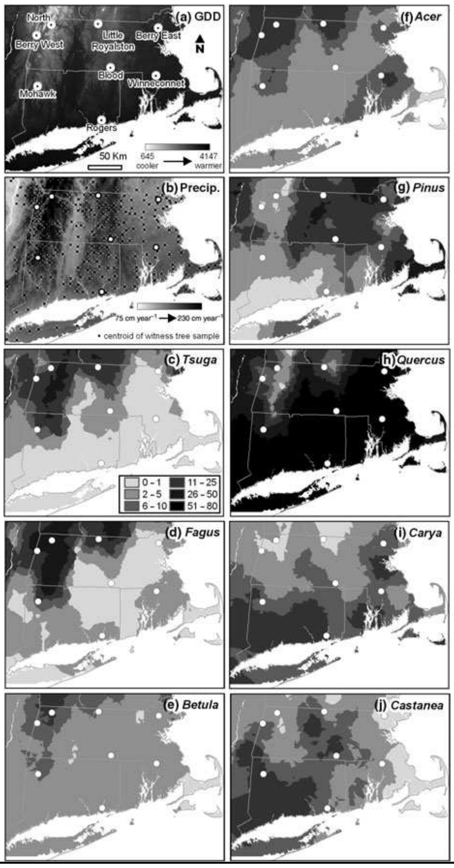


Figure 26: Vegetation responses to variations in temperature (a) and annual precipitation (b). The major canopy trees in Southern New England have different abundances according to climatic conditions; shading and legend refers to the relative frequency of the given species. (Oswald et al., 2007)

Like Oswald et al. (2007), I also observed a shift in the major tree species moving from region to region in terms of both relative importance values and forest type (Fig. 15, 16). This shift can explained to some extent by climatic differences because there is variation in both annual precipitation and average temperature among the four regions surveyed (Table 4). Petersham stands out from the other three regions because annual precipitation for this region is substantially higher than the other three regions. Martha's Vineyard is also climatically unique from the other regions because this is the only region where the average temperature does not fall below freezing during the coldest month of the year. Despite these differences, the overall climate in the four regions does not shift drastically from Martha's Vineyard to Petersham to Blue Hills and Levi Pond and thus cannot completely explain the unique composition observed in each region. Rogers (1982) also questions the role of climate in determining species composition. He sampled spring herb communities in hardwood-mesophytic forest in 5 different Midwestern states and found that climate was not a deciding factor in herb composition (Rogers, 1982).

5.4 Forest Structure

The forest structure is another potential source of environmental dissimilarity among regions and in fact, the density and size distribution of trees varies considerably by region (Table 7). Martha's Vineyard exemplifies how limited resources such as light, water and nutrients in the soil can result in a trade-off between density in the canopy and in the sapling layer. In the absence of large, canopy trees, more seedlings are able to take advantage of increased availability of light, water and nutrients and develop into the dense sapling layer (Table 7). In Petersham the reverse effect is observed with the highest average tree basal area of the three regions and the lowest sapling basal area.

This trade-off is relevant to the understory species richness because by limiting the resources available in the understory, large canopy trees may also restrict the number of different species able to persist. This trend is observed in the present study in the Blue Hills region; as the overall basal area for trees increased, the species richness in the understory declined (Fig. 9c). Basal area did not have a significant effect on the species richness in the understory for the regions of Martha’s Vineyard, Petersham, or Levi Pond. This contradiction may have a biological explanation or it may be the result of the sample size. Since the Blue Hills dataset had a much larger sample size and consequently, a higher statistical power than the other three regions sampled, it is likelier that the null hypothesis was rejected in Martha’s Vineyard, Petersham and Levi Pond.

In other studies as well, a negative correlation between tree basal area and understory richness has been confirmed (Hutchinson et al., 1999; Ford et al, 2000). Ford et al. (2000) also found that species evenness increased with increased basal area. Fountain (1980) did not find that tree basal area was significantly related to the diversity of herbaceous species; however his study compared understory diversity, not richness. Since diversity is a function of both richness and evenness, Fountain’s study could still reflect the results of Hutchinson et al. (1999) and Ford et al. (2000) if species richness and species evenness showed opposite trends in response to increased basal area (i.e. if species evenness increased with basal area and richness decreased with basal area). These results could potentially cancel each other out in the diversity calculation, resulting in no trend in species diversity with basal area.

5.5 Overstory Composition

The relative importance values of canopy trees are pertinent to understory studies because the canopy can determine understory richness and composition by altering light regimes and edaphic conditions. *P. strobus* and *T. canadensis* are two species of particular importance because they may have a pronounced effect on the environmental conditions in the understory. In both Petersham and Blue Hills *P. strobus* has a high relative importance value (Fig. 15). These two regions also have very high frequencies of both *P. strobus* and *T. Canadensis*, however these two species are notably absent from plots within Martha's Vineyard (Fig.14).

Both *T. canadensis* and *P. strobus* are associated with nutrient poor (Whitney and Foster, 1988) and more acidic soils than are found in hardwood stands (Barbier et al. 2008; Beatty, 1984). The light transmittance, or the photosynthetic photon flux, is estimated to be very low (less than 2%) in *T. canadensis* stands meaning that the understory receives a very low percentage of photosynthetic light (Barbier et al., 2008). Thus, by limiting the resources available to understory vegetation, these canopy species dictate understory growth, creating an environment where only a few hardy species are able to persist.

Given the limited conditions that are typically found beneath the *T. canadensis* canopy, it is not surprising that this species is associated low species richness in the understory. In the region of Blue Hills *T. canadensis* is negatively related to understory species richness (Fig.13b). Ellum et al. (2010) also found that as the basal area of eastern *T. canadensis* increases, the species richness significantly decreases.

T. canadensis also influences the composition of species in the understory. Beatty (1984) found that certain understory species were more apt to grow under a *T. canadensis* canopy than other species, which were found only in a hardwood dominated overstory. *T. canadensis* influenced areas had a higher abundance of *Acer spicatum, Aster acuminatus, F. grandifolia, Monotropa uniflora, Acer pensylvanicum*,and *Epifagus virginiana* (Beatty, 1984). However, this association is not apparent in the present study. *A. spicatum, A. acuminatus, F. grandifolia, M. uniflora,* and *A. pensylvanicum* were all identified in the present study; however these species did not show any preference for *T.*

canadensis forests; in fact all five of these species were recorded in a broad range of forest types.

5.6 Soils

While differences in climate, forest structure and overstory composition can explain the unique species composition observed in each region to some extent, these variables are not the only factors at play. Rogers (1982) found that herb communities spanning five Midwestern states were influenced most strongly by soil variables. I also found that several soil characteristics were significant determinants of understory composition; these characteristics include organic matter (%), nitrogen (%), C/N ratio, extractable calcium, sulfur, potassium, magnesium, iron, manganese, aluminum, zinc and sodium (Fig. 10; Table 6).

Organic Matter and Nitrogen

The percentage of organic matter in the soil distinguishes between high-nutrient requiring, mesic species and low-nutrient requiring species common in drier soils. In their characterization of upland sites in the hardwood and conifer ecosystems of the Cyrus H. McCormick Experimental Forest, Pregitzer and Barnes (1984; 1985) characterized the vegetation at sites with the highest organic matter by mesic, high-nutrient requiring species. Some of these species include *A. saccharum* and *viola spp (*1984; 1985) and *Caulophyllum thalictroides* (Spies and Barnes, 1985). These species are correlated with high organic matter values in the present study as well (Fig. 10). In addition to these species, I also found that *Betula alleghaniensis, Picea rubens, Goodyera spp. Mitchella repens, Hamamelis virginiana, Maianthemum canadensis,* and *Lycopodium obscurum* were strongly correlated with high organic matter levels.

At the other end of the organic matter gradient are low-nutrient requiring, dry-soil species. Pregitzer and Barnes (1984; 1985) classified low organic matter sites by *Vaccinium spp* and other dry shrubby species. The same trend is observed in the present study since species with the strongest negative correlation with organic matter were common to the sandy soils of Martha's Vineyard (Fig. 10). This observation is also supported in the present study by the low distribution of soil organic matter in the Martha's Vineyard region compared with the other three regions (Fig. 18).

The percentage of nitrogen in the soil is closely correlated with the percentage of organic matter and many of the same high-nutrient requiring mesic species (Fig. 10). Pregitzer and Barnes (1984) found that of all sites surveyed, those with the highest nitrogen content included the same *A. saccharum* and *Viola spp.* dominated sites that also had high organic matter values. *Polygonatum spp.* (Pregitzer and Barnes, 1984), *Caulophyllum thalictroides* (Spies and Barnes, 1985), *Gymnocarpium spp.* (Pregitzer and Barnes, 1982; Wali and Krajina, 1973), *Cornus canadensis, Lycopodium complanatum*, and *Aralia nudicaulis* (Wali and Krajina, 1973), are additional species that are correlated with nitrogen-rich soils.

The species listed above were correlated with nitrogen-rich soils in the present study as well. In addition to these species, I also found that *Trillium undulatum, polygonatum pubescens, Viburnum acerfolium, Phegopteris hexagonoptera, Castanea spp., Osmunda claytonia, Dennstaedtia puncliobula*, and *Aralia nudicalis* illustrated the strongest correlation with high nitrogen levels in the soil (Fig. 10). Interestingly, all of the species with an affinity for nitrogen cited by Pregitzer and Barnes (1984), Pregitzer and Barnes, (1982), and Wali and Krajina (1973) in addition to the species with the strongest correlation with soil nitrogen levels in the present study, were sighted in the Levi Pond region. This correlation between Levi Pond and specie with an affinity for nitrogen is not surprising considering that the average percent of nitrogen in Levi Pond is almost 2.5 times higher than Martha's Vineyard's value (Fig. 21b).

Nitrogen, like organic matter is also negatively correlated with low-nutrient requiring, dry species. Pregitzer and Barnes classified sites with the lowest nitrogen values as "excessively well-drained" and characterized these sites by the presence of *Vaccinium spp*. and *Acer rubrum* (1982) and *P. strobus, Maianthemum canadense* and *Athyrium filix-femina* (1984). I also observed a negative correlation between soil nitrogen levels and species such as *Vaccinium corymbosum* that are more commonly found on drier sandy soils (Fig. 10). *A. rubrum* was also slightly negatively correlated with soil nitrogen levels in the present study, however there is a discrepancy between the present study and the results of Pregitzer and Barnes (1984). I did not find that *P. strobus, Maianthemum canadense* and *Athyrium filix-femina* were also associated with low nitrogen levels in the soil. This conflict may be attributed to the fact that both of these species are super-generalists and can persist in a wide range of soil conditions (Wali and Krajina, 1973)).

Carbon-to-Nitrogen Ratio

The C/N ratio is negatively correlated with the soil nitrogen levels and organic matter levels and as a result, this variable is also negatively correlated with the mesic species with high nutrient requirements common in nitrogen-rich and high organic matter sites. Bellemare et al. (2002) determined that *Tiarella cordifolia, Parthenocissus quinquefolia* and *Dryopteris marginalis* were all significantly and negatively related with the C/N ratio in the soil. I also found that *T. cordifolia, P. quinquefolia* and *D. marginalis* were negatively correlated with C/N ratio (Fig. 10).

At the other end of the C/N gradient, Bellemare et al. (2002) found that *F. grandifolia* had a significant positive relationship with the C/N ratio. In the present study as well, *F. grandifolia* illustrated a slightly positive correlation with the C/N ratio. However, none of the species observed in the present study indicated a strong correlation with a high C/N ratio (Fig. 10). Regionally, a distinction can be made between the high C/N ratio regions of Blue Hills and Martha's Vineyard and lower C/N ratio values that may be found in Petersham and Levi Pond (Fig. 19). This regional difference may explain why species common to the rich mesic forest were sighted mostly in the Levi Pond region and dry low-nutrient requiring species were able to persist in the high C/N ratio regions of Blue Hills and Martha's Vineyard.

The C/N ratio also influences the understory in terms of species richness. In Blue Hills, C/N ratio is negatively related to understory richness (Fig. 20c). This trend was also observed by Small and McCarthy, 2005.

Macro and Micronutrients

Nitrogen is not the only soil macronutrient with the potential to determine species composition in the understory; the percentage of extractable calcium and the concentration of extractable sulfur, potassium and magnesium are also significant determinants of understory vegetation (Fig. 10). Extractable calcium has the same influence on understory composition as nitrogen and organic matter and is also strongly associated with rich mesic species. Spies and Barnes (1985) found that high calcium sites had a high abundance of *A. saccharum* and *C. thalictroides.* I also found that these two species were slightly correlated with higher calcium levels. However in the present study, *Onoclea sensibilis*, *Acer pensylvanicum, Lycopodium complanatum,* and *Euthamia caroliniana* illustrated the strongest correlation with extractable calcium levels.

Patterns in species composition at the other end of the calcium spectrum are not as easy to define. Wali and Krajina (1973) found that calcium-poor sites were composed of "dry, well-drained soils" and sandy outwash material. *Melampyrum lineare* is one species correlated with dry soils and calcium-poor sites (Wali and Krajina, 1973). In contrast, Spies and Barnes (1985) observed *T. canadensis* and *Clintonia spp.* in the highest abundances at plots with the lowest calcium values. While these two species may be found in dry nutrient-poor soils they are not as characteristic of these soil conditions as *Melampyrum lineare* and can be found in a broad range of soil conditions.

The present study supports the observations made by Wali and Krajina (1973) because I also found that calcium-poor soils are more likely to be inhabited by low-nutrient requiring, dry soil species. In the present study, *Melampyrum lineare* was correlated with low extractable calcium whereas the low calcium species identified by Spies and Barnes (1985),*T. canadensis and Clintonia spp,* did not correlate with low extractable calcium in the present study (Fig. 10).

Sulfur and potassium are two other important macronutrients that influence species composition in the understory. These two variables are closely associated with each other and with the following understory species: *Betula papyrifera, Viburnum cassinoides, Tsuga Canadensis, Abies balsamea,Pinus strobus, Lycopodium tristachyum, Aster acuminatus, Cypripedium acaule* and *Quercus rubra* (Fig. 10). Unfortunately, there is a gap in the literature regarding the effects of extractable sulfur and potassium in the understory species composition and thus there is no way to compare our findings with other studies.

Magnesium is another important macronutrient which is strongly correlated with *Pinus resinosa, Chimaphila umbellata, Betula populifolia, Berberis thunbergii, Potentilla spp., Houstonia radicata, Populus grandifolia, Plantago rugelli, Calamagrostis canadensis, Tragopogon pratensis, Juniperus communis,* and *Prunus pensylvanica* (Fig. 10). Again, while the literature exploring the influence of magnesium on understory vegetation is lacking, there is an interesting pattern within the present dataset. While only 11 weedy or invasive species were noted in the present study (see appendix IV for a full list), four of these species are correlated with extractable magnesium. *P. rugelii, H. caerulea, T. pratensis,* and *B. thunbergii* are all weedy or invasive species according to USDA Plant Database.

The extractable zinc, manganese and iron in the soil are three micronutrients that were also identified as significant variables influencing species composition in the understory (Fig. 10, Table 6). Zinc and manganese are correlated both with each other and with *Ostrya virginiana, P. quinquefolia,* and *Aster spp* (Fig. 10). Unfortunately, few studies focus explicitly on the effects of micronutrients on understory species composition so it is difficult to compare any observations from the present study with other research. It is also possible that these variables reflect a regional difference in extractable zinc and manganese more than a compositional trend in the understory. This is plausible given that these two soil variables are most strongly correlated with species sighted in Levi Pond where zinc and manganese were much higher than in Martha's Vineyard and Blue Hills (Fig. 22a, b).

There is also a trade-off between iron and aluminum levels in the soil. Iron is most strongly correlated with the dry-low nutrient requiring species identified in Martha’s Vineyard (Fig. 10). Aluminum on the other had is more strongly correlated with broad spectrum of species observed in Petersham, Blue Hills and Levi Pond (Fig. 10).

Sodium also appears in the ordination as an influence on understory composition however, it is possible that this variable, like zinc and manganese, is reflecting a regional difference more than an understory compositional change. None of the species observed illustrate a strong correlation with this soil variable, however species sighted in the Blue Hills region are slightly correlated with this variable (Fig. 10). This association is also reflected in the distribution of sodium levels from region to region; Blue Hills on average had 2.5 times higher soil sodium values than Petersham or Levi Pond (Fig. 24)

5.7 Disturbance History

The New England forest bears a long history of disturbance by humans. While historic disturbances may have occurred in the distant past, in many cases both the landscape and the understory composition bear the scars for years to come. All four regions experienced some degree of historic disturbance, however the scale and type of disturbance is variable by region. Plots on Martha’s Vineyard exhibited the most severe signs of disturbance as result of the oak moth. Additionally, these plots occurred on land owned either by the Polly Hill Arboretum or the Nature Conservancy and as a result were subject to past agricultural use and present-day recreational use. Coppiced hardwoods were ubiquitous throughout the region suggesting a historic timber harvest (Wessels, 1997). Historic fires or presumed controlled burning was also evidenced at two plots.

Like Martha's Vineyard, the region of Petersham is characterized by an abundance of cultural features. These features include stone walls, trail and roads which suggest both historic land use and current use though the maintenance of trails. This region has also been subject to past timber extractions as evidenced by the abundance of multi-stemmed hardwoods in and around plots.

The Blue Hills region was also historically harvested and continues to be used for small scale timber extraction projects today. Cut stumps were noted in most Blue Hill plots alluding to the presence of current timber harvest in this region. The abundance of stone walls snaking through plots also indicates that this region was likely cleared for agriculture in the past.

In contrast to the other regions sampled, only three plots at Levi Pond are near notable cultural features and these cultural features were limited to very old roads that had clearly not been used for years. The presence of multi-stemmed hardwood trees in most plots does suggest historic timber harvest however these events were most likely small scale and heterogeneous in the landscape since multi-stemmed hardwoods were noted only in a few of the plots sampled. Additionally, the presence of pit-and-mound topography in almost half of the plots suggests that the Levi Pond forest has remained largely intact and only moderately disturbed. One small scale disturbance that was noted in the Levi Pond region is the ash decline or "ash dieback" (White Ash: USDA Plant guide). While the direct cause of ash decline may be the result of multiple variables, infection from mycoplasma-like organisms is considered one of the primary causes of this disturbance (White Ash: USDA Plant guide, 2010). Although ash decline was evident in a few of the plots at Levi Pond, this natural disturbance does not come close to matching the magnitude and severity of the oak decline on Martha's Vineyard.

Unfortunately, disturbance history was not factored into data analysis via ordination but we may conclude that disturbance is at least partially responsible for the species composition in each region based on the presence or absence of certain invasive or weedy species (Table 8). While all four regions did possess non-native, weedy species; the presence of these species is clearly more abundant in Martha's Vineyard and Blue Hills than at Petersham and Levi Pond.

The abundance of non-native weeds in these plots is likely the result of the conditions created post disturbance. The two most heavily disturbed regions sampled also possessed the highest number of non-native and weedy species. Holle and Motzkin (2007) also found that previously cultivated sites and those with a history of soil disturbance have a higher occurrence of non-native plant species than undisturbed sites (Holle and Motzkin, 2007).

Interestingly, rare and threatened understory species were found in equal abundances in all four of the regions surveyed. Rare and threatened species are often a good indicator of disturbance history because, the reason these species are "rare" is because they have specific habitat requirements and are sensitive to any change in the environment around them. Additionally, there is often a negative relationship between invasive plants and rare or endangered plants (Jolls, 2003). This negative relationship is a consequence of the ability of opportunistic invasive species to take advantage of any light gaps and outcompete native flora for resources.

Given these extensive environmental constraints on rare and endangered plant species we may expect to see a higher number of rare and endangered plants in the intact Levi Pond forest and very few in the highly disturbed Martha's Vineyard region. However, rare and endangered plants were identified in three of the regions sampled including Martha's Vineyard and the Blue Hills region (Table 9).

While the presence or absence of invasive weedy species as opposed to rare and endangered species may be a useful indicator of disturbance history, the influence of disturbance can be detected on general species composition as well. Gerhardt and Foster (2002) found that undisturbed, woods had a higher occurrence of shade tolerant species such as *Clintonia borealis, Trillium undulatum* and *Coptis trifolia* while historic pasturelands supported more shade-intolerant species. In the present study as well, *C. borealis, T. undulatum* and *C. trifolia* were most frequent in the relatively undisturbed Levi Pond region though this conclusion is purely qualitative.

In another study, D'Amato et al (2008) used indicator species analysis to determine that *A. nudicaulis, D. intermedia,* and *V. alnifolium* are significant indicator species of undisturbed, old-growth *T. canadensis* stands. Of these three species only *A. nudicaulis* occurred in our dataset and this herb was so widespread it is difficult to distinguish any site preference.

5.8 Conclusion

While the results of this study indicate that region is the most important underlying gradient determining understory composition, it is also clear that multiple factors are at play. Unfortunately, the relative influence that each of the factors examined exerts on understory composition is blurred by studies which take place in different geographic locations, forest types and utilize different data analysis methods.

The use of different data analyses is especially relevant since ordination techniques are both complex and variable in their results. Ordination serves as a valuable tool in community ecology and can be especially useful when applied to large datasets such as the present one. By organizing data along a gradient of variation, large datasets may be converted into a readable format for the ecologist. At the same time, users should be wary of replacing field observations and intuition with computer generated models.

Another source of ambiguity within the results of the present study can be attributed to the complexity and interconnectedness of the forest ecosystem. Forest systems are infinitely intricate; to try and identify the influence of one environmental variable over another is nearly impossible. The best we can do is examine the influence of these variables on a regional scale and look for patterns.

At the same time that these ambiguities exist, there are a few trends observed in the present study and other understory studies that transcend the regional and environmental gradients and influence understory vegetation in the same way. These trends include the positive association of calcium, nitrogen and organic matter with each other and with mesic species with high nutrient requirements. Nitrogen and organic matter also have a negative association with dry low-nutrient requiring species. The C/N ratio has the opposite associations as nitrogen and organic matter and is most strongly correlated with dry low-nutrient requiring species. Finally, the presence or absence of weedy and invasive plant species in the understory can be used as a useful indicator of historic or present disturbances.

5.9 Future Research and Work

One of the most obvious and most important improvements that could be made to this study would be increasing the number of plots sampled in all regions especially in Martha’s Vineyard, Petersham and Levi Pond. Not only do the sample sizes limit the reliability of the dataset, there are also statistical and ordination limitations on samples of a minimum size. As indicated by the species area curve for Martha’s Vineyard, Petersham, Blue Hills and Levi Pond the number of plots sampled in each region are not entirely representative of the regional species richness (Appendix VI)

In a continuation of this study it would also be important to more thoroughly examine the influences of historic disturbances on the understory vegetation. This study only touched on disturbance history briefly using remaining landscape clues as indicators of disturbance and relating these hints to the presence and absence of rare and weedy/non-native species. However, given a more detailed and thorough description of land use and disturbance data could be analyzed in ordination and statistical analysis. In the future it may be useful to employ GIS aerial photography from the past to fill in gaps in the historical data and to get a more comprehensive picture of when land was cleared and the scale of these clearing events.

Finally, just as this study will benefit from an increased sample size as additional plots are surveyed, the possibility of the same sites being revisited and sampled ten, twenty and potentially 100 years from now will contribute to the overall comprehensiveness and interest of this study. By adding the dimension of time, not only will it be possible to track changes in species composition on a temporal scale, but it also opens up the possibility of directly observing and the vegetation changes that correspond with each successional stage.

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Appendix I: Understory Species Key

ABIBAL	*Abies balsamea*	Balsam Fir
ACEPEN	*Acer pensylvanicum*	Striped Maple
ACERUB	*Acer rubrum*	Red Maple
ACESAC	*Acer saccharum*	Sugar Maple
ACESPI	*Acer spicatum*	Mountain Maple
ACTRUB	*Actaea rubra*	Baneberry
AMEARB	*Amelanchier arborea*	Serviceberry
AMELAN	*Anemone lancifolia*	Mountain Thimbleweek
ANEQUI	*Anemone quinquefolia*	Wood Anemone
ARANUD	*Aralia nudicaulis*	Wild Sarsaparilla
ARITRI	*Arisaema triphyllum*	Jack in the Pulpit
AROSPP	*Aronia sp.*	Chokeberry
ASTACU	*Aster acuminatus*	Whorled Wood Aster
ASTCOR	*Aster cordifolius*	Blue Wood Aster
ASTSPP	*Aster spp.*	Aster spp.
ATHFIL	*Athyrium filix-femina*	Lady Fern
BAZTRI	*Bazzania trilobata*	liverwort
BERTHU	*Berberis thunbergii*	Japanese barberry
BETALL	*Betula alleghaniensis*	Yellow birch
BETLEN	*Betula lenta*	Black Birch
BETPAP	*Betula papyrifera*	White Birch
BETPOP	*Betula populifolia*	Grey Birch
BOTVIR	*Botrychium virginianum*	Rattlesnake Fern
BROTEC	*Bromus tectorum*	Cheatgrass
CALCAN	*Calamagrostis canadensis*	Canada Bluejoint
CARCAR	*Carpinus carolinus*	American Hornbeam
CARGLA	*Carya glabra*	Pignut Hickory
CARSPP	*Carex sp.*	Sedge spp.
CARTOM	*Carya tomentosa*	Mockernut Hickory
CASSPP	*Castanea spp.*	Chestnut
CAUTHA	*Caulophyllum thalictroides*	Blue Cohosh

CHAANG	*Chamerion angustifolium*	Fireweed
CHIMAC	*Chimaphila maculata*	Striped Prince's Pine
CHIUMB	*Chimaphila umbellata*	Pipsissewa
CLEALN	*Clethra alnifolia*	Coastal Sweet Pepperbush
CLIBOR	*Clintonia borealis*	Blue Bead Lily
COPTRI	*Coptis trifolia*	Gold Thread
CORALT	*Cornus alternifolia*	Alternate Leaved Dogwood
CORCAN	*Cornus canadensis*	Bunchberry
CORCOR	*Corylus cornuta*	Beaked Hazelnut
CORFLO	*Cornus florida*	Flowering Dogwood
CRASPP	*Crataegus sp.*	Hawthorn
CYPACA	*Cypripedium acaule*	Moccasin Flower
DALREP	*Daliharda repens*	Robin Runaway
DENPUN	*Dennstaedtia punctilobula*	Hay Scented Fern
DESFLE	*Deschampsia flexuosa*	Hair Grass
DRYCAR	*Dryopteris carthusiana*	Spinulose Woodfern
DRYMAR	*Dryopteris marginalis*	Marginal Woodfern
DRYSPP	*Dryopteris spp.*	Woodfern spp.
EPIANG	*Epilobium angustifolium*	Fireweed
EPIREP	*Epigaea repens*	Trailing Arbutus
EQUSYL	*Equisetum sylvaticum*	Woodland Horsetail
EREHIE	*Erechtites hieracifolia*	American Burnweed
EUTCAR	*Euthamia caroliniana*	Slender Goldentop
FAGGRA	*Fagus grandifolia*	Beech
FRAAME	*Fraxinus americana*	White Ash
GALSEP	*Galium septenrionale*	Northern Bedstraw
GAUHIS	*Gaultheria hispidula*	Creeping Snowberry
GAUPRO	*Gaultheria procumbens*	Wintergreen
GAYBAC	*Gaylussacia baccata*	Black Huckleberry
GAYFRO	*Gaylussacia frondosa*	Blue Huckleberry
GERROB	*Geranium robertianum*	Geranium
GOOSPP	*Goodyera sp.*	Rattlesnake Plaintain

GRASPP	*Grape spp.*	Grape spp.
GRASS	*Poaceae*	Grass spp.
GYMDRY	*Gymnocarpium dryopteris*	Oak Fern
HAB SP	*Habenaria spp.*	Orchid
HAMVIR	*Hamamelis virginiana*	Witch Hazel
HEPAME	*Hepatica americana*	Roundlobe Hepatica
HOUCAE	*Houstonia caerulea*	Azure Bluet
HYPRAD	*Hypochoeris radicata*	Cat's Ear
ILELAE	*Ilex laevigata*	Smooth Winterberry
ILEOPA	*Ilex opaca*	American Holly
ILEVER	*Ilex verticillata*	Common Winterberry
JUNCOM	*Juniperus communis*	Juniper
KALANG	*Kalmia angustifolia*	Sheep Laurel
LAC SP	*Lactuca sp*	Lettuce
LILORC	*Lily/orchid*	Lily/orchid
LONCAN	*Lonicera canadensis*	American Fly Honeysuckle
LYCANN	*Lycopodium annotinum*	Lycopodium Annotinum
LYCCLA	*Lycopodium clavatum*	Lycopodium Clavatum
LYCCOM	*Lycopodium complanatum*	Lycopodium Complanatum
LYCLUC	*Lycopodium lucidium*	Lycopodium Lucidium
LYCOBS	*Lycopodium obscurum*	Lycopodium Obscurum
LYCSPP	*Lycopus sp*	Bugleweed/Horehound
LYCTRI	*Lycopodium tristachyum*	Lycopodium Tristachyum
LYOLIG	*Lyonia ligustrina*	Maleberry
LYSQUA	*Lysimachia quadrifolia*	Whorled Yellow Loosestrife
MAICAN	*Maianthemum canadense*	Canada Mayflower
MALSPP	*Malus sp*	Apple
MEDVIRG	*Medeola virginiana*	Indian Cucumber Root
MELLIN	*Melampyrum lineare*	Narrowleaf Coweheat
MITREP	*Mitchela repens*	Partridge Berry
MONHYP	*Monotropa hypopitys*	Pine Sap
MONUNI	*Monotropa uniflora*	Indian Pipe

MYRPEN	*Myrica pensylvanica*	Bayberry
ONOSEN	*Onoclea sensibilis*	Sensitive Fern
OSMCIN	*Osmunda cinnamomea*	Cinnamon Fern
OSMCLA	*Osmunda claytonia*	Interrupted Fern
OSMREG	*Osmunda regalis*	Royal Fern
OSMSPP	*Osmunda spp.*	Osmunda spp.
OSTVIR	*Ostrya virginiana*	Hophorn Beam
OXASPP	*Oxalis sp.*	Wood Sorrel
PANTRI	*Panax trifolius*	Dwarf Ginseng
PARQUI	*Parthenocissus quinquefolia*	Virginia Creeper
PHECON	*Phegopteris connectilis*	Long Beech Fern
PHEHEX	*Phegopteris hexagonoptera*	Broad Beech Fern
PICRUB	*Picea rubens*	Red Spruce
PINRES	*Pinus resinosa*	Red Pine
PINSTRO	*Pinus strobus*	White Pine
PLARUG	*Plantago rugelli*	Blackseed Plantain
PLASPP	*Plantago sp.*	Plantago sp.
POL SP	*Polygonum spp.*	Polygonum (vine)
POLACR	*Polystichum acrostichoides*	Christmas Fern
POLBIF	*Polygonatum biflorum*	Smooth Solomn's Seal
POLPUB	*Polygonatum pubescens*	Hairy Solomon's Seal
POLVIR	*Polypodium virginianum*	Polypody
POPGRA	*Populus grandidentata*	Bigtooth Aspen
POTSPP	*Potentilla sp*	Cinquefoil
PREALB	*Prenanthus alba*	White Rattlesnakeroot
PRETRI	*Prenanthus trifoliata*	Gall-of-the-earth
PRUPEN	*Prunus pensylvanica*	Pin Cherry
PRUSER	*Prunus serotina*	Black Cherry
PTEAQU	*Pteridium aquilinum*	Braken Fern
PYRASA	*Pyrola asarifolia*	Liverleaf Wintergreen
PYRROT	*Pyrola rotundifolia*	American Wintergreen
PYRSPP	*Pyrola sp.*	Wintergreen spp.

QUEALB	*Quercus alba*	White Oak
QUERUB	*Quercus rubus*	Red Oak
QUESTE	*Quercus stellata*	Post Oak
QUETUR	*Quercus turbinella*	Scrub Oak
QUEVEL	*Quercus velutina*	Black Oak
REDCAN	*Reed Canary Grass*	Reed Canary Grass
RHOVIS	*Rhododendron viscosum*	Swamp Azalea
RHUCOP	*Rhus copallina*	Winged Sumac
ROSBLA	*Rosa blanda*	Smooth Rose
ROSSPP	*Rosa sp.*	Rose
RUB SP	*Rubus spp.*	Rubus spp.
RUBALL	*Rubus allegheniensis*	Blackberry
RUBFLA	*Rubus flagellaris*	Dewberry
RUBFRU	*Rubus fruiticosus*	Blackberry
RUBHIS	*Rubus hispidus*	Dewberry
RUBIDE	*Rubus ideaus*	Red Rasberry
RUBOCC	*Rubus occidentalis*	Black Raspberry
RUMACE	*Rumex acetosella*	Sheep Sorrel
RUSHSPP	*Rush spp.*	Rush spp.
SASALB	*Sassafras albidum*	Sassafras
SMIRAC	*Smilacina racemosa*	False Solomon's Seal
SMISPP	*Smilax sp.*	Smilax
SOLRUG	*Solidago rugosa*	Goldenrod
SOLSPP	*Solidago sp*	Solidago sp.
SORDEC	*Sorbus decora*	Mountain Ash
SORSPP	*Sorbus sp.*	Sorbus sp.
SPISPP	*Spirea sp.*	Spirea
STRAMP	*Streptopis amplexifolius*	Claspleaf Twistedstalk
STRROS	*Streptopus roseus*	Twistedstalk
THENOV	*Thelypteris noveboracensis*	New York Fern
TIACOR	*Tiarella cordifolia*	Foamflower
TILAME	*Tilia americana*	American Basswood

TOXRAD	*Toxicodendron radicans*	Poison Ivy
TRAPRA	*Tragopogon pratensis*	Jack-go-to-bed-at-noon
TRIBOR	*Trientalis borealis*	Starflower
TRIERE	*Trillium erectum*	Red Trillium
TRIUND	*Trillium undulatum*	Painted Trillium
TRIVIR	*Triadenum virginicum*	Virginia March St. Johnswort
TSUCAN	*Tsuga canadesis*	Eastern Hemlock
VACANG	*Vaccinium angustifolium*	Lowbush Blueberry
VACCOR	*Vaccinium corybosum*	High Bush Blueberry
VEROFF	*Veronica officionalis*	Common Gypsyweed
VIBACE	*Viburnum acerifolia*	Mapleleaf Viburnum
VIBCAS	*Viburnum casseniodes*	With-rod
VIBDEN	*Viburnum dentatum*	Arrowwood
VIBLAN	*Viburnum lantanoides*	Hobblebush
VIOSPP	*Viola sp.*	Violet
VITSPP	*Vitis sp.*	Grape sp.

Appendix II: Tree Species Key

Abibal	*Abies balsamea*	Balsam Fir
Acepen	*Acer pensylnaicum*	Striped Maple
Acerub	*Acer rubrum*	Red Maple
Acesac	*Acer saccharum*	Sugar Maple
Acespi	*Acer spicatum*	Mountain Maple
Amespp	*Amelanchier arborea*	Serviceberry
Aronia	*Aronia sp.*	Aronia sp.
Betall	*Betula alleghensis*	Yellow Birch
Betlen	*Betula lenta*	Black Birch
Betpap	*Betula papyrifera*	Paper Birch
Betpop	*Betula populifolia*	Grey Birch
Carcar	*Carpinus Carolina*	Hornbeam
Carova	*Carya ovata*	Shagbark Hickory
Cartom	*Carya tomentosa*	Mockernut Hickory
Casden	*Castenea denata*	Chestnut
Clespp	*Clethra sp.*	Clethra sp.
Faggra	*Fagus grandifolia*	American Beech

Fraame	*Fraxinus Americana*	White Ash
Franig	*Fraxinus nigra*	Black Ash
Hamvir	*Hamamelis virginiana*	Witch Hazel
Illver	*Ilex verticillata*	Winterberry
Lyospp	*lyonia*	Lyonia
Myrpen	*Myrica pensylvanica*	Bayberry
Ostvir	*Ostrya virginiana*	Hop Hornbeam
Picrub	*Picea rubens*	Red Spruce
Pinres	*Pinus resinosa*	Red Pine
Pinstr	*Pinus strobus*	White Pine
Popgra	*Populus grandidentata*	Bigtooth Aspen
Poptre	*Populus tremuloides*	Quaking Aspen
Prupen	*Prunus pensylvanica*	Pin Cherry
Pruser	*Prunus serotina*	Black Cherry
Quealb	*Quercus alba*	White Oak
Queill	*Quercus ilicifolia*	Scrub Oak
Querub	*Quercus rubra*	Red Oak
Queste	*Quercus stellata*	Post Oak
Quevel	*Quercus velutina*	Black Oak
Rhovis	*Rhododendron viscosum*	Swamp azela
Robpse	*Robinia pseudoacacia*	Black Locust
Sasalb	*Sassafras albidum*	Sassafras
Tsucan	*Tsuga Canadensis*	Eastern Hemlock
Ulmrub	*Ulmus rubra*	Slippery Elm
Vaccor	*Vaccinium corybosum*	Highbush Blueberrry
Vibden	*Viburnum detatum*	Arrowwood Viburnum

Appendix III: Species Presence or Absence by Region

Species	Martha's Vineyard	Petersham	Blue Hills	Levi Pond
Shrubs				
Acer pensylvanicum		X	X	X
Acer spicatum		X		
Amelanchier arborea	X	X	X	X
Aronia sp.	X			
Berberis thunbergii			X	
Carpinus carolinus		X		
Castanea sp.		X		
Clethra alnifolia	X			
Cornus alternifolia				X
Cornus florida		X		
Corylus cornuta	X		X	
Crataegus sp.		X	X	
Gaylussacia baccata	X	X		
Gaylussacia frondosa	X			
Hamamelis virginiana		X	X	
Ilex laevigata			X	
Ilex opaca	X			
Ilex verticillata	X	X		
Juniperus communis			X	
Kalmia angustifolia	X		X	
Lonicera canadensis				X
Lyonia ligustrina	X			
Malus sp	X			
Myrica pensylvanica	X			
Ostrya virginiana	X	X		X
Prunus pensylvanica			X	
Quercus turbinella	X			
Rhododendron viscosum	X			
Rhus copallina	X			
Rosa sp.	X			
Rubus allegheniensis	X			
Rubus flagellaris	X			
Rubus fruiticosus			X	
Rubus hispidus	X		X	
Rubus ideaus			X	
Rubus occidentalis				X
Rubus sp.		X		X
Sorbus decora				X
Sorbus sp.		X	X	
Vaccinium angustifolium	X	X	X	X
Vaccinium corybosum	X	X	X	X
Viburnum acerifolia		X	X	
Viburnum casseniodes			X	X
Viburnum dentatum	X		X	
Viburnum lantenoides			X	X
Seedlings				
Abies balsamea			X	X
Acer saccharum		X	X	X
Betula alleghaniensis			X	X
Betula lenta	X	X	X	
Betula papyrifera			X	
Betula populifolia			X	
Carya glabra	X			
Carya tomentosa	X			
Castanea sp.		X		
Fagus grandifolia	X	X	X	X
Fraxinus americana		X	X	X
Picea rubens			X	X
Pinus resinosa			X	
Pinus strobus		X	X	X
Populus grandidentata			X	
Prunus serotina	X	X	X	X
Quercus alba	X	X		

Quercus rubus		X	X	X
Quercus stellata	X			
Quercus velutina	X	X		
Sassafras albidum	X			
Tilia americana		X		
Tsuga canadesis		X	X	X
Ferns				
Athyrium filix-femina		X		X
Botrychium virginianum				X
Dennstaedtia punctilobula	X	X	X	X
Dryopteris carthusiana			X	
Dryopteris marginalis		X	X	
Dryopteris sp.		X		X
Equisetum sylvaticum			X	
Gymnocarpium dryopteris				X
Onoclea sensibilis		X	X	X
Osmunda cinnamomea		X	X	X
Osmunda claytonia		X	X	X
Osmunda regalis			X	
Phegopteris connectilis				X
Phegopteris hexagonoptera			X	
Polypodium virginianum		X	X	
Polystichum acrostichoides		X		X
Pteridium aquilinum	X	X	X	X
Thelypteris noveboracensis	X	X		X
Herbs				
Actaea rubra				X
Amemone lancifolia			X	
Anemone quinquefolia	X			
Aralia nudicaulis	X	X	X	X
Arisaema triphyllum		X		X
Aster acuminatus			X	
Aster cordifolius			X	
Aster sp	X	X		X
Bazzania trilobata	X			
Caulophyllum thalictroides				X
Chamerion angustifolium	X			
Chimaphila maculata	X			
Chimaphila umbellata			X	
Clintonia borealis			X	X
Coptis trifolia		X	X	X
Cornus canadensis		X	X	X
Cypripedium acaule		X	X	
Daliharda repens			X	
Epigaea repens	X		X	
Epilobium angustifolium	X			
Erechtites hieracifolia	X			
Euthamia caroliniana				X
Galium septenrionale	X			
Gaultheria hispidula	X			
Gaultheria procumbens	X	X	X	X
Geranium robertianum				X
Goodyera sp.			X	X
Habenaria spp.	X			X
Hepatica americana		X		
Houstonia caerulea			X	
Hypochoeris radicata	X			
Lactuca sp	X			
Lycopus sp			X	
Lysimachia quadrifolia	X			
Maianthemum canadense	X	X	X	X
Medeola virginiana	X	X	X	X
Melampyrum lineare	X	X	X	
Mitchela repens		X	X	X
Monotropa hypopithys		X	X	
Monotropa uniflora	X	X	X	X
Panax trifolius			X	

Parthenocissus quinquefolia	X	X		
Plantago rugelli			X	
Plantago sp.			X	
Polygonatum biflorum		X	X	X
Polygonatum pubescens		X		X
Potentilla sp			X	
Prenanthus alba				X
Prenanthus trifoliata				X
Pyrola asarifolia			X	
Pyrola rotundifolia	X			
Pyrola sp.			X	
Rosa blanda				X
Rubus occidentalis				X
Rumex acetosella	X		X	
Smilacina racemosa	X		X	X
Solidago rugosa	X			
Solidago sp	X			
Spirea sp.			X	
Streptopis amplexifolius				X
Streptopus roseus		X		X
Tiarella cordifolia				X
Toxicodendron radicans	X			
Tragopogon pratensis			X	
Triadenum virginicum			X	
Trientalis borealis	X	X	X	X
Trillium erectum		X		
Trillium undulatum			X	X
Veronica officionalis				X
Viola sp.		X	X	X
Grammoids				
Bromus tectorum			X	
Calamagrostis canadensis			X	
Carex spp.	X		X	X
Deschampsia flexuosa			X	
Phalaris arundinacea	X	X		
Poa spp.	X	X		X
Rush spp.	X		X	
Club Mosses				
Lycopodium annotinum		X		X
Lycopodium clavatum			X	X
Lycopodium complanatum		X		X
Lycopodium lucidium			X	
Lycopodium obscurum		X	X	X
Lycopodium tristachyum			X	
Vines				
Polygonum sp.				X
Smilax sp.	X			
Vitis sp.	X			

Appendix IV: Weedy/Invasive Species

Species	Martha's Vineyard	Petersham	Blue Hills	Levi Pond
Rubus ideaus			X	
Plantago rugelii			X	
Epigaea repens	X		X	
Houstonia caerulea			X	
Hypochoeris radicata	X			
Epilobium angustifolium	X			
Chamerion angustifolium	X			
Geranium robertianum				X
Berberis thunbergii			X	
Parthenocissus quinquefolia	X	X		
Rubus fruiticosus			X	
Total	5	1	6	1

Appendix V: Rare and Threatened Species

Species	Martha's Vineyard	Petersham	Blue Hills	Levi Pond
Cornus florida				X
Polygonatum biflorum			X	
Pyrola asarifolia	X		X	
Galium septenrionale	X			
Sorbus decora				X
Rhododendron viscosum	X		X	
Total	3	0	3	2

Appendix VI: Species limits curve for Martha’s Vineyard, Petersham, Blue Hills, and Levi Pond.

While the species area curves for the four regions do suggest that the species richness is reaching a constant all four regions, the curve has not yet reached a plateau and therefore is not entirely representative of species richness. The dashed line indicates the species confidence interval +/- two standard deviations.