

**The Dynamics of Temperate Forest Fragmentation:
an Examination of Susceptibility to Woody Invasive Species**

by

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When an ecosystem is fully functioning, all the members are present at the assembly. To speak of wilderness is to speak of wholeness.

- Gary Snyder

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Although my personal perspective is less extreme, I offer E.O. Wilson's sentiment that "there's nothing more romantic than biogeography".

Abstract: Forest fragmentation and the invasion of non-native species are two current threats to global biodiversity. We investigate whether fragmentation increases the susceptibility to woody invasive species in ten remnants (2 to 126 ha) of Eastern deciduous forest. We counted all woody individuals in plots located in belt transects at the edge and center of each fragment and midway between. While 40% of edge individuals are invasive, interior regions have fewer invasives (14%). Species richness, abundance of individuals, and the percentage of invasive species decline significantly from both the edges to the centers of the fragments and with increasing fragment area. These patterns result from increased susceptibility to invasive species in edge regions and in smaller fragments. The increase in non-native species with decreasing fragment area does not correspond to an equivalent decline in the native species community, suggesting that non-native species may colonize an empty habitat niche associated with the fragment edge. However, the interiors of larger fragments had a richer community of native species. Overall community diversity and evenness indices do not vary with fragment size, which suggests their ineffectiveness in assessing the integrity of fragmented forests. The diversity and evenness indices do, however, reflect the expansion of the non-native species community with decreasing fragment area. Our results provide support for conservation efforts dedicated to preserving large tracts of eastern deciduous forests in order to minimize the invasion and dominance by non-native woody plants.

Introduction:

Forest fragmentation has been described as one of the most pressing threat to global biodiversity (Wilcox and Murphy 1985, Stork 1997, Raven and McNeely 1998). Fragmentation induces transformations of the physical structure of communities that compel changes in species composition and distribution. As much as 40% of eastern deciduous forests exists as small isolated woodlots in the midst of commercial, agricultural, and residential properties (Yahner 1995). Many of fragments are severely affected by the invasion of non-native species (Schulze *et al.* 1996). It is among these isolated eastern deciduous fragments that this study has been conducted.

We study the effects of fragmentation on invasive species density and distribution in fragments of mixed deciduous hardwood in Williamstown, MA. To elucidate the dynamic interactions between forest fragmentation and the presence of invasive species, we address three questions. We consider the relationship between the density of invasive species and the following three factors: (1) distance from the edge of the fragment; (2) fragment size; and (3) species richness or species diversity of the fragment. We examine the correlation of species composition with these factors by censusing vegetation at three distances from the edge of ten habitat fragments spanning a spectrum of areas from 1ha to 126ha.

Although fragmentation and the associated losses of biodiversity occur globally, much research has focused on hot spots, areas of tremendous biodiversity, that are primarily located in tropical areas (Douglas 1998). While concentrating fragmentation studies on regions of rich biodiversity incurring colossal rates of destruction is justified, fragmentation also presents a tremendous threat to temperate ecosystems. The lesser degree of alarm with which the fragmentation of temperate forests, such as eastern deciduous forests, has been viewed may be attributed to the greater population densities and broader geographic ranges of temperate species. Additionally, much of the most severe fragmentation is historic, having initiated with European arrival in North America in the 17th century (Wilcove *et al.* 1986). However, the destruction of 95-97% of old growth forests throughout the continental United States provides cause for concern.

I first review the existing degree of understanding of the dynamics of forest fragmentation. Forest fragments remain isolated among a sea of agricultural and residential

land, compelling comparison to isolated oceanic islands and application of the theory of island biogeography. The edges of the fragments are human-induced *ecotones*, transition zones between community types. At the ecotone between forest and open land, forests are subject to microclimates and seed inputs unlike those present in the forest interior. The plants that thrive at forest margins are often opportunistic, pioneer species, many of which are non-native to the fragmented region. The presence of non-native species may cause further alterations in species composition and species richness through resource competition and alteration of their microenvironments.

Forest Fragments as habitat islands

An underlying question of community ecology involves patterns of species distributions in space. Much of the initial work in this area of community ecology is summarized by Preston's *species-area relationship*, which suggests that community species richness is an exponential function of the available area of habitat. The relation assumes the form

$$S=cA^z$$

where S denotes species richness, A denotes area, and z denotes a community parameter indicating the breadth of species ranges or how rapidly new species are added with increasing area (Preston 1962). The capacity of larger areas to sustain more species serves as the underlying premise for the *equilibrium theory of island biogeography*, developed by MacArthur and Wilson (1967). According to island biogeography, the number of species on an island is a function of the island's colonization rates and extinction rates. The immigration rate will decline with increasing distance from adjacent islands due to the increasing distance from the source pool. The extinction rate will decrease as island size increases, due to a greater ease of obtaining resources and evading predators on larger islands (MacArthur and Wilson 1967). If the positions of islands are selected stochastically, larger islands will tend to possess greater habitat heterogeneity (Yahner 1995).

The theory of island biogeography has been applied to forest fragmentation by relating species of true oceanic islands to those of isolated forest patches. The theory has proven successful in capturing the trends in species immigration and extinction of a variety of fragmented habitats (see review in Simberloff 1988, also Harris 1984). Island biogeography theory has been effectively used to address changes in species composition

associated with tropical rain forest fragmentation. The most prominent of these studies is the Biological Dynamics of Fragmentation project, a long term study of fragmentation conducted on land cleared for grazing in the Brazilian Amazon (Lovejoy *et al.* 1986, Bierregaard *et al.* 1992, Lovejoy and Oren 1981).

Despite the success of numerous studies in using island theory to address habitat fragmentation, questions remain as to the validity of applying island biogeography to the study of habitat fragmentation. A primary issue of contention is that the barriers for movement between habitat islands (ie. mountains or roads) may be extremely distinct from those of ocean islands (ie. open water) (Margules *et al.* 1982). While the ocean separating habitat islands is inhospitable to many species, the lands between forest fragments may be marginally accommodating for species. Hence, the scale of isolation and the inter-fragment matrix may differ markedly (Doak and Mills 1994). Whittaker (1998) cites non-random patterns of community assemblage as rational for preferring to address fragmentation with empirical observation over theoretical analysis. While empirical studies may better suit the design of particular conservation reserves, the application of island biogeography theory to habitat fragmentation remains essential to understanding the fundamental dynamics of fragmentation.

When applying the theory of island biogeography to habitat fragmentation, the time since isolation must be considered. Saunders (1991) observed that species richness depends upon time since isolation. Often, a newly formed fragment initially contains more species than it is capable of sustaining without access to the resources of adjacent forests. A loss of species termed *species-relaxation* will occur until the fragment reaches a sustainable level of species richness (Saunders 1991). Successful reproduction and maintenance is necessary for the survival of the remaining species.

An increasing incidence of habitat fragmentation associated with human land use has resulted in an increasing number of species existing as metapopulations (New 1997). *Metapopulations* are assemblages of local populations sustained by a balance of the extinction and colonization (Levins 1970 cited in Hill, Thomas, and Lewis 1996). Metapopulations are characterized by the following four conditions: (1) local breeding populations occupy discrete habitat patches, although individuals are exchanged through relatively infrequent migration; (2) the small local populations network to form a larger

population with a longer duration than any local population; (3) patches are sufficiently connected to allow recolonization; and (4) sufficient spatial and environmental variation exists to prohibit simultaneous extinction of all local populations (Hanski and Kuussaari 1995). The *rescue effect* enacted by metapopulations allows the separated groups to periodically serve as sources or sink of species; when a species becomes locally extinct, individuals from another group will recolonize the essentially vacated community niche. In this manner, the effective area of a habitat fragment may be augmented (Thomas and Hanski 1997).

Implication of Island Theory for Conservation Biology

Island biogeography has been used in the debate, which has become referred to as SLOSS (single large or several small), which addresses which reserve design methodology is more effective in furthering conservation initiatives (Wilcox and Murphy 1985). While it is undisputed that more and larger reserves should universally be preferred, the SLOSS debate treats conservation priority in cases of limited resources. The foremost of the initial attempts to apply the principles of island biology to reserve design was Diamond's (1975) suggestion that, in the absence of empirical data, reserves should be preferred which are larger, less separated, circular rather than elongated, and connected by corridors (Figure 1).

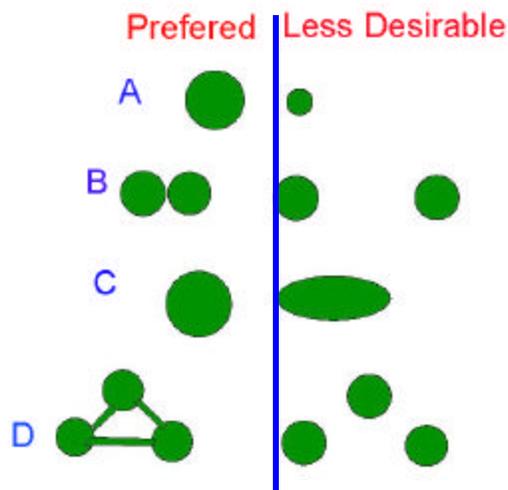


Figure 1: Diamond (1975) suggested that in the absence of empirical data, reserves should be preferred which are larger (A), less separated (B), circular rather than elongated (C), and connected by corridors (D).

Simberloff and Abele (1976) rebutted the assertions by claiming that the application of island biogeography to reserve design was premature and that the species-area relationship (SAR) is actually neutral in deciding between a single large and several small reserves. In homogenous habitat, a large reserve will indeed be able to support more species than several small reserves. However, environmental heterogeneity significantly determines species composition on relatively small scales. Hence, depending on the degree of overlap in species composition between reserves, several small reserves may support more species than a single large reserve. Several small reserves would be stochastically likely to include a greater number of habitat types (Simberloff and Abele 1976).

While many accept Simberloff and Abele's SAR reasoning, they criticize their argument's failure to consider a spectrum of other conservation concerns. Researchers warn of the danger of using species richness as a reserve selection criterion in the absence of concern for particular species. Diamond (1976) stresses the need for minimum population size considerations because (1) some habitats only exist on large patches; (2) food supplies may be seasonally or spatially patchy; (3) low population densities of some species may cause low recolonization potential; and (4) hot spots of high resources only constitute a fraction of habitat. Maintaining his support of large reserve areas, Diamond (1976) suggests that optimal reserve design entails a large reserve accompanied by smaller reserves. The small reserves would be intended to avoid environmental catastrophe and provide habitat for species excluded from the larger patch by competition (Diamond 1976).

As source populations will seldom be available in actual reserve designs, Terborgh (1976) claims that logic suggests minimizing extinctions. Further, extinctions may initially effect the most vulnerable species in consistent order across smaller reserves (Terborgh 1976). Cole (1981) constructed a model (although with somewhat questionable methods) that countered the conclusions of Simberloff and Abele (1976). Wilcox and Murphy (1985) criticize the assumption of Simberloff and Abele (1976) that most species are fairly innocuous to fragmentation. They stress the distinction between habitat fragmentation and the issue of SLOSS. While fragmentation concerns species relaxation, the SLOSS issue involves which reserve configuration will support more species following relaxation (Wilcox and Murphy 1985).

Diamond's (1975) selection criteria favoring large and connected reserves appears generally desirable. Reflecting on the irreversibility of fragmentation and the large-scale habitat requirements of some species (Sullivan and Shaffer 1975), we suggest that large conservation reserves are essential to the preservation of biodiversity. The synergistic effects of loss of area (as dictated by species-area relationships) and fragmentation (including isolation as addressed by island biogeography as well as edge effects) may render a single large tracts of land preferable to several smaller tracts (Whittaker 1998).

An emerging concept in considerations of habitat patches is that of the vegetation *matrix* surrounding habitat islands. The density and type of vegetation between forest patches is important in determining the ease with which species are able to move between fragments. In areas with poor inter-fragment potential for migration, corridors function as strips of habitat that connect habitat fragments by allowing for species movement. The effectiveness and desirable characteristics of corridors vary widely according to the type of habitat and species composition (Saunders 1991). Indeed, corridors may actually be detrimental to some species that would thrive better in isolation (Whittaker 1998).

Indirect Effects of Fragmentation

The formation of a new ecotone at the transition from the edge of the forest into the surrounding cleared land causes a profusion of *edge effects* (Wales 1972). Murcia (1995) cites three general types of edge effects: abiotic environmental changes, direct biological effects, and indirect biological effects. Direct biological effects include shifts in the abundance and distribution of species subject to degrees of physiological tolerance to physical edge conditions such as desiccation, temperature, and wind. Indirect effects propagate through changes in species interactions compelled by the changing physical edge conditions (Murcia 1995). Microclimate, vegetation structure, and floristic composition delineate edge habitats (Williams-Linera *et al.* 1998). Although numerous studies have calculated edge width for fragments of particular microclimates and species compositions, no general method exists for estimating edge width (Matlack and Litvaitis 1999). However, the ratio of the area of edge to the total area of the fragment has been found to be instrumental in configuring spatial vegetation patterns (Chen *et al.* 1996).

Abiotic Edge Effects

Microclimate changes are small scale variations in the surrounding climate caused by alterations of a forest's physical characteristics. The open agricultural or residential land surrounding forest fragments incurs more ground solar radiation during the day as well as increased atmospheric reradiation at night than the forest sub-canopy, which is cooler, moister, and less variable. This microclimate dichotomy creates a temperature and moisture gradient perpendicular to the forest edge (Murcia 1995). Higher radiation levels permeate the edge of the forest. This increase in radiation varies according to the edge aspect. While a south facing edge may receive 180-200 hours of sunlight during mid-summer months, the corresponding north facing edge may receive only 20-60 hours (Geiger 1966 cited in Ranney 1977). This difference in radiation accounts for the more pronounced edge effects observed along southern edges (Palik and Murphy 1990). A synthesis of tropical forest fragmentation presents the range of microclimate alteration at forest edges as occurring within 15-60m. Physical microclimate changes such as wind extend as far as 100m (Laurence *et al.* 1997).

Increased radiation also elevates edge temperatures above those of forest interiors. The high albedo (reflectance) of cleared lands, which may be 50% greater than that of forests, results in increased energy along the forest edges (Colwell 1974 cited in Ranney 1977). The wind that sweeps across open lands also permeates the forest edges. Increases in temperature and wind velocity coupled with the lesser evapotranspiration in open lands decreases air as well as soil moisture (Murcia 1995). An additional source of abiotic effects is the introduction of chemical compounds such as fertilizers from croplands into adjacent forests (Murcia 1995).

Direct and Indirect Biological Effects

Increased solar radiation may augment plant growth along the fragment edges. Understory cover density was observed to increase from 15% at forest interiors to 40% along forest edges (Barrick 1945 cited in Ranney 1977). Altered abiotic conditions along the forest margins may favor the colonization of shade-intolerant, pioneer species. Plants exhibiting pioneer traits are disproportionately non-native species.

The ability of plants to germinate in the altered abiotic conditions will also determine species composition. Changes in light input alone achieved through patch clearing may differentially favor the germination of weedy species (Nee and May 1992). A study

conducted in fragments of Brazilian rainforest found that a native herb, *Heliconia acuminata*, was between 3 and 7 times more likely to germinate in continuous forests than in forest fragments of 1 to 10 ha (Bruna 1999). A study of the distribution of shade tolerant tree seedlings in 1, 10, and 100 ha fragments of tropical rainforest observed a decline in seedling density towards the edge of the fragment and as the size of the fragment decreased (Benitez-Malvido 1998). Edge effects were found to be more responsible for the observed trends than area loss. A decrease in seed rain was attributed to increased seed mortality, reduced seed output and dispersal, high seed predation, and lower seedling establishment (Benitez-Malvido 1998).

Interior forest species may not be as limited by edge microclimate as by competition from edge species (Palik and Murphy 1990). The edges will often receive greater seed input due to the transport of wind dispersed seeds between fragments (Ranney *et al.* 1981). Additionally, edges may attract seed-dispersing herbivores to forage the augmented herb cover. Birds are able to find many nesting sites and food sources in the multi-level vegetation of forest edges (Matlack and Litvaitis 1999). Hence, augmented fruit and seed dispersal may increase the relative densities of animal and bird disperse species, many of which are berry producing invasive species (Cox 1999). Models suggest that dispersal ability is the most essential determinant of invasive spread (Higgins *et al.* 1999).

The traits cited as promoting propagation along forest edges are largely characteristic of invasive species. These traits include abundant seed production, wide seed dispersal, the ability to germinate under a variety of conditions, rapid growth, preference for high light environments, the ability to withstand disturbance, and strong competitive abilities (Cox 1999). In a study of transitions along a forest-field gradient, a principle component analysis found the first two components to be related to the forest edge (Meiners and Pickett 1999). Accordingly, species richness, the Shannon-Weiner diversity index, and the percent total cover increased from the forest interior to edge in the study. The edge also possessed greater heterogeneity of vegetation structure. Much of this increase in species richness and diversity may be attributed to colonization by invasive species (Meiners and Pickett 1999). Hence, one should couple considerations of species richness and diversity with knowledge of the composition of edge vegetation in order to accurately assess vegetation changes associated with fragmentation (Saunders 1991).

Invasive Species

The majority of fragmentation studies emphasize the loss of native species rather than colonization by invasive species (for an exception, see Brothers and Spingarn 1993). I use the terms non-native and invasive species interchangeably throughout this paper to indicate species that are non-indigenous members of the local plant community (although not all non-native plants have invasive propagation patterns). The competitive ability of many invasive species presents a serious threat to native biota. In accordance with the theory of island biogeography, the reduced selection pressures subjected on island biota may render the island more susceptible to invasion (Carlquist 1974). Reduced abundance of young trees and seedlings is often attributed to either fragmentation of populations or competition with introduced species. Such is the case for a threatened native tree, *Dombeya acutangula*, on La Reunion Island in the Indian Ocean (Gigord *et al.* 1999). Although forest edges and fragmentation often allow for the invasion of non-native species, in several cases, the isolation of forest fragments has prevented invasion by non-native species. One observation of greater invasive cover within forests of greater area and connectivity occurred in the case of an invasive honeysuckle shrub, *Lonicera maackii* (Hutchinson and Vankat 1998).

The spread of invasive species generally occurs through two means: populations either advance steadily or establish isolated populations from an initial center of introduction (Shigesada and Kawasaki 1997, Baker 1986). While the first of these strategies is independent of disturbance, the spatial and temporal scales of disturbance orchestrate the second (Bazzaz 1986). In a study of the forest colonization of *Lonicera maackii*, small populations propagated through a series of small dispersal events for approximately ten years; at that time, a dramatic population expansion occurred due to the advent of seed reproduction by the initial colonizers (Deering 1999).

In most systems, disturbance, (including clearing and fire), encourages alien invasion by reducing light and resource competition (Brothers and Spingarn 1993). Although disturbed habitats may be the most susceptible to invasion by non-native species, in some communities a degree of disturbance is essential to maintaining ecosystem integrity, a notion encapsulated by the *intermediate disturbance hypothesis* (Roberts *et al.* 1995). The edge response of the forest may hinder further invasion. A dense wall of vegetation that develops in the increased radiation of the forest edge ultimately reduces interior light levels and wind

speed and hinders the entrance of seed disperses (excepting birds to a degree) (Brothers and Spingarn 1993). Despite the hope offered by this finding for the integrity (associated with factors such as ecosystem health or sustainability) of small fragments, the fear remains that future assaults on native biota may arise among shade tolerant non-native species (Brothers and Spingarn 1993).

Issues of Fragment invasion

Distance from the Fragment Edge

The primary question which this study intends to address is the manner in which the density of invasive species changes along a transect from the edge to the interior of habitat fragments. We anticipate that invasive density will decrease towards the interior of the fragments because light and seed inputs will dwindle. Although few studies have explicitly considered the relationship between invasive density and distribution and degrees of habitat fragmentation, precedence for this study is provided by a study conducted in 7 Indiana old growth forest stands ranging in size from 7 to 23 ha. Vegetation was censused along five belt transects dispersed from the edge to the center of the fragment with consideration granted to edge aspect (Brothers and Spingarn 1993). 37 of the 58 non-native species censused among the 7 fragments were observed only on the exterior transect, while an additional 6 non-native species did not extend beyond 2m into the fragment. The mean species richness of invasives declined from 11.1% to 1.5% from the exterior transect to the transect extending 8m into the interior. At a distance of 50m from the edge, only 10% of the plots harbored even a single non-native species. Invasive species density decreased sharply beyond the edge, and the invasive species that did manage to permeate into the interior were generally small, isolated, and non-reproducing individuals (Brothers and Spingarn 1993).

Although edge effects have been observed to end abruptly in several studies, no distinct discontinuity existed between the edge and interior of forest fragments in Wisconsin (Ranney *et al.* 1981). However, vegetation beyond 10-15m into the fragments possessed characteristics of interior forests (Ranney *et al.* 1981). Matlack (1994) found edge species distribution to correspond with a distinct climatic gradient. While most edge species were confined to within 5m of the forest margin, some more shade tolerant species reached their peak densities as far as 40m, the greatest distance censused, into the fragments of eastern deciduous forest.

The maximum edge penetration of a sugar maple and beech dominated forest fragment was found to be 45m and 5m, on the south and north aspects, respectively (Palik and Murphy 1990). Meiners and Pickett (1999) observed that non-native species were restricted to within 20m of the forest edge. A review of edge effects suggested that edge effects generally do not extend beyond 50m into the fragment (Murcia 1995). Previous research involving *Lonicera maackii* also supports the decline in invasive species presence from the edge to the interior of forest fragments (Luken and Goessling 1995, Rose and Fairweather 1997). While the most dramatic edge effects are fairly well contained, subtler effects extend much farther. Subtle effects have been observed to permeate up to 300m into Brazilian fragment interiors (Laurance *et al.* 1998).

Fragment Area

Our experiment also intends to test whether the density of invasive species is correlated to patch size. As discussed above, invasives are anticipated to be more abundant at the edges of fragments. As smaller patches have a greater ratio of edge to interior area (Haila 1999) (Figure 2), the density of invasives is anticipated to be correlated to patch size. Additionally, if seed dispersal is the determining factor of invasive distribution, the seeds of invasive species will be able to reach the interior of the small forest fragments more readily than that of large fragments. The size of the patch may also effect the fragment's ability to withstand disturbance (Zuidema, Sayer, and Dijkman 1996).

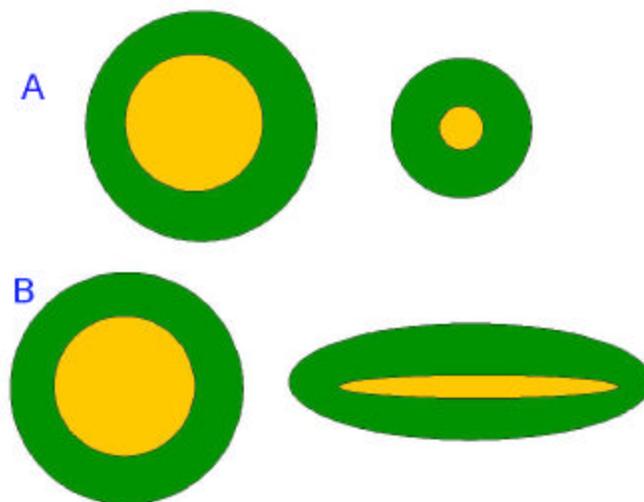


Figure 2: Given an equal edge width, fragments that are (A) smaller or (B) less circular will have a greater ratio of edge area to interior area.

Small fragment may lack interior forest types entirely. Observation of edge effects in 1 ha and 10 ha fragments as well as continuous section of Brazilian rainforest supported this assertion (Malcolm 1994). Data from a study of fragmented woodlots in Wisconsin were fit to a species-area curve. Total woody species richness was observed to increase with increasing woodlot size to approximately 2.3 ha. This area was interpreted as the threshold above which interior forest types may be differentiated. Accordingly, the lesser species richness of fragments with areas greater than 2.3 ha may be attributed to the exclusion of invasive species (Levenson 1981). Another study of Wisconsin fragmentation estimated a threshold of 3 ha for the initiation of interior forest (Ranney *et al.* 1981). These estimated threshold areas correspond well with that of 2 ha estimated for a mature oak forest in New Jersey (Forman and Elfstrom 1975 cited in Levenson 1981). A 4.7 ha sugar maple and beech dominated forest was estimated to consist of 41% edge conditions (Palik and Murphy 1990). A study of fragments of Australian bushland ranging in size from 5 to 200ha found that the correlation between remnant size and integrity was due to the greater habitat heterogeneity present in larger patches (Gilfedder and Kirkpatrick 1998).

A mathematical "core-area" model based on data from an 18-year study of Brazilian fragmentation is employed by Laurance *et al.* (1998) to estimate the critical fragment area below which edge effects become prominent. This area threshold was estimated to be between 100 and 400 ha in the Brazilian rainforest, depending on the shape of the fragment. However, despite the degradation of small fragments by edge effects, fragments with areas below this threshold do afford substantial conservation contributions. Conversely, the effects of fragmentation may be considerable in much larger fragments (such as 1000 ha), particularly if the fragment shape distinctly deviates from circular (Laurance *et al.* 1998).

Fragmentation Dynamics of Species Richness and Diversity

A lingering question in the study of fragmentation involves whether invasive density is correlated to the species richness or species diversity of fragment. Although the presence of a correlation may be empirically considered through simple field observations, the causes of any observed correlation between species richness and diversity and invasive cover are difficult to isolate. Observed correlations may result from differential invasion in fragments with either high or low species diversity and richness or, alternately, changes in forest

composition induced by the presence of invasives. The association between community stability, including resistance to invasion, and species diversity continues to be debated (Case 1991). In his classic text on invasivity, Elton (1958) suggested that the resistance to invasion of a community increases with species richness. However, a theoretical treatment yielded the converse prediction (May 1973). Two recent models fail to resolve this discrepancy. One model suggests that communities can increase resistance to invasion through increasing species number and thus the strength and variance of interspecific competition (Case 1991). Strongly interacting species deter invaders due to their low densities. Dependence on species richness invokes the theory of island biogeography as a determinant of invasivity (Case 1991). A model of the spread of invasive plants in South Africa predicts that augmented native plant diversity may open a community to invasion (Higgins *et al.* 1999).

Empirical support has been gathered in support of each of these concepts. A long-term study of an herb invasion in a mountain beech community found that species rich sites experienced a greater incidence of invasion (Wiser *et al.* 1998). Conversely, a study of grassland ecosystems found that increased species richness increases resistance to invasion (Tilman 1997). This discrepancy may be able to be resolved by considering functional diversity rather than species diversity parameters (Huston 1997).

The presence of non-native plants has generally been found to decrease species richness and diversity (Woods 1993). A study of the invasion of a non-native honeysuckle, *Lonicera tatarica*, in four New England forests showed a decline in the herb cover, species richness, and the density of tree seedlings when the *L. tatarica* cover exceeded 30% (Woods 1993). The study, however, highlighted the influence of the environmental conditions in determining invasive behavior. In Williamstown's Hopkins forest, which possesses more acidic and less nutrient rich soil than the other 3 forests, *L. tatarica* cover was directly correlated with herb cover and species richness (Woods 1993). Examination of all the invasives in the forest community of Williamstown will allow for further exploration of this trend.

Distribution Patterns in Space and Time

Distinct life characteristics of invasive species may lend to distribution patterns that are differentiated from those of native species. Due to possibly greater seed dispersal and resistance to environmental variation, invasive species may have greater ranges than the

native species. However, this effect may be countered by the observation that invasive species tend to possess clumped distributions.

The density of invasives may also correlate with the time since last disturbance of the habitat patch. The extended life cycles of forest species, particularly trees, may delay a forest's response to fragmentation (Haila 1999). Due to the opportunistic quality and capacity for effective resource competition of many invasive species, which may be r-selected species, the density of invasives in recently disturbed patches may be anticipated to be high. Alternatively, the time required for invasives to establish may compel invasive density to be low in recently disturbed patches. A study of the invasion of a non-native honeysuckle, *Lonicera maackii*, observed a ten-year delay in population explosion (Deering 1999). If greater abundance of invasives along forest margins is primarily due to dispersal limitations, the importance of the edge in determining the distribution of early successional forests may be eliminated as the forest matures. Wisser *et al.* (1998) documented the invasion of mountain beech forests by an invasive herb in a long-term study spanning 23 years. The frequency of the invasive herb in observation plots increased from 11% to 43% and eventually reached 57% in 1970, 1985 and 1993, respectively. Over the span of observation, the subset of possible habitats occupied by the herb increased as dispersal limitations were overcome through time. While edge-related patterns were observed to be most prominent along newly created edges within eastern deciduous forests, edge patterns sometimes remained persistent along edges following 55 years of succession (Matlack 1994).

Summary

Having reviewed the literature providing precedence for the current study, we now consider the relation of the current study to the existing body of work addressing fragmentation and the invasion of non-native species. Much work has been conducted regarding species loss due to fragmentation and the influence of edge effects on species composition. Although some general theory regarding fragmentation exists, overarching trends may linger unacknowledged. Studies addressing the invasion of non-native species have emerged only relatively recently (Brothers and Spingarn 1993). Although many studies have attempted to formulate characteristics that describe either the environments that are preferentially invaded or the plants that are capable of this invasion, few comprehensive theories of invasion have been developed (Cox 1999). The microenvironment and resource

availability changes induced by fragmentation often augment the competitive advantages of invasive species. Thus, a clear link exists between the study of fragmentation and the study of invasive colonization. Few studies address this interrelation. The current study attempts to expound upon the relationship between fragmentation and invasion by non-native species in the context of the eastern deciduous forest. By doing so, we will be linking two of the most severe current threats to global biodiversity.

Methods:

Forest Description and History

The study was conducted in eastern-deciduous forests fragment patches in Williamstown, Berkshire County, Massachusetts (42° 42' 43" N, 74° 12' 22" W). The study fragments were located in a broad, low elevation valley enclosed by the Taconic range to the west and Mount Greylock and other adjacent peaks to the east. Forests in Williamstown have incurred a fate similar to that of other eastern deciduous forests since European settlement: initial expanses of relatively virgin forests were cleared for agriculture and resource extraction until the late 1800's at which point forests reestablished. Development and agriculture fragment much of the present forests. Indeed, 40% of all eastern deciduous forests currently exists as small, isolated woodlots (Yahner 1995).

Shortly after the initial colonization of Williamstown in 1753, the Williamstown forest cover was reported to be 98% (Brooks 1974). By 1800, the town's population of 2086 had cleared 20,000 acres of land, leaving only 33% of the town's land forested. A decline in farming beginning in the 1850's allowed fields and pastures to develop into second growth forests (Brooks 1974). Forest cover expanded to 64% and 66% in 1952 and 1972, respectively (Brooks 1974). Although the population of Berkshire County expanded by 36% during this time interval, the percent of agriculture and open land decreased from 21 to 15 percent between 1952 and 1972 (Brooks 1974). Many of the reestablishing forests occur as woodlots that were logged at least into the 1970's (Saterson 1977). A study of the forest history of Williamstown revealed a shift in beech (*Fagus grandifolia.*) and maple (*Acer spp.*) abundance from presettlement to the present. While Williamstown's forests initially consisted of 42% beech and 18% maple, the dominance had shifted to 18% and 35%, respectively, by 1977, accompanied by an increased abundance of birch (*Betula spp.*) and ash (*Fraxinus spp.*) (Saterson 1977).

Of the approximately 1200ha of land within Williamstown, we estimate that approximately 70% currently exists as forests. This estimate is based upon the area of land classified as forest in the Massachusetts GIS (geographic information system) 1997 land-use classification. This assessment corresponds to Weatherbee's (1996) estimate of 70% for the average forest cover of the towns within Berkshire County. At least 8.9% of the forests within Williamstown currently exist as small, isolated patches (as estimated with land use

classifications, see figure 3). This figure may be an underestimate, because the tracts considered to be continuous include some fragmentation by roads and patches only connected by narrow corridors. The high proportion of continuous forest cover within Williamstown may be attributed to the steep terrain surrounding the central valley (figure 4). A town ordinance prevents building at elevations above a prescribed height in order to protect watershed quality.

Regions of the forest study fragments are progressing through secondary succession, a redevelopment of the forest following disturbances such as timber harvest, agricultural clearing, or fire. Eastern deciduous forest succession initiates with the establishment of seedlings of shade-intolerant, pioneer species including aspen (*Populus spp.*) and black cherry (*Prunus serotina*) (Yahner 1995). This initial establishment is followed by species with intermediate shade tolerance such as white oak (*Quercus alba*), northern red oak (*Quercus rubra*), yellow birch (*Betula alleghaniensis*), and red maple (*Acer rubrum*). The forest gradually reaches a mature state indicated by an increasing incidence of shade tolerant species including sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*). These species will dominate a relatively stable community until the reoccurrence of disturbance (Yahner 1995). A stable, late successional community develops from several decades to a few hundred years following the initiation of secondary succession (Yahner 1995). Although some small patches of older forests may exist among the study fragments, we estimate that the majority of the forest fragments are 75 to 150 years old. Several of the fragments include clear signs of former agricultural uses, such as stone walls, stone foundations, and trails.

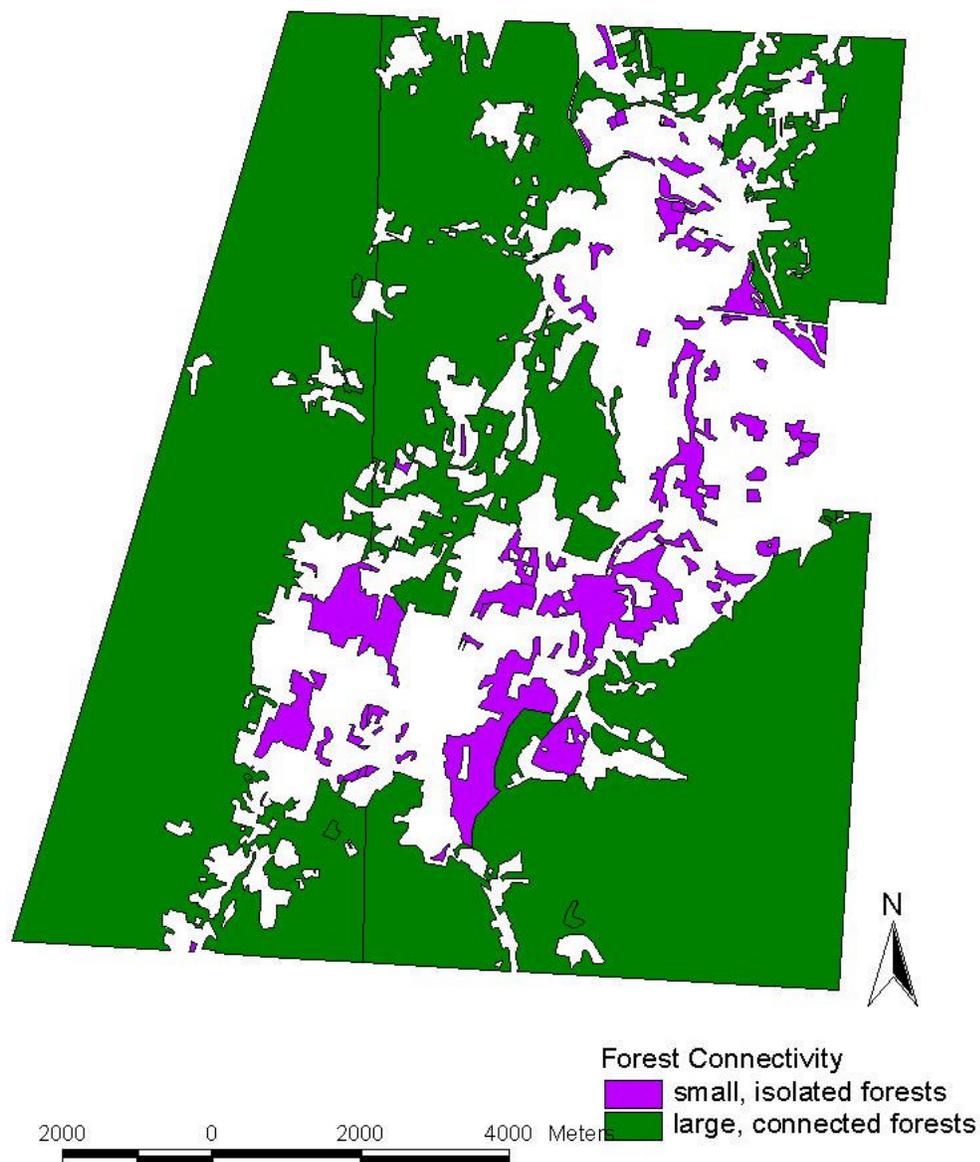


Figure 3: The regions of Williamstown’s forests that exist as small, isolated fragments (purple), as larger, contiguous tracts (green), and as non-forested land (white). The forest patches were defined using the Massachusetts GIS 1997 landuse classification. Roads may actually fragment some forest regions depicted as continuous. Some continuous regions may be only connected by narrow corridors.

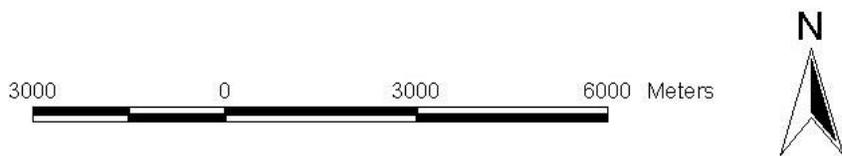
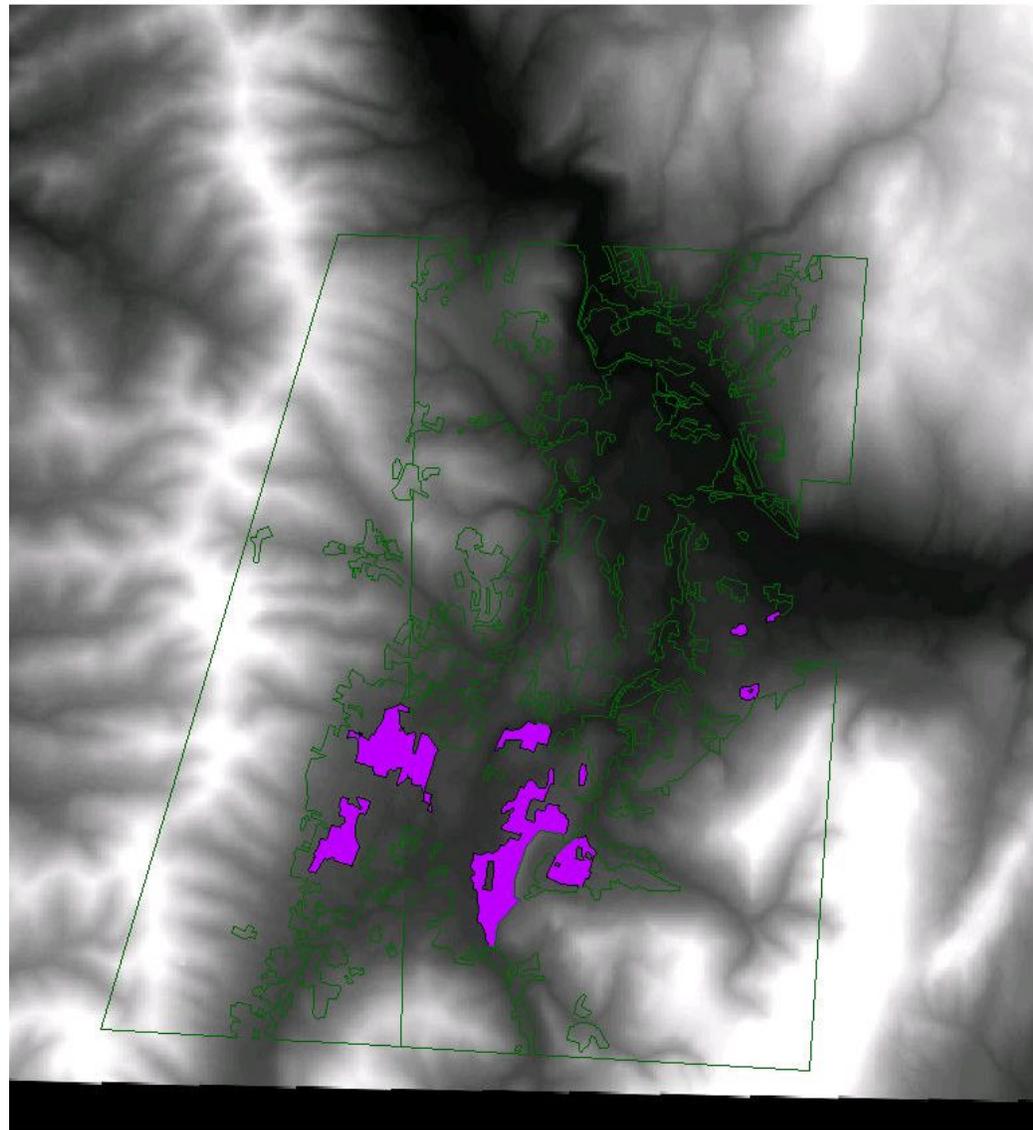


Figure 4: The valley in which Williamstown is situated is confined by the Taconic Crest to the west and Mt. Greylock and adjacent peaks to the east. In this digital elevation model depiction of Williamstown, the areas of lighter shading represent higher elevations. The Massachusetts GIS 1997 Williamstown landuse polygons (green) are overlain and the locations of the 10 study fragments are shown (purple).

Study Fragment Selection

Our study included censusing of ten temperate hardwood forest fragments, ranging in area from 2 to 126ha. We chose fragments that were approximately circular in shape, without narrow bottleneck sections or long, narrow projections. We preferred fragments with only slight inclinations and a southern edge that was distinct and roughly parallel to a west-east transect. Fragments were isolated from other forested regions by at least 100m, although exceptions are noted in the fragment descriptions. While uncultivated agricultural land or pastures delineated the majority of fragment edges, road corridors bordered several fragments. Due to the limited number of potential study fragments within a feasible distance from the center of Williamstown, the fragments deviate from these selection criteria as noted in the fragment descriptions.

We used graphical information system (ESRI ArcView 3.1 GIS) and remote sensing (Research Systems ENVI 3.1) technologies to locate the study fragments. The fragments were initially identified using the Massachusetts GIS 1997 landuse classification layer in GIS (figure 5). The GIS landuse layer provided areas and perimeters for the polygons classified as forests. Massachusetts GIS developed the landuse layer by interpreting 1:25000 aerial photographs taken in 1971 and 1985. The layer has since been updated with aerial photographs from 1990 and 1991/1992 (MassGIS, <http://www.state.ma.us/mgis/lu-doc.htm>). We used the GIS roads layer to locate the fragments on a paper 1971 USGS landuse map, in which the landuse polygons were depicted on a Williamstown and Berlin quadrangle topo map. We examined the fragments in GIS using digitized aerial photographs with 5 meter resolution (figure 6). As final criteria for fragment selection, we used a satellite (SPOT Landsat) image of Williamstown with 20m resolution in the ENVI image processing program. We combined the three satellite bands into a color composite image indicating the degree of reflectance of the land surface. The remote sensing image revealed the extent of forest cover and heterogeneity (figure 7).

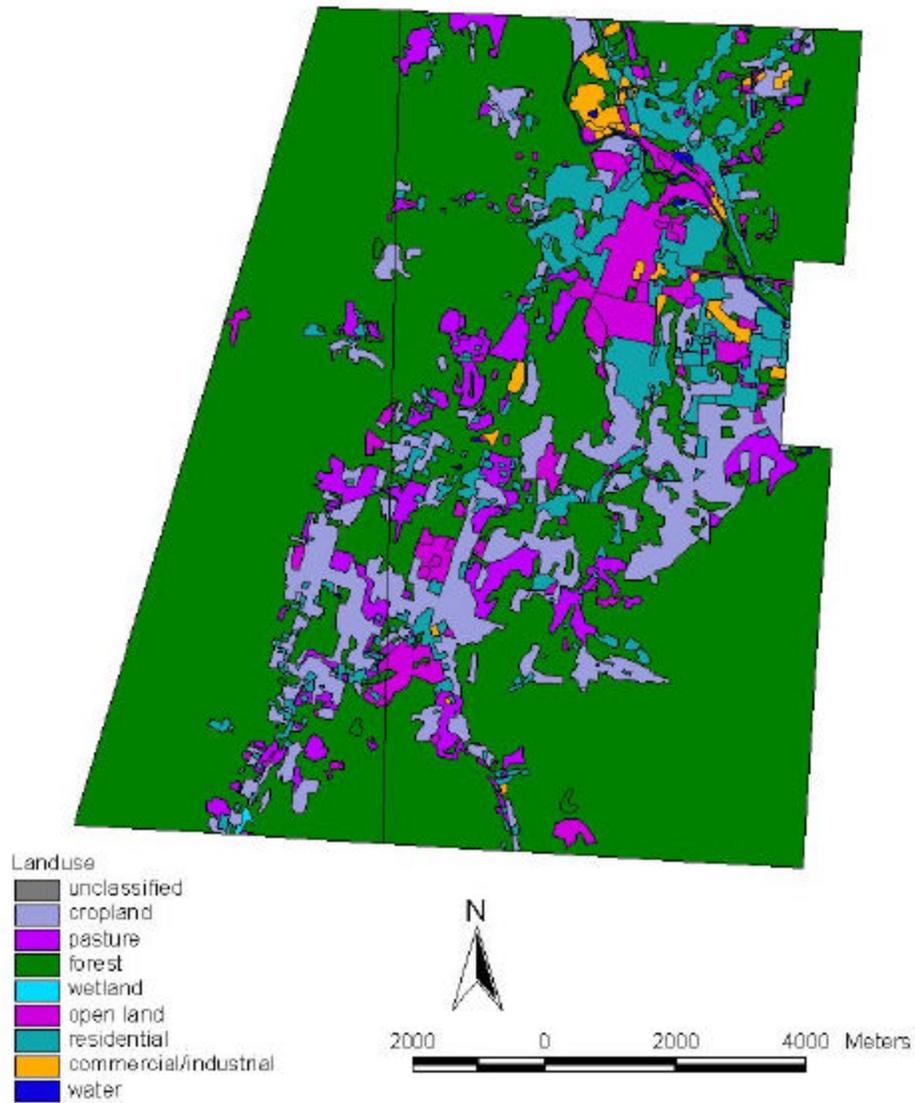


Figure 5: A map of Williamstown landuse based upon the delineations of the Massachusetts GIS 1997 landuse map showing cropland (lavender), pasture(light magenta), forest (green), wetland (light blue), open land (dark magenta), residential (medium blue), commercial or industrial, (yellow) and water (dark blue).

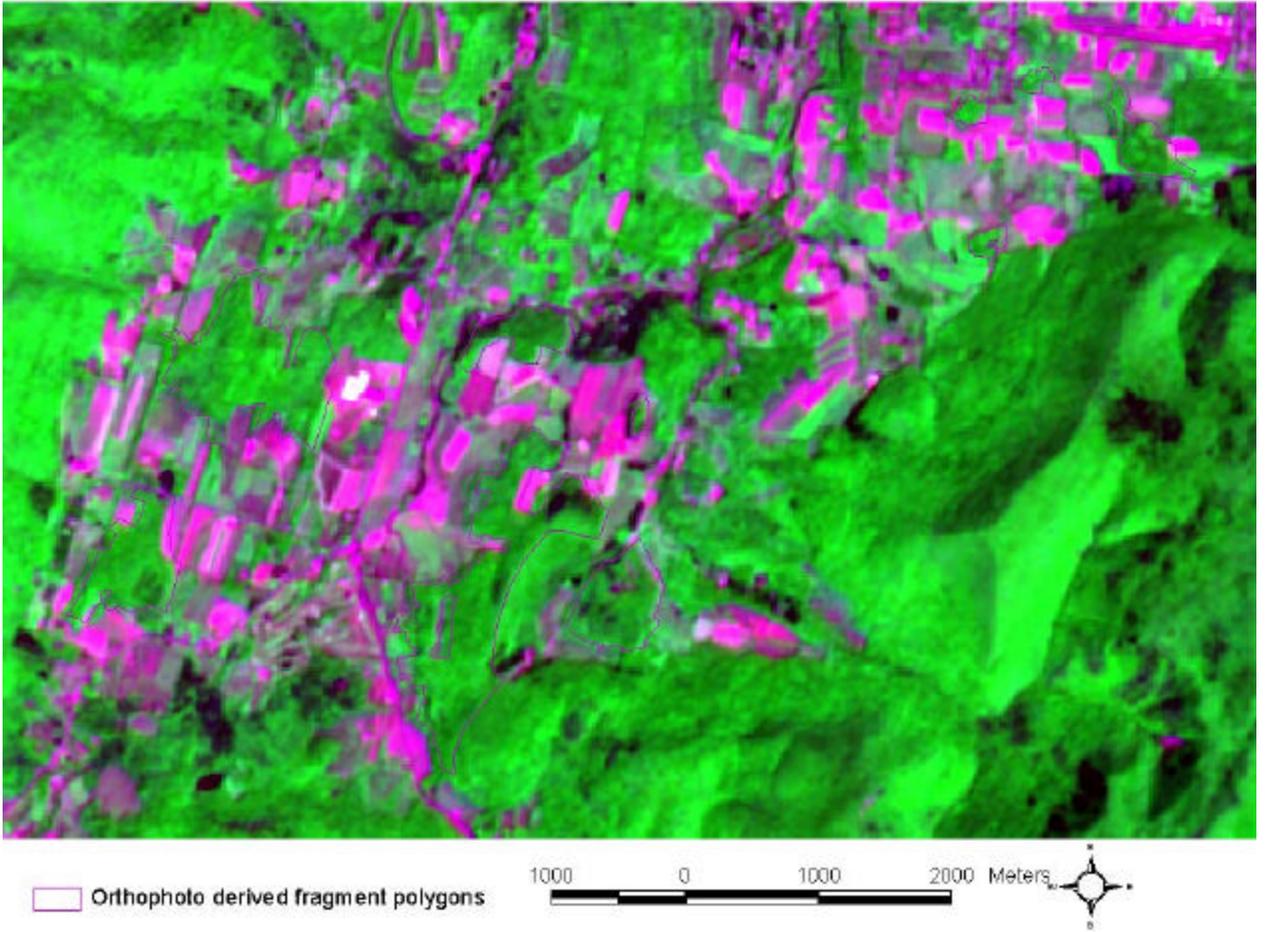


Figure 7: A satellite (SPOT Landsat) image of Williamstown with 20m resolution with the study fragments outlined in purple. The image is a color composite of the intensity of reflectance reported by 3 satellite bands. Open lands (and other high reflectance areas) are magenta and forested (low reflectance) areas green. A lack of correspondence between forest edges on the satellite image and the drawn polygons results from both the lesser resolution of the satellite image and inaccuracies in associating the satellite image with ground points. The causes of misalignment were confirmed by checking one fragment boundary using a GPS (geographic positioning system).

Fragment Descriptions

The study fragments ranged in area from 2 to 126 ha (figure 8). We categorized fragments as small (2 to 5ha), moderate (5 to 25 ha), and large (25 to 126 ha) sized in order to facilitate data interpretation. We chose 5 ha as a conservative threshold above which a fragment is able to sustain more stable, interior forest types (Levenson *et al.* 1981 and Ranney *et al.* 1981). While there were three of each small and moderately sized fragments, the large size category included four fragments. All study fragments (except those with unknown history: the Chenail South, Mt. Hope East, and Hopper fragments) are predominantly primary forest, meaning that they have not been completely cleared, although the fragments have been exposed to variable degrees of disturbance (H. Art, *personal communication*). Descriptions of each of the study fragments, presented from smallest to largest, follow. Directions to the fragments are given in Appendix A.

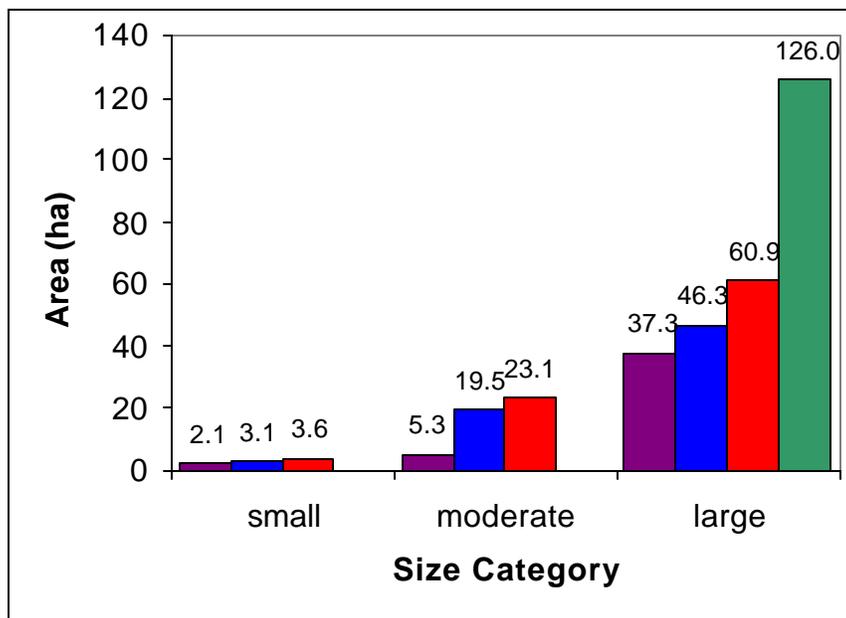


Figure 8: The areas of the ten fragments in hectares. The fragments are categorized as small (2 to 5 ha), moderate (5 to 25 ha), and large (25 to 126 ha).

Small Fragments (Figure 9)

Airport plot: This oblong fragment is located between agricultural pastures and land cleared for an airport. A downward slope begins near the 10m boundary of the edge transect and continues down into a streambed. Beyond the stream, the slope rises up to level ground upon which the middle transect is located in a mid-successional forest composed of birches (*Betula spp.*), ironwood (*Carpinus caroliniana*), and maples (*Acer spp.*) as well as some aspen (*Populus tremuloides*). Between the middle and interior transects, the forest abruptly shifts to being dominated by shrubs and small trees including hawthorns (*Crataegus sp.*) and buckthorns (*Rhamnus spp.*), suggesting the possibility of recent disturbance. While much of the plot is primary, disturbances such as woodlot grazing have occurred. Hawthorn (*Crataegus sp.*) is indicative of old pastures (H. Art, *personal communication*). Although some large trees are present, remnants of stone walls suggested an agricultural history.

Mt. Hope east: This fragment occupies a flat hilltop surrounded by a residence and grassy fields. The north side of the fragment is dominated by softwood species. An old boiler is present in the northern section of the fragment. Due to the narrow width of the fragment and a desire to avoid the effects of the west-east edge, two plots of the middle and interior transects are located behind the other three plots.

Chenail south: Cows are able to enter this fragment from their surrounding pastures. A clearing in the northeast corner of the fragment harbors a small house that was absent from the land use maps. The middle and interior transects were positioned somewhat west of the edge transect in order to avoid a steep slope both to the north of the edge transect and south of the middle and interior transects.

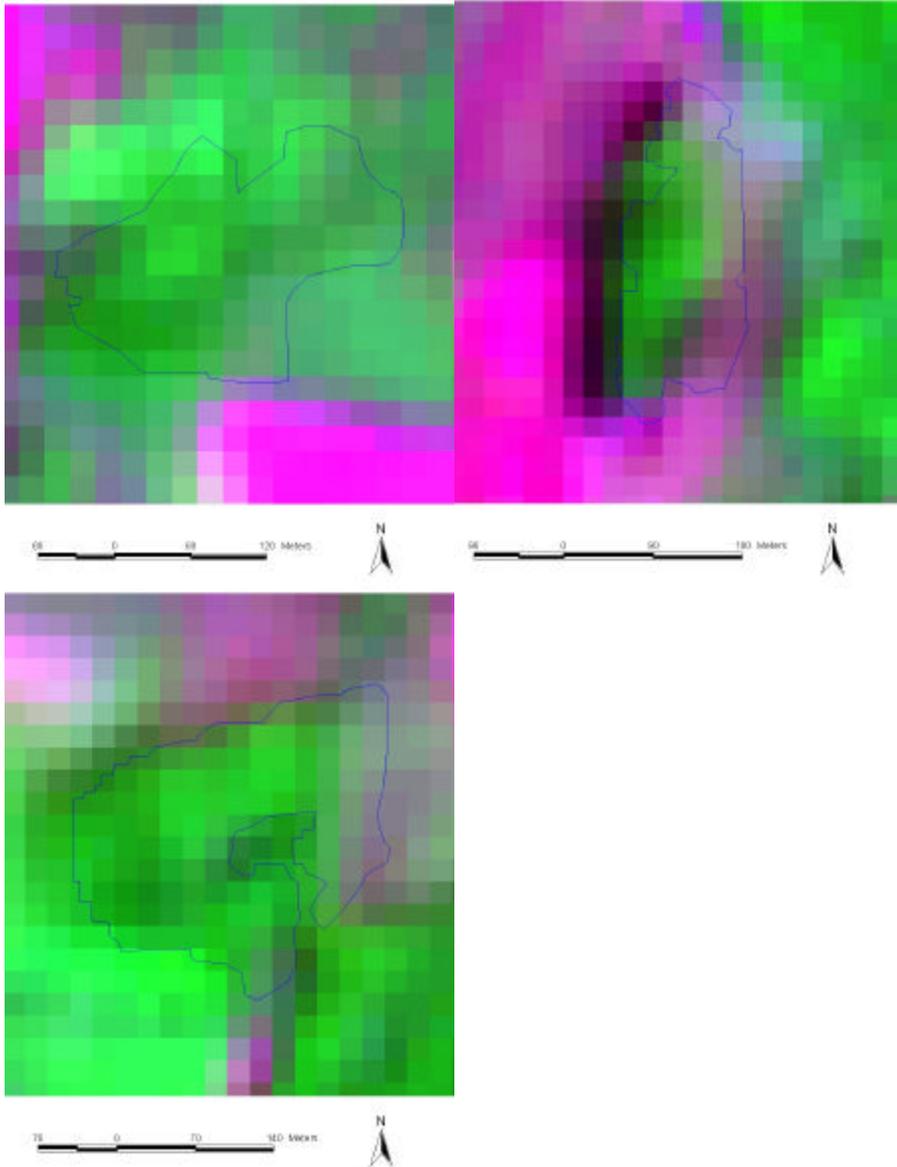


Figure 9: Landsat TM 30m resolution satellite images of the three small forest fragments. Arranged left to right, top to bottom, in order of increasing fragment area, the fragments are the airport plot, Mt. Hope east, and Chenail South.

Moderate Fragments (Figure 10)

Chenail north: This primary forest fragment is located just north of the Chenail south fragment and is also surrounded by cow pastures. An intermittent-stream bed is present near the eastern edge of the transects. The interior plot is shifted north slightly to avoid a wagon trail. A stone foundation is located west of the interior transect.

Luce Road: The southern edge of this fragment is confined by a low-traffic dirt road beyond which is a reservoir. While a portion of the remaining boundary borders a cornfield, fallow fields surround the rest. A decrepit, large-mesh wire fence spans the southern edge. The elevation of the fragment drops sharply into a valley beyond the interior transect. Although most of the fragment is primary, the northern portion was logged in the Spring of 1998 (H. Art, *personal communication*). Some areas of the fragment include coniferous vegetation. A number of down trees in the interior transect may have influenced plant composition in some plots.

Mt. Hope west: Portions of this predominantly primary fragment have been used for woodlot grazing (H. Art, *personal communication*). An old building is located at the western edge of this fragment, which is surrounded by open fields. The middle transect was shifted west to avoid a clearing associated with another buildings. Wagon paths traverse the fragment, although none were in the study transects. The middle transect is located on a moderate to steep downward slope. The interior transect is at the base of this slope. A large section of relatively narrow forest extends west-east beyond the region containing the transects.

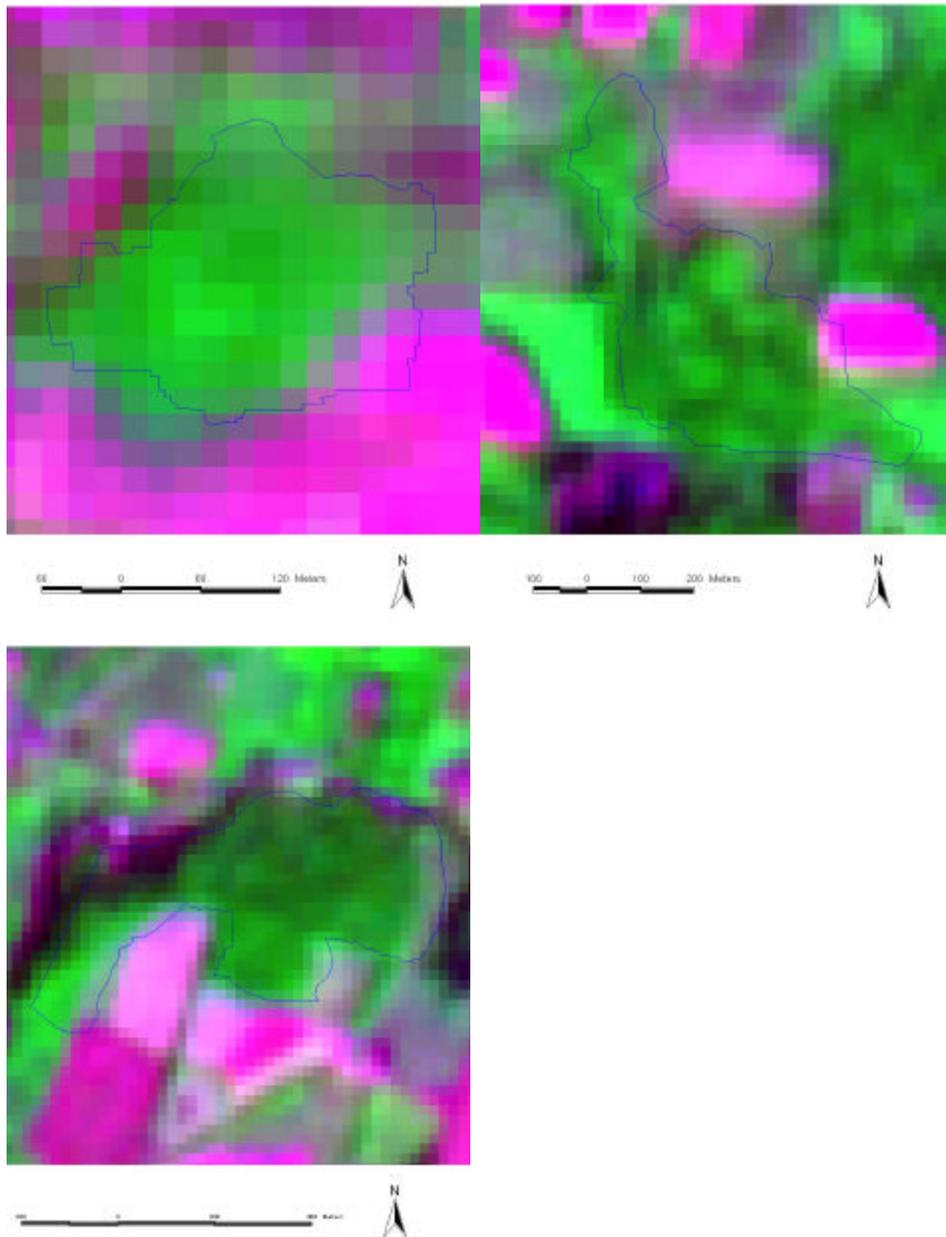


Figure 10: Landsat TM 30m resolution satellite images of the three moderate sized fragments. Arranged left to right, top to bottom, in order of increasing fragment area, the fragments are Chenail north, Luce Road, and Mt. Hope West.

Large Fragments (Figure 11)

Hopper Road: While residences delineate the western and north edges of this fragment, open fields border the remainder. The southeast corner of the fragment is connected to the large, contiguous forest at the base of Mount Greylock by a narrow swath of vegetation. However, the vegetation appears too sparse and narrow to affect fragment dynamics by

servicing as a corridor for the movement of animals. Two of the edge plots did not run along the same west-east parallel as the other three plots due to a non-linear edge. A wide-mesh wire fence spans the eastern portion of the edge transect. A stream runs west-east through the fragment beyond the interior transect.

Sloan Road: Open fields and residences border the fragment, excepting the northern edge, which is fragmented by a road. The large fragment size and absence of visible disturbances may be attributed to its being managed by a local land trust. As such, there was a trail in its northern region. The northern region has experienced past disturbance, likely from woodlot grazing (H. Art, *personal communication*).

Greylock Highschool: While the fragment is mainly primary forest, woodlot grazing occurred in an area referred to as the east knob (H. Art, *personal communication*). Roads, fields, and the high school at the southeastern edge delineate the fragment margins. As this fragment is also managed by a land trust, a trail runs along the fragment's edge. A river flows west-east just south of the interior transect. Two of the interior transect plots were shifted somewhat westward to avoid a trail.

Deer Ridge: Fallow agricultural fields confine the southern and western edges of this mainly primary fragment, while residences delineate the north and eastern edges. An old road running north-south marks the center of the plot. The transects are located to the west of this road. The land generally slopes downward from the road westward. Some other signs of prior human disturbance, such as stone walls are visible. While the southern section of the fragment is owned by the state, the northern section is part of the Mt. Hope Farm property. The edge transect does not run precisely west-east, but is actually oriented north-west to south-east. A substantial river flows slightly further into the fragment beyond the edge plot. The middle and interior transects are oriented approximately west-east; due to the large size of the fragment, We did not recognize a need for parallel orientation with the edge plot. The middle and interior plots are located at a higher elevation than the edge plot and slope marginally downward to the west.

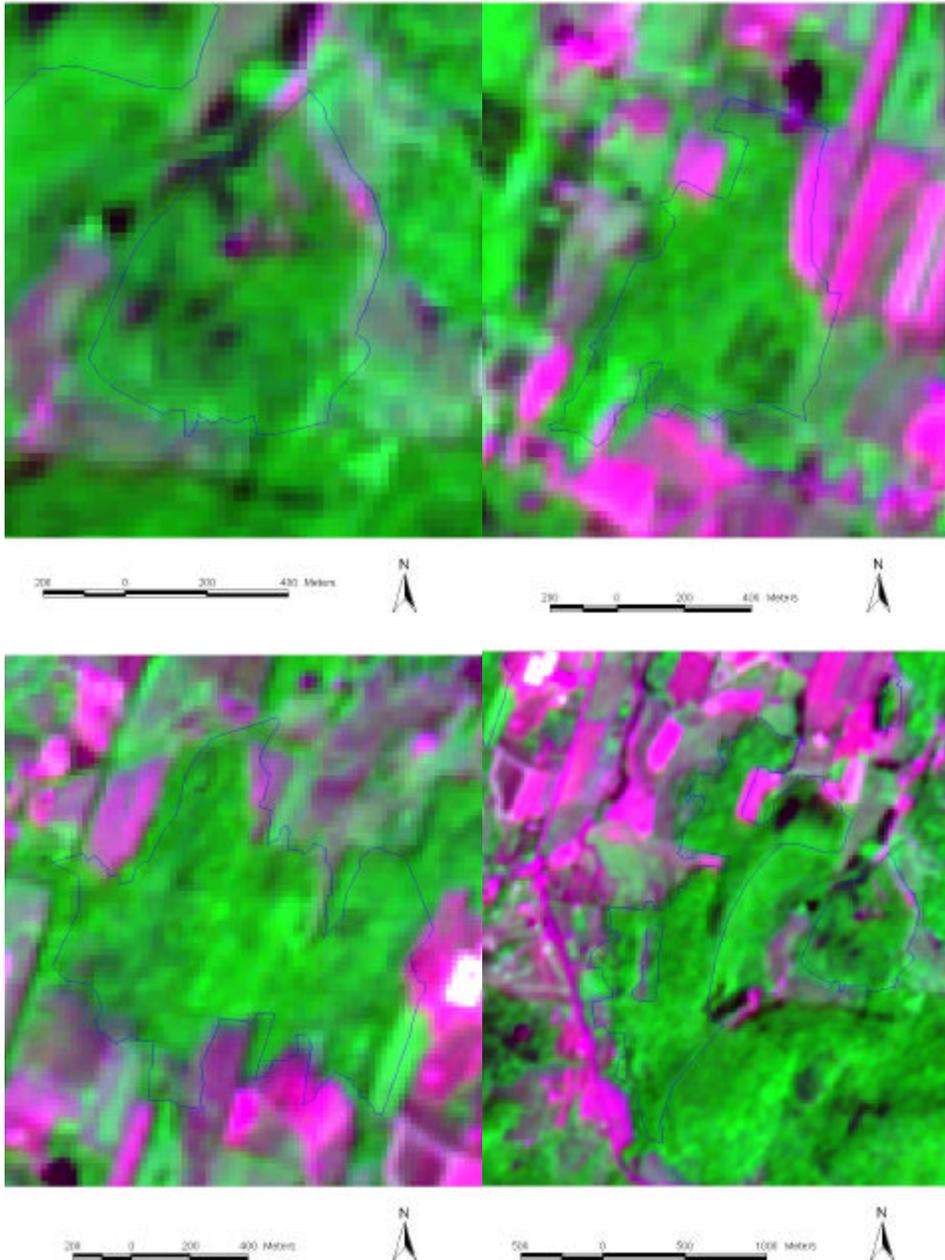


Figure 11: Landsat TM 30m resolution satellite images of the four large sized fragments. Arranged left to right in order of increasing fragment area, the fragments are Hopper Road, Sloan Road, Greylock, and Deer Ridge.

Experimental Design

We censused woody vegetation along three transects within each of the ten study fragments. The outer edges of the three transects were located at the edge of the fragment, the center of the fragment, and midway between. We located the edge transect along a relatively linear edge section of at least 50m and as near to the midpoint of the fragment’s southern

exposure as possible. The southern edge was chosen to maximize edge effects. Southern edges may incur enhanced edge effects due to their greater duration of sun exposure (Palik and Murphy 1990). Middle and interior transects were oriented parallel to and directly behind the edge transect (figure 12). We assessed the distance of the north-south axis of each fragment using the measuring tool in ArcView GIS. Areas at the northern edge that were significantly narrower than the remainder of the fragments were excluded from the distance measurements. Where noted in the above fragment descriptions, we positioned the middle and interior transects at distances deviating from their measured intended location in order to avoid extreme disturbances (such as old wagon trails) that were uncharacteristic of the fragment.

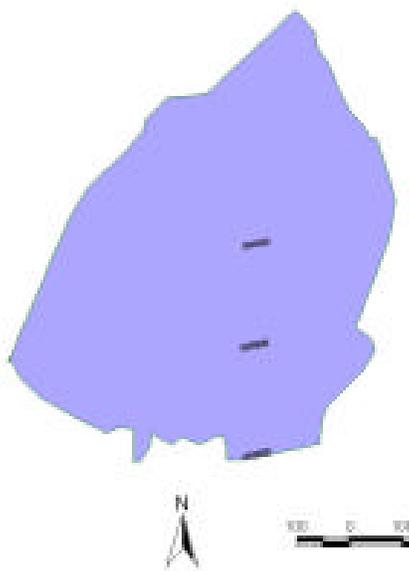


Figure 12: A map of the Hopper fragment showing the experimental design. In each of the 10 study fragments, a transect was located along the southern edge, at the center of the fragment, and midway between. The three transects were aligned parallel to each other. The middle and center of each plot was located using a GIS measuring tool.

The west-east transect axis consisted of ten 5m contiguous plots. An outer and inner row of plots each extending 5 m were located along this axis (figure 13). We eventually combined the ten 5mX5m plots along the outer and inner transect into two rows of 10mX5m plots by combining adjoining plots along the west-east axis. While data collection was facilitated by the 5mX5m plot size, combining the data reduced the effects of environmental heterogeneity.

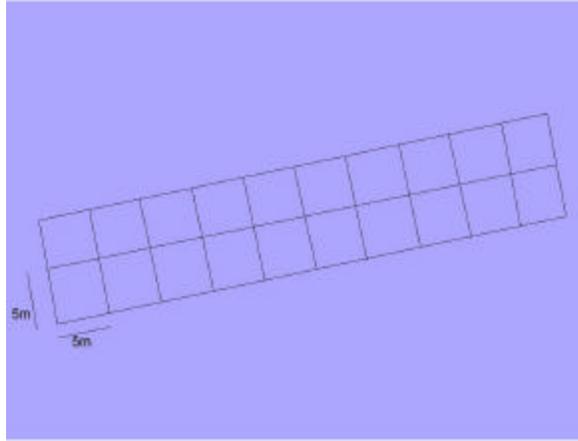


Figure 13: Each of the three transects within a fragment consisted of both an outer and an inner row of ten 5mx5m plots.

We identified to species all woody shrubs that were taller than .25m and trees that were taller than waist height (approximately 1.0 m). Species were distinguished as trees or shrubs by growth habit. Species that characteristically have a single dominant trunk and lack low branches were considered to be trees. We classified trees as either seedlings or mature trees: we considered individuals with diameters (dbh) less than (12 cm) to be seedlings. We counted consolidated clumps of stems as single shrub individuals. We conducted vegetation censusing in a random plot ordering from late September through mid November. We censused approximately half of the fragments following the occurrence of substantial leaf loss.

Analysis

We defined tree and shrub species as either native or non-native according to Weatherbee (1996). For each plot, we grouped tree and shrub species to determine the species richness, total number of individuals, percent invasive species (number invasive species/ total number of species), and percent invasive individuals (number invasive individuals/ total number individuals). As no significant differences were observed between the outer and inner rows of the middle and interior transects, we combined the outer and inner row data for much of our analysis. We calculated diversity indices as detailed below.

Our statistical analysis accounted for the non-independent sampling associated with the similar environmental conditions of the 10 contiguous plots within each transect. Non-independence is accommodated by using the transect as a clustering variable for the plots. We used the survey regression functions of the Stata 6.0 (Stata Corporation) statistics

and data analysis program. The problem of non-independence of plots can generally be accommodated using regression terms for the fragment, region, and the cross of the fragment and region. However, as the regression matrix columns corresponding to the area of the fragments (which we wished to use as a predictor variable) were not linearly independent from those of the fragment dummy variables, we instead used the survey regression functions to predict on the plot level. Survey regressions account for sampling clusters of non-independent entities within a population (such as surveying blocks of houses within a town). The model residuals were checked for an approximately linear distribution in order to meet the assumptions of normally distributed error with mean zero for linear regressions. All percentages were square-root transformed in order to avoid the lack of linearity of percentage errors.

The two forms of analysis presented consider fragment area to be either a continuous or discrete variable. It is infeasible for either to illustrate the clustered design graphically. Instead, when fragment area was considered to be a continuous variable, regression graphs show parameters in relation to fragment area as the independent variable and each data point in the figure is the mean of the ten plots within each transect. Although only showing the mean results in some loss of information, it avoids making incorrect visual conclusions due to the clustering of plots. The linear trend lines depicted are only approximations as they are based on the transect means. We present the regression table for the survey linear regression model, showing the significance level and r^2 -value for the overall model. We tabulate the coefficient, standard error, and p-value for each effect in the model. The coefficient, derived from the regression equation, assesses the contribution of each effect in determining the value of the response variable. We also present whether the slope of the trendline for each independent relationship is significantly different from zero (as calculated with a survey regression).

In the graphs showing fragment area or region as a discrete variable, data are means of the observations for each plot within each transect. The standard errors shown are smaller than actual errors because they fail to account for non-independence of plots. Significant pairwise differences were calculated using a survey regression. Some cases are not differentiated pairwise despite the appearance of significant differences based on error bars due to the portrayal of error without accounting for non-independence.

Diversity and evenness indices were calculated on the transect level due to the relatively small size of the plots. Thus, the diversity and evenness indices did not involve a clustered experimental design. The data were analyzed using linear regressions and ANOVAS in JMP 3.2.6 (SAS Institute) or Stata 6.0.

Species richness, evenness, and diversity

Although most ecologists agree that it is desirable to invoke the notion of *species diversity* to distinguish between communities with equal species richness but different community compositions, uncertainty arises in methods for assessing species diversity (Hurlbert 1971). Many indices of diversity have been developed to gauge community heterogeneity, most of which are wrought with mathematically undesirable qualities and are difficult to interpret (Peet 1974). Hurlbert (1971) has gone so far as to claim that species diversity has become a “non-concept” due to its various and disparate definitions. Species diversity is generally held to be composed of two components: the richness of species and the evenness of species abundances (Peet 1975). In our assessment of species diversity, we use Hill’s diversity numbers which are generally more interpretable than the commonly used Simpson and Shannon (also referred to as Shannon-Weaver or Shannon-Wiener) indices from which they are derived (Ludwig and Reynolds 1988). We use the unbiased form of Simpson’s index, which ranges from 0 to 1 and gives the probability that two species drawn at random from a population belong to the same species. If n_i is the number of individuals of the i^{th} species, n is the total number of individuals and S is the total number of species in the sample, then Simpson’s unbiased estimator (Simpson 1949) assumes the form:

$$I = \sum_{i=1}^s \frac{n_i(n_i - 1)}{n(n - 1)}$$

Shannon’s index, which is based on information theory, indicates the average “uncertainty” in predicting the species to which a randomly chosen individual belongs. Shannon’s index is as follows (Shannon and Weaver 1949):

$$H' = -\sum_{i=1}^s \frac{n_i}{n} \ln \frac{n_i}{n}$$

Hill’s diversity numbers assess the “effective number of species” in a sample, which is the degree to which proportional abundances are distributed among species (Hill 1973). The

diversity numbers are in units of number of species, where N1 and N2 indicate the number of abundant and very abundant species, respectively. As diversity decreases, both diversity numbers N1 and N2 approach 1 (Hill 1973):

$$N1 = e^{H'}$$
$$N2 = 1/\mathbf{I}$$

where H' = Shannon's Index and \mathbf{I} = Simpson's Index

Some ecologists avoiding compounding species richness and evenness in diversity indices in favor of analyzing the two parameters independently (Ludwig and Reynolds 1988).

Although we provide analysis of the diversity numbers N1 and N2, treating species diversity and evenness independently is our primarily approach employed. We use the modified Hill's ratio to assess species evenness. The ratio, which is the fraction of very abundant to abundant species, approaches zero as the dominance of a single species increases (Alatalo 1981). The modified Hill's ratio (E) has the advantage of being independent of species richness of the sample, unlike the commonly applied J' of Pielou (Peet 1974):

$$E = \frac{N2 - 1}{N1 - 1}$$

The N1 and N2 diversity numbers as well as the modified Hill's ratio were calculated by considering the species in the entire transect. This eliminated the stochastic effects of the small sizes of plots.

Results:

27.8% of the 61 tree and shrub species present in the study fragments were invasive (Appendix B). Our observations included 32 native tree species, 12 native shrub species, 2 non-native tree species, and 15 non-native shrub species (figure 14).

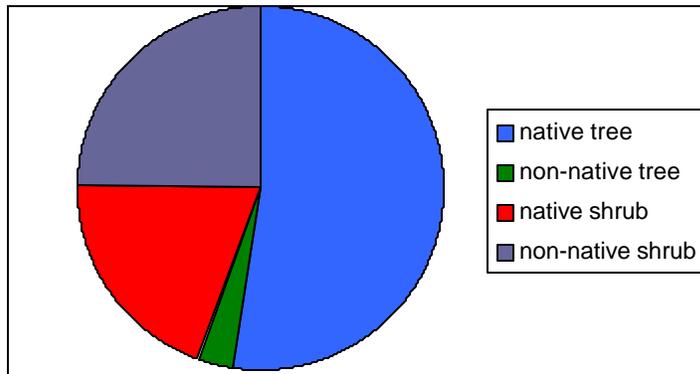


Figure 14: The combined proportion of native and non-native tree and shrub species censused in all the study fragments.

Edge Effects

Fragment edges have significantly more invasive plants than the interior. While, on average, 40% of the individual plants sampled in the edge transect are invasive, middle and interior regions have fewer invasives (19% and 14%, respectively). The percent of invasive species also declines with mean values of 36%, 16%, and 19%, respectively (Figure 15). While both the percent invasive species and individuals significantly differentiated the edge from the middle and interior regions, the middle and interior regions were not significantly different (Table 1).

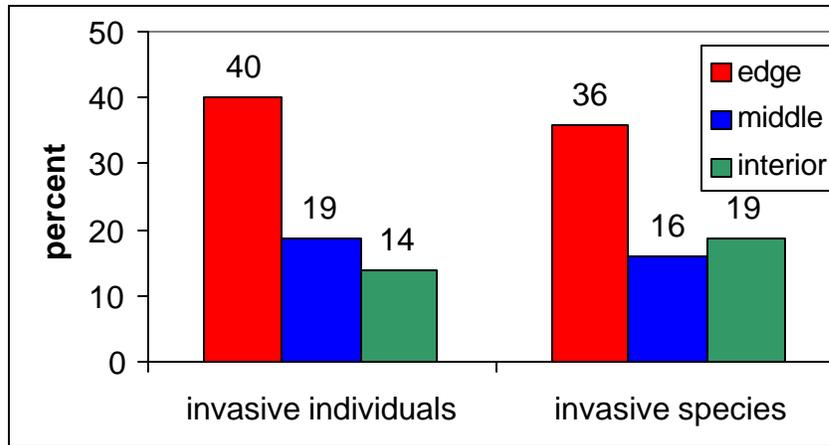


Figure 15: Both the percent of invasive individuals and invasive species decline significantly from the edge to the interior of the fragments. Data are mean of the values for the 10 fragments. The percent invasive individuals and percent invasive species of the edge region are significantly differentiated from both the middle and interior regions.

Table 1: A survey linear regression model ($p=.0254$, $r^2=.1396$) showing that percent of invasive individuals and invasive species decline significantly from the edge to the interior of the fragments.

	coef	std. Err.	p-value	* sig at $p<.05$ ** sig at $p<.01$
percent invasive individuals		$p=.0254$	$r^2=.1396$	
edge-middle	0.219	0.0969	0.031	*
edge-interior	0.267	0.0956	0.009	**
middle-interior	0.0476	0.0945	0.618	
percent invasive species		$p=.0341$	$r^2=.1633$	
edge-middle	0.2517	0.117	0.04	*
edge-interior	0.3145	0.1165	0.012	*
middle-interior	0.0627	0.1108	0.575	

The influence of edge effects was observed to decline beyond the outer row (0 to 5m) of the edge transect to the inner row (5 to 10 m) (Figure 16). The species richness and number of individuals decline significantly beyond 5m into the fragment (Table 2). The degree of differentiation between the outer and inner rows was independent of size class. The decline in percent invasive species and individuals between the outer and inner rows was non-significant but suggestive. The effect of area was removed from the model for each parameter and was significant in all cases (Table 2). When treating the trendlines independently for each position (outer or inner) and parameter, each response was

significantly correlated with area, excepting the trends for species richness and number individuals (Figure 16). The outer and inner rows of the middle and interior transects did not possess differentiated species richness, number individuals, percent invasive species, or percent invasive individuals.

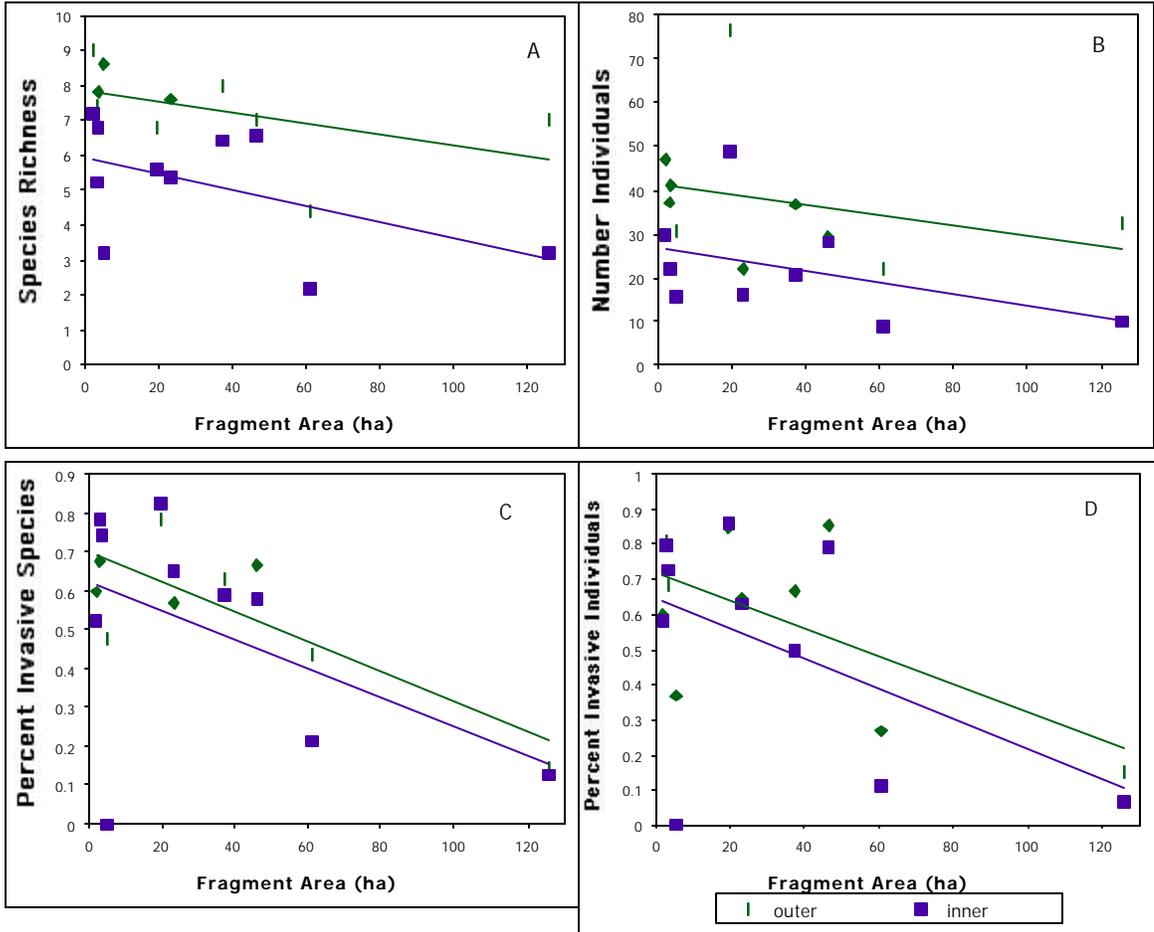


Figure 16: The (A) species richness, (B) number individuals, (C) percent invasive species, and (D) percent invasive individuals for the outer (0-5m) (green) and inner (5-10m) (purple) rows of the edge region. Data are means of the ten 5x10m² plots in the 10 study fragments. Although the outer and inner rows of the middle and interior transects were not significantly differentiated (data not shown), the outer row parameters are significantly higher than those of the inner row of the edge transect (Table 2). When treating each trendline individually, species richness, number individuals, percent invasive species, and percent invasive individuals were significantly correlated with area excepting the trends for species richness and total number individuals for the outer row. The outer and inner rows are not significantly different from each other unless the effect of area is removed (Table 2).

Table 2: A survey linear regression model ($p=.0008$, $r^2=.2959$) examining the significant differences in community parameter values between the outer and inner rows.

	coef	std. Err.	p-value	* sig at p<.05
species richness		$p=.0008$	$r^2=.2959$	** sig at p<.01
outer-inner	-2.180	0.459	0.001	**
area	-0.019	0.008	0.042	*
number individuals		$p=.0009$	$r^2=.2547$	
outer-inner	-15.320	2.375	0.000	**
area	-0.126	0.055	0.048	*
percent invasive species		$p=.0007$	$r^2=.2925$	
outer-inner	-0.069	0.237	0.054	
area	-0.004	0.001	0.007	**
percent invasive individuals		$p=.0018$	$r^2=.2472$	
outer-inner	-0.083	0.039	0.062	
area	-0.004	0.001	0.013	*

Area Effects

Species richness, the number of individuals, and percent invasive species and individuals decreased with larger fragment sizes and from the edge to the interior of the fragments (Figure 17). Regression models incorporating fragment area and region were highly significant in their ability to account for trends in species richness, percent invasive species, and percent invasive individuals. The regression model for number individuals was suggestive, while non-significant (Table 3). Despite the significance of the overall models, the degree of significance of the individual terms varies. While increasing area was not significantly correlated with decreases in the number of individuals ($p=.152$) in the regression model, this correlation was significant for species richness ($p=.037$), percent invasive species ($p=.000$), and percent invasive individuals ($p=.000$). While the trend of decreasing community parameter values with increasing fragment area was significantly differentiated between the edge and both the middle and interior transects in all cases, the trend was not significantly differentiated between the middle and interior transects for any parameter (Table 3).

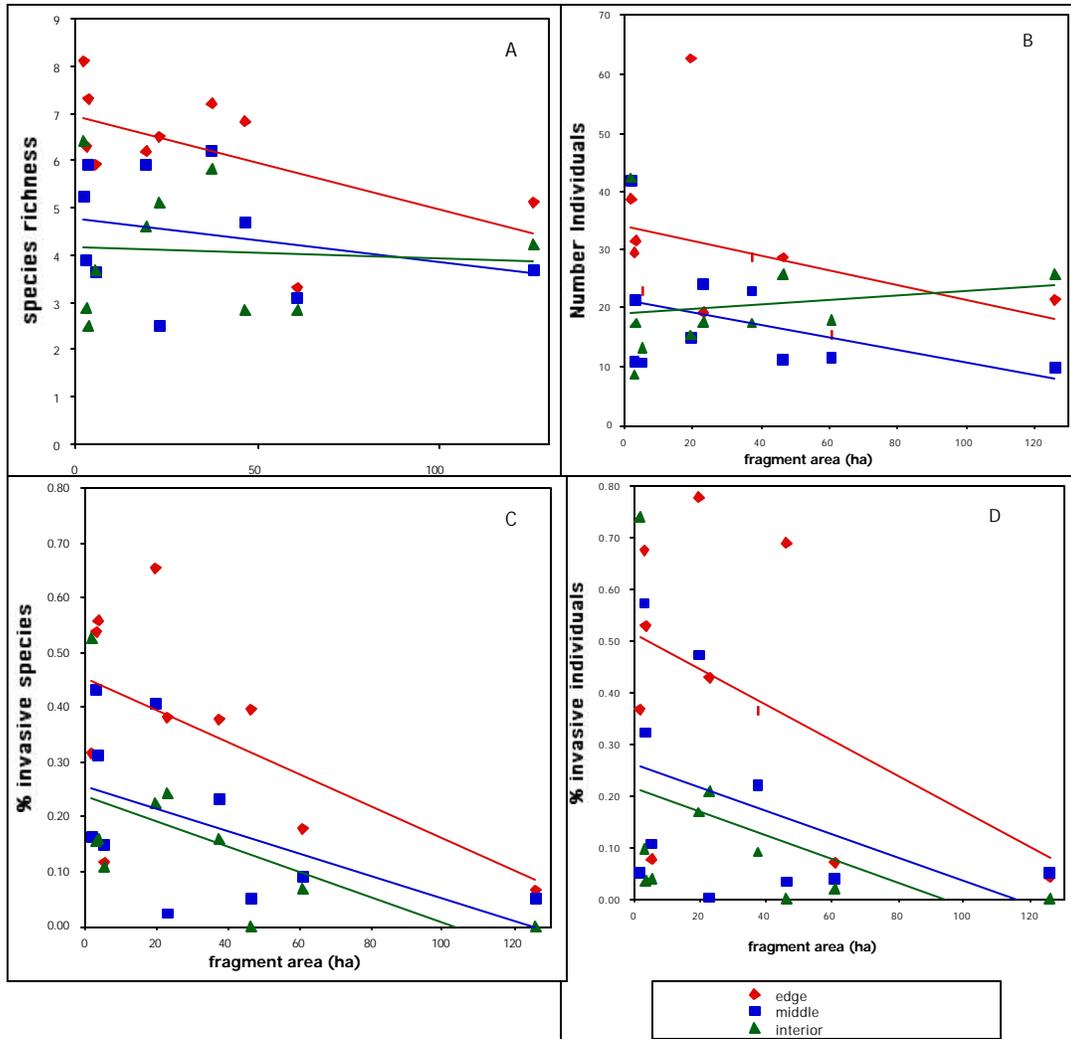


Figure 17: The (A) species richness; (B) number individuals; (C) percent invasive species; and (D) percent invasive individuals in relation to fragment area for the edge (red), middle (blue), and interior (green) transects of each forest fragment. Data points are means for the 10 sampling plots in each transect for the 10 forest fragments. When considering the regression lines individually, the slopes are significantly different from zero for all four measures in the edge region, for species richness and percent invasive species and individuals in the middle region, and only for the percent invasive species in the interior region. The regression lines were not significantly differentiated between fragment regions for any parameter.

Table 3: A survey linear regression model that significantly differentiates the contributions of fragments region in predicting the species richness, number individuals, or percent invasive species and individuals.

	coef	std. Err.	p-value	* sig at p<.05		** sig at p<.01		
Species Richness		p=.0001	r ² =.192		Percent invasive species	p=.0000	r ² =.308	
area	-0.010	0.005	0.037	*	area	-0.003	0.000	0.000 **
edge-middle	2.190	0.556	0.000	**	edge-middle	0.267	0.074	0.001 **
edge-interior	1.800	0.519	0.002	**	edge-interior	0.219	0.077	0.008 **
middle-interior	-0.390	0.573	0.502		middle-interior	-0.047	0.076	0.536
Number Individuals		p=.061	r ² =.138		Percent invasive individuals	p=.0001	r ² =.312	
area	-0.064	0.043	0.152		area	-0.003	0.001	0.000 **
edge-middle	9.640	4.920	0.060	*	edge-middle	0.315	0.099	0.003 **
edge-interior	11.890	4.770	0.019	*	edge-interior	0.252	0.100	0.017 *
middle-interior	2.250	4.160	0.593		middle-interior	-0.063	0.097	0.522

Larger fragments appear to have decreased susceptibility to invasive species at the edge region, as a significant correlation exists between increases in area and increases in species richness (p=.042), number individuals (p=.048), percent invasive species (p=.007), and percent invasive individuals (p=.013) (Table 4). The distances from the fragment edge to the middle and interior transects are proportional to the size of the fragment. Because of this compounding of distance to the fragment edge and fragment area for the middle and interior regions, the observation of the effects of fragmentation in the edge region is notable. Larger forest fragments had significantly greater area to perimeter ratios (figure 18).

Table 4: The effect of area on edge parameters in a survey linear regression model. The effect of area is most pronounced at the edge region. Although the distance into the fragment of the middle and interior transects vary with fragment size, the trends for the universally located edge fragment lend strength to our conclusions regarding the effect of fragment size on the four considered parameters.

	coef	std. Err.	p-value	* sig at p<.05
species richness				** sig at p<.01
area	-0.019	0.008	0.042	*
number individuals				
area	-0.126	0.055	0.048	*
percent invasive species				
area	-0.004	0.001	0.007	**
percent invasive individuals				
area	-0.004	0.001	0.013	*

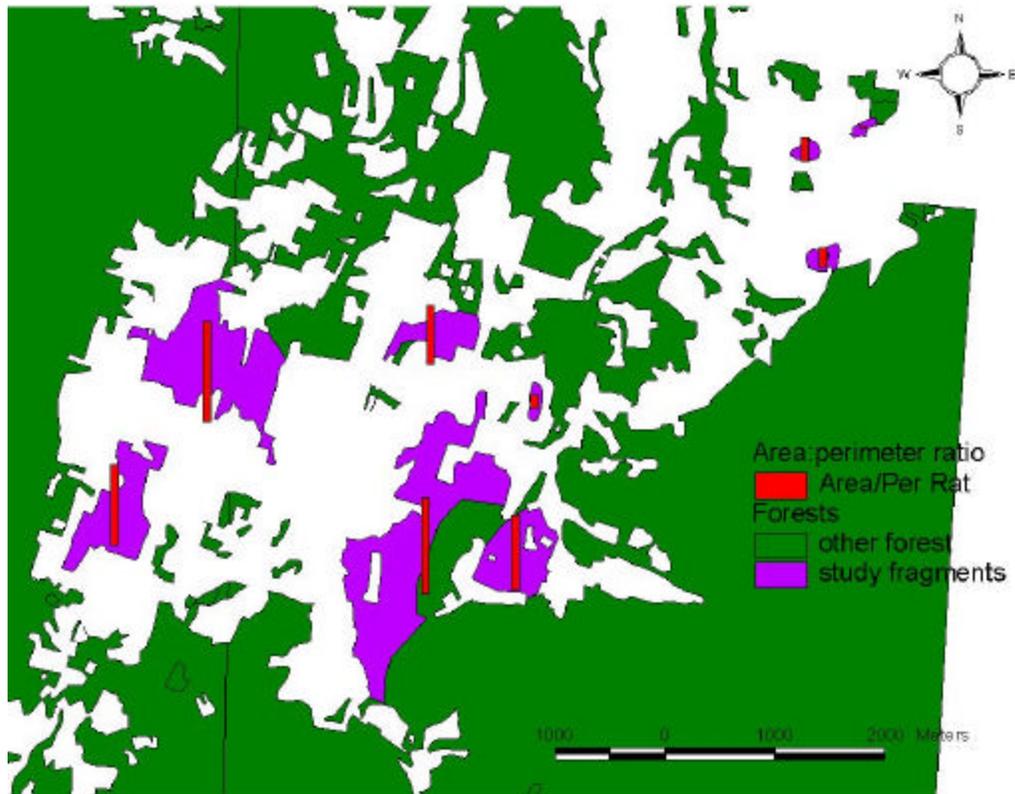


Figure 18: Area to perimeter ratios (longer red lines indicate larger area/perimeter ratios) for the forest study fragments (purple). The larger fragments are observed to possess greater area to perimeter ratios than the smaller fragments.

Area is significantly correlated with species richness when considering native and invasive species independently (Figure 19). Regression analysis significantly differentiates the trends for native and invasive species and the trend for the edge region from that of the middle and interior regions (Table 5). When considering the correlation with area for each combination of vegetation type (native or invasive) and region independently, the species richness of invasive edge and middle species decreased significantly with increasing fragment area. The converse trend was observed for the native community in the interior region; the species richness of the interior native community increased significantly with increasing fragment area ($p=0.022$). This trend is also perceptible, though non-significant, for the edge and middle regions. The abundances of native and invasive species are significantly differentiated ($p=0.007$) when considered across all fragment regions, but fragment area is not a significant factor in the regression model (Figure 20). Only the number individuals of the edge and middle regions are significantly differentiated in the regression model ($p=0.019$).

(Table 6). When considering the trends independently for each type and region combination as with species richness, the relationship between number individuals and area was significant for invasive edge and middle species. Corresponding to the trend observed for native, interior species richness, the number of native individuals in the edge region increased significantly ($p=.000$) with increasing fragment area.

Neither the species richness nor abundance of native species is significantly correlated with fragment area or fragment region. However, when invasive species are considered independently, the effect of fragment area and region of invasive species richness and abundance is accentuated beyond that observed in the general model (Table 7). Increasing fragment area is observed to be a significant deterrent of species invasion, as increasing area is a significant effect for reducing both the species richness ($p=.000$) and number individuals ($p=.016$) of invasive species. While the invasive species richness of the edge region was significantly differentiated from both the middle and interior regions, the number of invasive edge individuals was only significantly differentiated from the middle region (Table 7).

Table 7: A survey linear regression analysis of the invasive species exclusively further clarifies the trends observed in figures 19 and 20. As the species richness and number of native species is observed to be largely unaffected by area, the significance of the correlation between species richness and abundance of invasive species and fragment area is greater than that of the combined model. The survey linear regression models relating native species richness and abundance with area and fragment region are not significant.

	coef	std. Err.	p-value	* sig at $p<.05$
species richness		$p=.0000$	$r^2=.3937$	** sig at $p<.01$
area	-0.015	0.003	0.000	**
edge-middle	1.390	0.363	0.001	**
edge-interior	1.530	0.387	0.000	**
middle-interior	0.140	0.322	0.667	
number individuals		$p=.0299$	$r^2=.2044$	
area	-0.089	0.035	0.016	*
edge-middle	11.760	4.443	0.013	*
edge-interior	10.450	5.195	0.054	
middle-interior	-1.310	3.027	0.668	

Species Diversity and Evenness

Fragment size category did not significantly influence overall diversity and evenness, although the transect did have a significant effect on N1 ($p=.0291$), N2 ($p=.0499$), and the MHR ($p=.0534$) (Figure 21). The diversity and evenness indices tended to increase from the interior to the edge of the fragments. While pairwise comparisons of N1, N2, and the MHR

were significantly (or highly suggestively) differentiated the edge transect, the middle and interior regions were not significantly differentiated (Table 8). The trend of greater diversity and evenness indices values in the edge transect is most accentuated in the small fragments (Figure 22). Considering only the small fragments, the transect is a significant effect for N1 ($p=.0374$), N2 ($p=.0163$), and the MHR ($p=.0229$). The edge transect was significantly differentiated, according to pairwise comparisons, from the middle and interior transects. Transect position did not have a significant effect when the moderate and large sized plots were considered independently (Figure 22).

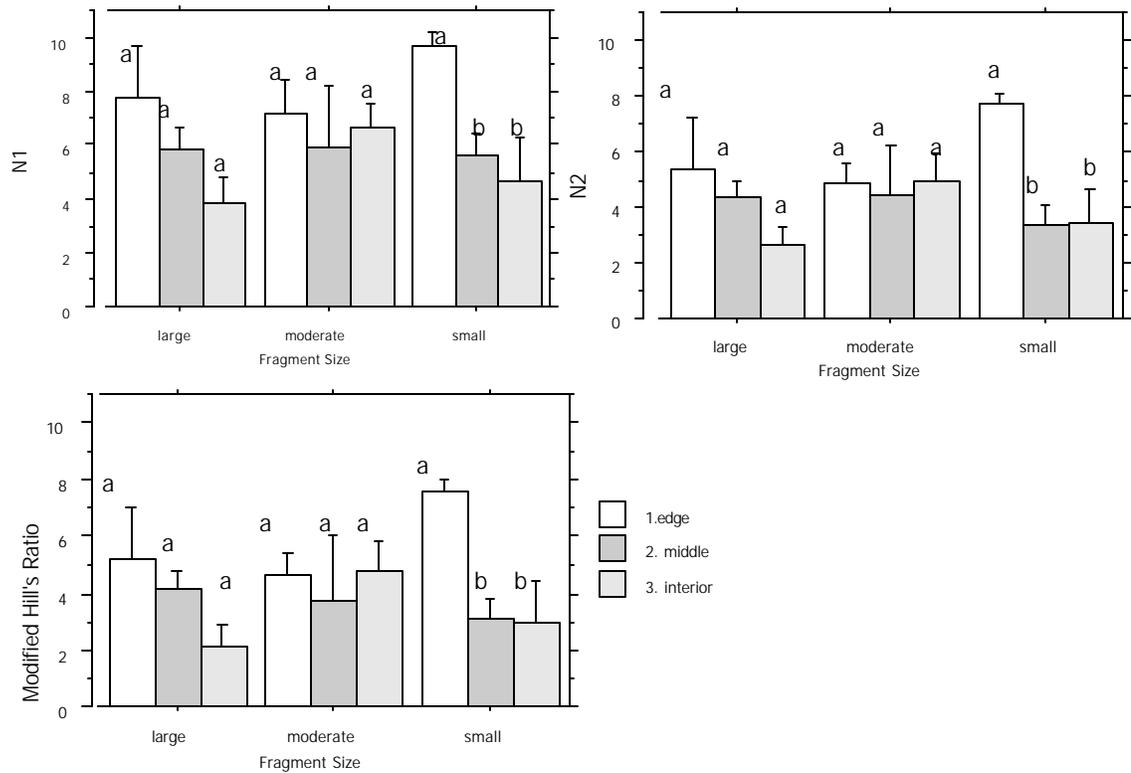


Figure 21: The species diversity (Hill's diversity numbers N1 and N2) and evenness (Modified Hill's ratio) of the fragments considering transect and size category. Fragment regions with different letters within each size class and diversity or evenness measure are significantly different at $p=0.05$. While fragment size class does not significantly influence overall diversity and evenness, the transect does have a substantial effect on N1 ($p=.0291$), N2 ($p=.0499$), and the Modified Hill's Ratio ($p=.0534$) (Pairwise comparisons compiled in table 8). The parameters are shown as means ($n=3,4$) with one standard error.

Table 8: The p-values for Fisher's LSD pairwise comparisons between transect for the diversity and evenness indices.

Transect	N1	N2	Modified Hill's Ratio
Edge- middle	0.048	0.058	0.063
Edge- interior	0.001	0.02	0.021
Middle-interior	0.449	0.607	0.604

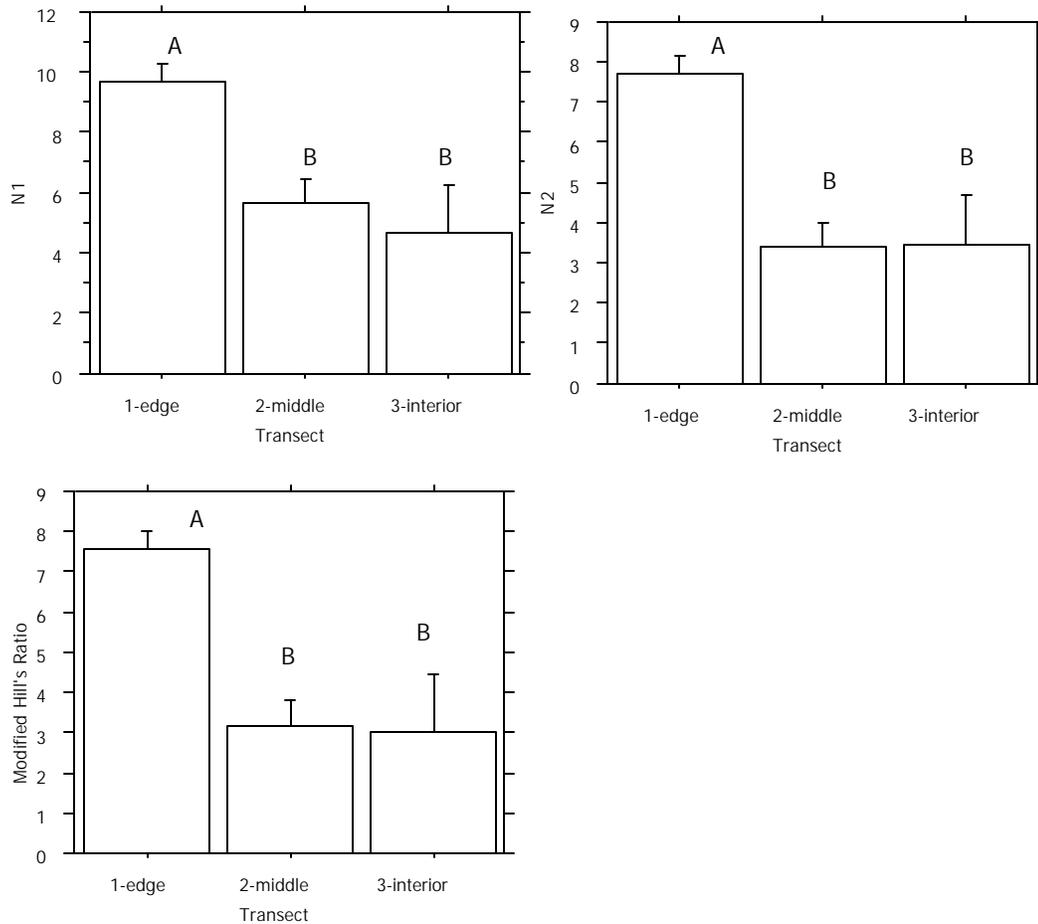


Figure 22: The trend of greater diversity and evenness indices values in the edge transects is most accentuated in the small fragments. Considering only the small fragments, the fragment region is a significant effect for N1 ($p=0.0374$), N2 ($p=0.0163$), and the Modified Hill's Ratio ($p=0.0229$). Different letters indicate cases that are significantly different ($p < 0.05$). The transect did not have a significant effect when the moderate and large sized plots were considered independently. Data are means ($n=3,4$) with one standard error.

No significant relationship between the diversity (N1 and N2) and evenness indices (MHR) and fragment area (as a continuous variable) exists when considering native and invasive species together. However, regression models incorporating the effects of area and fragment region were significant predictors of the diversity and evenness indices for the invasive species community (Figure 23, Table 9). Area was significantly inversely correlated with N1, N2, and MHR for non-native species in the regression models. The models significantly differentiated the higher indices for the edge region from those of the middle regions for each diversity and evenness index, while the edge and interior regions were also significantly differentiated for N1. The regression models for native species, granting consideration to area and fragment region, were not significant. When considering the trends for each combination of fragment region and vegetation type (native or invasive) individually, significant declines in N1, N2 and the Modified Hill's Ratio are observed with increasing fragment area for the invasive species of some fragment regions. The N1 diversity number decreases with increasing area for the non-native species of the edge ($p=.0032$) and middle transects ($p=.0649$). A similar trend is observed for N2 for the non-native species of the edge ($p=.0081$) and interior ($p=.0546$) transects. A significant ($p=.0004$) decrease in the Modified Hill's ratio occurs with increasing fragment area for non-native species of the edge transect. There were no significant trends when examining the effects of fragment area on the diversity and evenness indices for native species in each region independently (Figure 23).

Table 9: A survey linear regression model that considers the influence of fragment area and region on the diversity and evenness indices of the non-native community.

	coef	std.err.	p-value	* sig at p<.05
N1	p=.0008	r ² =.4348		** sig at p<.01
area	-0.015	0.004	0.002	**
edge-middle	1.176	0.347	0.002	**
edge-interior	0.803	0.373	0.042	*
middle-interior	-0.373	0.373	0.328	
N2	p=.0067	r ² =.433		
area	-0.018	0.006	0.003	**
edge-middle	0.971	0.357	0.013	*
edge-interior	0.553	0.381	0.161	
middle-interior	-0.418	0.387	0.293	
Modified Hill's	p=.0007	r ² =.5304		
area	-0.030	0.007	0.000	**
edge-middle	1.287	0.458	0.010	**
edge-interior	0.836	0.461	0.084	
middle-interior	-0.451	0.477	0.354	

Dominance and Distribution of Invasive Shrubs

Shrub species richness and number of individual shrubs declined from the edge to the interior of the fragments (Figure 24). While the number of trees tended to increase in a converse (but non-significant) manner from the fragment edge to interior, there was no clear trend for tree species richness between the fragment regions (Figure 24, Table 10).

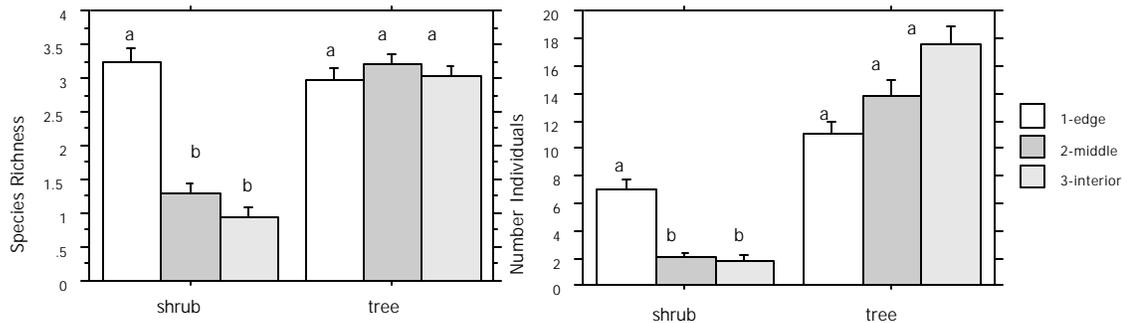


Figure 24: The (A) species richness and (B) number of individuals of shrubs and trees for the edge, middle, and interior regions of the forest fragments. Data are means of the ten plots in each of the ten fragments with one standard error. Transect regions within each vegetation type category with different letters are significantly different at p=.05. Fragment region significantly affected species richness and number individuals, while significantly differentiating trees and shrubs (Table 10).

Table 10: A survey linear regression model that uses fragment region and vegetation type (tree or shrub) to predict species richness and number individuals.

	coef	std. Err.	p-value	* sig at p<.05 ** sig at p<.01
species richness			$p=.0000$	$r^2=.1963$
tree-shrub	1.243	0.339	0.001	**
edge-middle	0.875	0.285	0.005	**
edge-interior	1.130	0.273	0.000	**
middle-interior	0.255	0.264	0.342	
number individuals			$p=.0000$	$r^2=.2697$
tree-shrub	10.596	1.837	0.000	**
edge-middle	1.080	1.793	0.552	
edge-interior	-0.685	1.649	0.681	
middle-interior	-1.765	2.112	0.410	

Native shrubs decline beyond the edge transect to remain stable in the middle and interior of the fragment. However, invasive shrubs continue their decline beyond the middle region to an abundance approximately equal to that of native shrubs in the interior region (Figure 25). These trends apply to both species richness and number of shrubs. In survey linear regression models considering the species richness and abundance trends for the three vegetation types together, the edge region was significantly differentiated from the middle and interior regions for both species richness and abundance (Table 11).

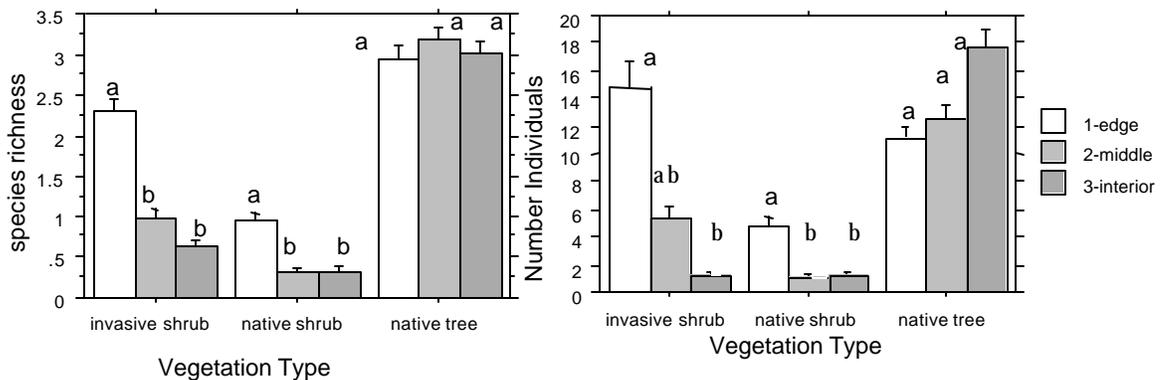


Figure 25: The (A) species richness and (B) number of individuals of invasive and native shrubs and native trees for the edge, middle, and interior forest fragment regions. Data are means of the ten plots in each of the ten fragments with one standard error. Fragment regions within each vegetation type with different letters are significantly different at $p=.05$. A survey linear regression model considers whether the edge, middle, and interior regions had significantly different species richness and abundance for each vegetation type (Table 11).

Table 11: A survey linear regression model that examines the contributions of fragment region and vegetation type for predicting the species richness and number individuals.

	coef	std. Err.	p-value	* sig at p<.05
species richness		p=.000	r ² =.460	** sig at p<.01
edge-middle	0.580	0.188	0.004	**
edge-interior	0.750	0.179	0.000	**
middle-interior	0.170	0.174	0.336	
nat tree-nat shr	2.520	0.191	0.000	**
nat tree-inv shr	1.746	0.283	0.000	**
nat shr-inv shr	-0.777	0.166	0.000	**
number individuals		p=.000	r ² =.201	
edge-middle	3.880	1.889	0.049	*
edge-interior	3.486	1.665	0.045	*
middle-interior	-0.400	1.581	0.802	
nat tree-nat shr	11.430	1.596	0.000	**
nat tree-inv shr	6.653	2.655	0.018	*
nat shr-inv shr	-4.770	1.980	0.022	*

While more species of invasive shrubs are present in more fragmented areas, the species richness of native trees and shrubs are not significantly influenced by fragment area (Figure 26). In a survey linear regression model incorporating vegetation type, area, and fragment region, the decrease in species richness with increasing fragments area was significantly differentiated from the edge to the middle and interior regions (Table 12). When considering the trendlines for each vegetation type and fragment region combination independently, the species richness of invasive shrubs decreased significantly with increasing area for all regions (Figure 26). Although the individual trendlines were not significantly differentiated between the regions, in a regression model considering exclusively invasive shrubs, increasing area was significantly correlated with decreasing species richness (p=.000) in a manner that significantly differentiated the edge from the middle and interior regions (Table 13). The individual trendlines and regression models for native shrubs and trees were not significant.

Table 13: Most of the observed trends for species richness in figure 26 may be attributed to correlation between the species richness of invasive shrubs and fragment area. Area and fragment region were used to predict the species richness of invasive shrubs in the following survey linear regression model. The regressions for the species richness of native shrubs and native trees alone were not significant.

	coeff	Std. Err.	p-value	* sig at p<.05
species richness		p=.0000	r ² =.4160	** sig at p<.01
area	-0.013	0.003	0.000	**
edge-middle	1.330	0.353	0.001	**
edge-interior	1.690	0.318	0.000	**
middle-interior	0.360	0.250	0.160	

While more invasive shrub individuals are present in more fragmented areas, the species richness of native trees and shrubs do not correlate with fragment area (Figure 27). The number individuals was significantly greater in the middle than in the interior regions and was significantly differentiated between vegetation types in a survey linear regression model incorporating vegetation type, area, and fragment region (Table 14). Fragment area was not a significant effect in the model. When considering the trendlines for each vegetation type and fragment region combination independently, the number individuals of invasive shrubs decreased significantly with increasing area for the edge and interior regions (Figure 27). Although the individuals trendlines were not significantly differentiated between the regions, in a regression model considering exclusively invasive shrubs, increasing area exerted a significant influence in decreasing the number individuals (p=.015) that was significantly differentiated between the edge and interior regions (Table 15). The individual trendlines and regression models for native shrubs and trees were not significant.

Table 15: Most of the observed trends for number individuals observed in figure 27 may be attributed to correlations between the number individuals of invasive shrubs and fragment area. Area and fragment region were used to predict the number individuals of invasive shrubs is the following survey linear regression model. The regression for native shrubs was suggestive but not significant overall ($p=.0874$), although it did distinguish the edge region from the middle ($p=.010$) and the interior ($p=.014$) regions. The regression for native trees was not significant.

	coeff	Std. Err.	p-value	* sig at $p<.05$
number individuals		P=.0184	$r^2=.2342$	** sig at $p<.01$
area	-0.083	0.032	0.015	*
edge-middle	9.460	4.793	0.058	
edge-interior	13.480	4.433	0.005	**
middle-interior	4.020	2.204	0.078	

Three dominant invasive shrubs are prominent in the fragments' woody species community. When the abundances of barberry (*Berberis thunbergii*), honeysuckle (*Lonicera spp.*), and buckthorn (*Rhamnus spp.*) are considered together, they account for 22.3% of all woody individuals sampled across all fragments and all regions. These three invasive species also represent 43.7% of shrub individuals and 54.3% of invasive shrub individuals. Figure 28 shows the percentage of all woody individuals, all shrubs, and invasive shrubs accounted for by the combined abundances of barberry, honeysuckle, and buckthorn with respect to fragment region and fragment size. The percentages for all three measures consistently decline from the fragment edges to interiors, although the percentage of invasive shrubs is approximately equal for the middle and interior regions (Figure 28a). All three measures of community importance of these species consistently increase as fragment size decreases (Figure 28b). The significance and degree of variation between the fragment sizes and regions for the percent presence of the three dominant invasive shrubs is summarized in a regression table (Table 16). Although none of the regression models incorporating fragment size or region are significant overall, there are some significant differences between individual region and size terms.

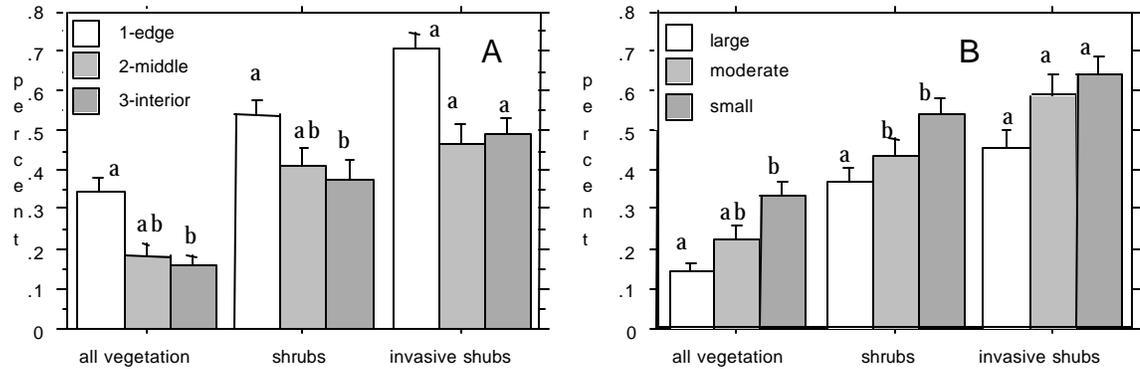


Figure 28: The percent of all woody plants, all shrubs, or invasive shrubs that the three dominant invasive shrubs, barberry (*Berberis thunbergii*), honeysuckle (*Lonicera spp.*), and buckthorn (*Rhamnus spp.*), account for. The data are shown with respect to (A) fragment region and (B) fragment size category. Data are means of the ten plots in each of the ten fragments with one standard error (not accounting for the clustered experimental design). Categories within each measure of community importance with different letters are significantly different at $p=.05$.

Table 16: The effects of fragment region and fragment size are considered independently in the following survey linear regression analysis that predicts the community importance of three dominant invasive shrubs.

	coef	std. Err.	p-value	* sig at $p<.05$	** sig at $p<.01$	
all vegetation		$p=.1159$	$r^2=.0972$			invasiveshrubs
edge-middle	0.172	0.099	0.093		$p=.0646$	$r^2=.0776$
edge-interior	0.218	0.103	0.043 *		0.128	0.051
middle-interior	0.046	0.090	0.613		0.288	0.133
		$p=.0905$	$r^2=.0924$		0.027	0.142
small-moderate	0.048	0.131	0.717		$p=.2556$	$r^2=.0440$
small-large	0.199	0.091	0.037 *		-0.008	0.137
moderate-large	0.151	0.118	0.211		0.192	0.132
		$p=.1333$	$r^2=.0602$		0.200	0.134
all shrubs		$p=.1333$	$r^2=.0602$			
edge-middle	0.164	0.122	0.190			
edge-interior	0.247	0.117	0.044 *			
middle-interior	0.082	0.113	0.473			
		$p=.2626$	$r^2=.0369$			
small-moderate	0.070	0.131	0.597			
small-large	0.181	0.107	0.100			
moderate-large	0.111	0.133	0.410			

The percent of woody plants accounted for by the three dominant invasive shrubs declines with increasing area. This trend is significant for the middle region and suggestive for the edge and interior regions when each region is considered independently (Figure 29). When incorporating the effects of area and fragment region in a regression model, the influence of increasing area on decreasing the percent of the invasive shrubs is significant ($p=.000$) in a manner that significantly differentiates the trend for the edge region from that of the middle and interiors (Table 17).

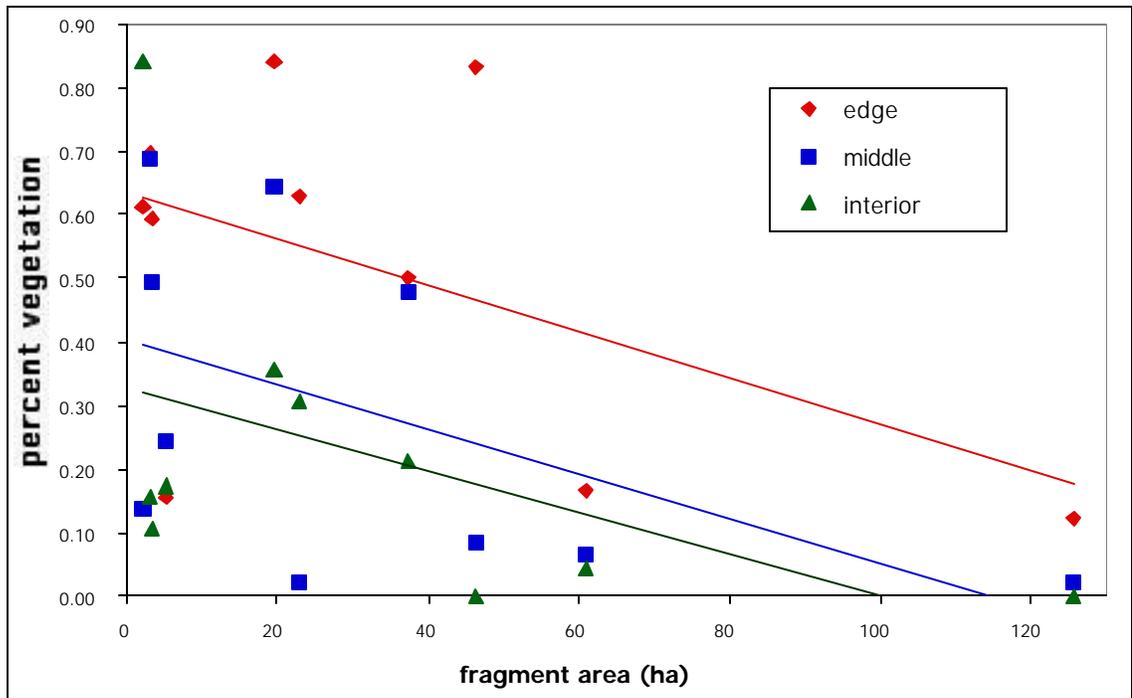


Figure 29: The percent of all woody plants accounted for by the following three dominant invasive shrubs: barberry (*Berberis thunbergii.*), honeysuckle (*Lonicera spp.*), and buckthorn (*Rhamnus spp.*) in the edge (red), middle (blue), and interior (green) regions. Data points are means of ten plots within each transect for the ten fragments. The percent invasives of the middle region considered independently is significantly inversely correlated with area ($p=.038$). The correlations with area for the percent invasives in the edge and interior regions are suggestive, while not significant ($p=.057$ and $p=.114$, respectively).

Table 17: A survey linear regression model using fragment area and region to predict the community importance of the three dominant invasive shrubs ($p=.0001$, $r^2=.2761$).

	coeff	Std. Err.	p-value	
percent				
area	-0.003	0.001	0.000	**
edge-middle	0.280	0.098	0.000	**
edge-interior	0.280	0.098	0.008	**
middle-interior	0.055	0.093	0.560	

* sig at $p<.05$
** sig at $p<.01$

The patterns of fragment invasion are different among the three dominant invasive species (Figure 30). While barberry has the greatest overall presence, it is less evenly distributed across fragment sizes and regions than honeysuckle or buckthorn. While the communities in several regions of variously sized fragments are composed of nearly 25% barberry, the percentage of honeysuckle generally remains below 10% while that of buckthorn generally remains below 15%. The fragment interiors have significantly fewer barberry individuals than the edge regions. The plant communities of large fragments appear to be highly resistant to invasion by barberry, as there are very few barberry individuals in any region of the large fragments. In regression models incorporating the effect of fragment size and region on the abundances of each of the three invasive shrubs, the models for honeysuckle and buckthorn were suggestive, while not significant, with p-values of .288 and .0891, respectively. The edge and middle transects were significantly differentiated for buckthorn ($p=.031$). Fragment size and region did significantly influence the dominance of barberry in the community (Table 18).

As with the percent of community vegetation, fragment size and region were only significant predictors of the number of invasive shrub individuals for barberry ($p=.0001$) (Figure 31). The large and small fragments had significantly different barberry abundances ($p=.000$). The models for honeysuckle and buckthorn were suggestive, but non-significant, with p-values of .230 and .084, respectively. Although regression models predicting both percent community composition and number invasive individuals using fragment size, region, and invasive species as predictor variables, were significant ($p=.003$ and $p=.001$, respectively), the three dominant invasive shrubs were not significantly differentiated pairwise (Figure 31).

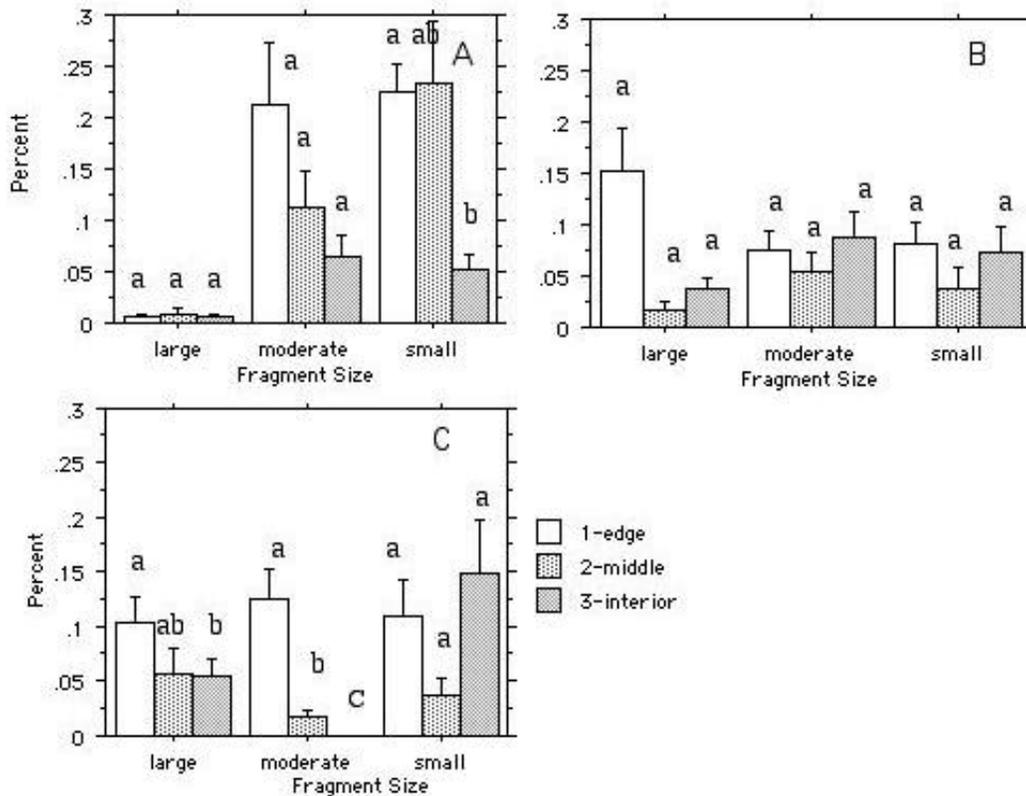


Figure 30: The percent of all woody plants accounted for by one of the following three dominant invasive shrubs: (A) barberry (*Berberis thunbergii*), (B) honeysuckle (*Lonicera spp.*), and (C) buckthorn (*Rhamnus spp.*). The data are shown with respect to both fragment region and fragment size category. Data are means of the ten plots in each of the ten fragments with one standard error. Fragment regions within a fragment size category with different letters are significantly different at $p=0.05$. In survey linear regression models incorporating the effect of fragment size and region on the abundances of each of the three invasive shrubs, the models for honeysuckle and buckthorn were suggestive, while not significant, with p -values of .288 and .0891, respectively. The edge and middle transects were significantly differentiated for buckthorn ($p=0.031$). Fragment size and region did significantly influence the dominance of barberry in the community (Table 18). Although a regression model predicting percent community composition using fragment size, region, and invasive species as predictor variables, was significant ($p=0.003$), the three dominant invasive shrubs were not significantly differentiated pairwise.

Table 18: A survey linear regression model examining the contributions of fragment region and size to determining the percent of woody plants accounted for by barberry ($p=0.002$, $r^2=0.2422$).

	coef	std. Err.	p-value	
percent barberry		$p=0.002$	$r^2=0.2422$	* sig at $p<0.05$
edge-middle	0.007	0.052	0.897	** sig at $p<0.01$
edge-interior	0.078	0.037	0.044	*
middle-interior	0.071	0.045	0.122	
small-moderate	0.012	0.077	0.876	
small-large	0.164	0.041	0.000	**
moderate-large	0.152	0.066	0.030	*

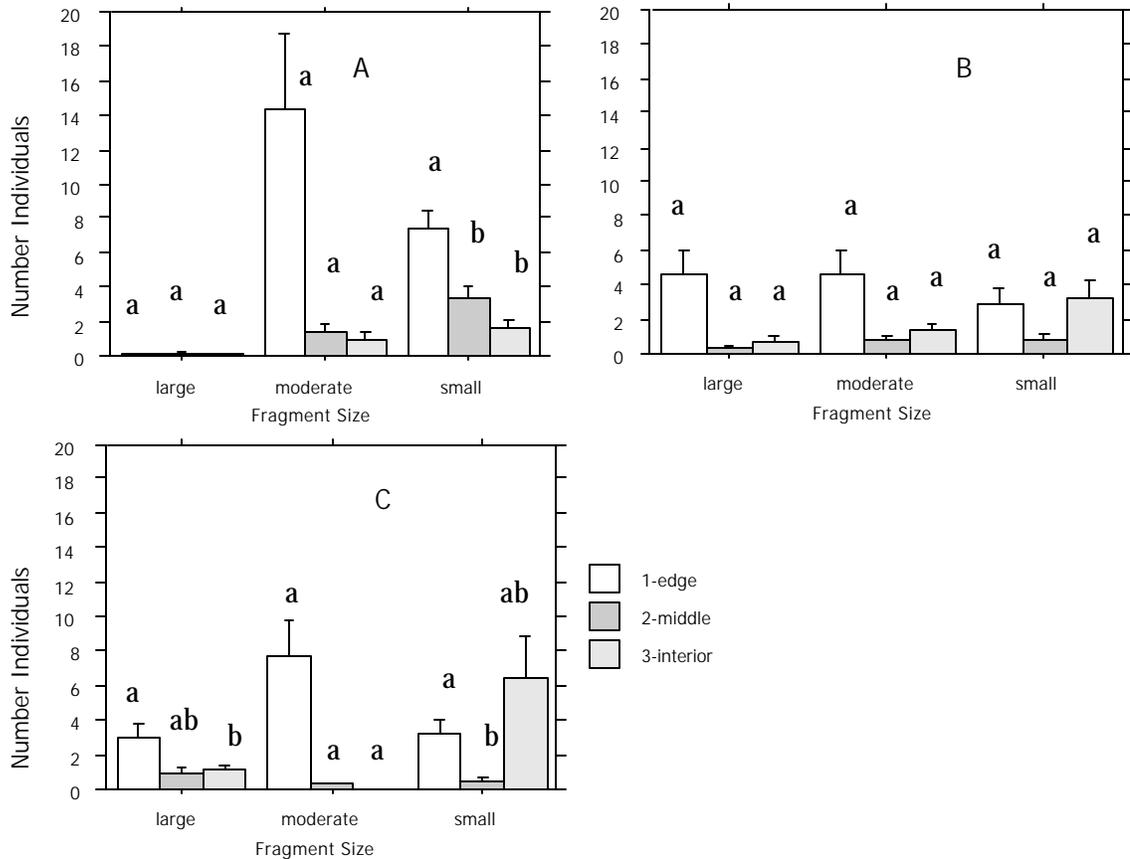


Figure 31: The absolute number of (A) barberry (*Berberis thunbergii*), (B) honeysuckle (*Lonicera spp.*), and (C) buckthorn (*Rhamnus spp.*). The data are shown with respect to both fragment region and fragment size category. Data are means of the ten plots in each of the ten fragments with one standard error. Fragment regions within a fragment size category with different letters are significantly different at $p=0.05$. As with the percent of community vegetation, fragment size and region were only significant predictors of the number of invasive shrub individuals for barberry ($p=0.0001$). The large and small fragments had significantly different barberry abundances ($p=0.000$). The models for honeysuckle and buckthorn were suggestive, but non-significant, with p -values of .230 and .084, respectively. Although a regression model predicting the number of invasive individuals using fragment size, region, and invasive species as predictor variables, was significant ($p=0.001$), the three dominant invasive shrubs were not significantly differentiated pairwise.

Discussion:

Invasive woody species are prominent in the vegetation of Williamstown, MA. Invasive species accounted for 27.8 percent of the woody species observed in this study. This estimate of woody invasive species corresponds to that of Weatherbee (1996) who placed the figure at 27 percent in 1995 for the entirety of flora in Berkshire County. Weatherbee's (1996) estimate represented a ten percentage point increase over the 17 percent reported in 1922 for the region. While she noted the addition of 35 native species in the interim, 107 non-native species were introduced.

Edge Associated Gradients of Invasion

The introduction and expansion of invasive species in Williamstown's remnant woodlots are severely influencing their forest composition, most extensively in small fragments and at the edge regions. The 40 percent of edge individuals or 36 percent of edge species in the study fragments that are non-native are a testament to the severity of the threat to the forest ecosystems associated with fragmentation. These numbers may be greater than those of some other studies because we exclusively considered the southern edges, where there may be a greater presence of invasive species. Brothers and Spingarn (1993), who studied all the vegetation in seven patches of Southern Indiana old-growth forest, attributed the greater non-native presence along southern and western edges to microclimate influences such as increased exposure to sunlight. While they observed a mean of 11.1 non-native species in edge transects, the number of non-native species fell to 1.5 at 8m into the fragment. While 86% of edge transects were occupied by non-native species, non-native species were present in only 22% of the transects located 8m into the fragments. The dynamics of the fragments examined in this study may be differentiated from those observed by Brothers and Spingarn (1993) as bird-dispersed invasive shrubs, with their effective dispersal capabilities and substantial abundance, were largely absent from their study.

The decline in invasives in the middle and interior fragment regions suggests that edge effects decline towards the centers of the fragments. While the percentage of invasive species and individuals in the middle transect are approximately half the values for the edge transect, the community importance of the invasive species does not decline significantly between the middle and the interior region. The trend of decreasing species richness and diversity (as assessed with the Shannon index) with increasing distance from the edge of the

fragment was also observed by Meiners and Pickett (1999) in a study of all the vegetation along a forest-field gradient in an eastern deciduous forest.

A decline in total species richness, number individuals, and percent invasive species and individuals initiated between the outer (0-5m) and inner (5-10m) rows of the edge transect. The decline in species richness and number individuals was more pronounced than the decline in invasive species presence. The experimental design of this study does not allow determination of whether the decline in species richness occurs as an abrupt transition beyond the edge region (considered to be 10m in this study) or as a more gradual transition. These declines in the magnitude of edge effects correspond to observed changes in microclimate parameters (Brothers and Spingarn 1993). In relation to the forest edge, the microclimate 2m into the forest had light levels reduced to 1% of edge levels and air and soil temperatures were reduced, while relative humidity increased (Brothers and Spingarn 1993).

Increased Susceptibility to Invasion in Smaller Fragments

The declines in total species richness, number individuals, and percent invasive species and individuals with increasing fragment area indicate that resistance to invasion by non-native species appeared to be greater in larger fragments. The decline in percent invasive species and individuals was substantial. While a lesser, but significant, trend was observed for overall species richness, the trend was not significant for the number individuals.

Most of the increased resistance to invasion of larger fragments occurred in the edge region. The middle and interior transects are located at distances from the edge of each fragment that are proportional to the size of each fragment (see methods section). Thus, it could be feasible that the observed decrease in species richness, number individuals, and percent invasive species and individuals with increasing fragment area for the middle and interior transects may simply be a function of measuring these parameters at greater distances from the edge in larger fragments. Indeed, our experimental design does not allow me to reject the hypothesis that the effect of fragment area in the middle and interior regions is simply a function of sampling method. However, because the location of the edge region does not depend on fragment area, the trend of decreasing species richness, number individuals, and percent invasive species and individuals with increasing fragment area for

the edge region can only be attributed to increased susceptibility to invasion in fragments of smaller area.

A hypothesis for the trends observed for species richness, number individuals, and percent invasive species and individuals is that larger fragments have greater seed sources for native species. A greater abundance of native seeds may allow for more native species establishment even in the presence of a constant input of invasive seeds. Fragments with larger areas may contain more native species according to the species-area relationship. Greater resistance to disturbance (ie. lesser tree falls) in the larger fragments may also increase their resistance to invasion. The lesser effect of fragment size in the interior of the fragments lends hope that interior types are able to persevere relatively unaltered in fairly small fragments.

My observation of a linear relationship between community richness or diversity parameters and fragment area is contrary to some previous research. Several other studies have shown a unimodal relationship between fragment area and parameters such as species richness, number individuals, and diversity (Levenson 1981, Ranney *et al.* 1981). These studies suggest that a threshold area exists above which a forest fragment is able to sustain interior forest conditions. The threshold area for temperate hardwood forests was estimated to be approximately 2 to 3 ha (Levenson 1981, Ranney *et al.* 1981). Below this threshold, the species richness of a forest plot should increase with increasing fragment area due to the greater area of edge, which adds considerable heterogeneity. Above the threshold, the species richness of the plots is expected to remain constant or decrease with increasing fragment area. Observed decreases in species richness may be attributed to a lesser proportional area edge, greater community stability afforded by greater area, or lesser edge effects (Levenson 1981).

The resolution of the data in this study does not allow determination of the threshold area concept, as only three fragments with areas of less than 5 ha were examined. Despite being unable to assess whether a threshold exists within small areas, this study shows no indication of a distinct threshold at areas greater than 5 ha. Within the trends of decreasing species richness, number individuals, and percent invasive species and individuals, the data do not reveal any discontinuities that would suggest that a threshold area for supporting interior forest types. As the data only represent three variably separated regions in each

transect, the discontinuity may occur in a fragment region not censused by the edge, middle, or interior transects. This lack of a threshold area suggests that the transition to interior forest types is gradual rather than abrupt. Additionally, interior and edge forest types may be differentially distinguished in different fragments due to peculiarities of microclimate or vegetation.

The decreasing species richness and number individuals with increasing fragment area are primarily due to the exclusion of invasive species. To determine the factors accounting for the decreases in species richness and number individuals, we considered the species richness and number individuals for native and invasive species independently. The trends are clearly different for native and non-native species. While the species richness of invasive species decreases with increasing fragment area, the species richness of native species increases with increasing fragment area. The increase in native species with increasing fragment area is rather slight and only significant for the interior transect. An analogous trend is observed for the number of native and invasive individuals. The increases in native species presence in the interior region of larger fragments suggest that either the native species may be displaced by the invasion of non-native species or that the greater stability of larger communities allows for a richer forest with a greater number of species and individuals. Although we did not analyze the size of individuals, the forest successional stage and time since disturbance may influence the species richness and number of individuals.

Given the small magnitude of the decrease in native species richness and abundance in the interiors of small fragments, our results suggest that invasive species are primarily invading empty community niches rather than displacing native species. These empty community niches result from changes in forest structure along edges induced by fragmentation. The propagation of invasive species to canopy gaps in the forest interior may displace native shrubs and suppress native tree seedlings, as a canopy gap is less likely to represent an empty community niche than is an introduced forest edge. Whereas the interior forest may be considered to be composed of a single canopy community and a single understory community, cross sectioning of the forest by fragmentation introduces additional potential habitat. The increased access to the understory shrub layer associated with fragmentation provides ideal nesting sites for birds that serve as dispersal vectors of berried

invasive seeds (Matlack and Livaitas 1999). The forest edges afford increased access for other seed dispersing species including mammals (Cox 1999). In addition to increased seed input of invasives at the forest edge, many invasive species are r-selected and thus well suited to colonize a newly introduced edge environment with their abundant seed production, wide seed dispersal, ability to germinate in diverse environments, and rapid growth. The characteristics of non-native species that allow for success in the edge environments include a preference for high light environments and an ability to withstand disturbance. The success of invasive species in the edge environments may result in reduced native herb cover and reduced native seedling recruitment (Cox 1999).

It is unclear why an empty niche would exist within a community as natural edges have traditionally existed. However, the structure of human-induced edges differs from that of natural edges. While natural edges have undergone succession at the margin of the forest, an interior type forest canopy remains when human-induced edges are formed. The attributes that delineate natural edges, such as changes in environmental conditions or barriers such as rivers, differ from those of human-induced edges. The high richness and abundance of non-native species may be self-limiting through density-dependent mechanisms. The great abundance of invasive species at the edge region may create a barrier to light and disturbances (associated with elements such wind and animals). This vegetation barrier may limit the penetrance of edge effects, ultimately restricting the dominance of non-native species (Brothers and Spingard 1993).

The Capacity of Diversity and Evenness to Reflect Community Changes

The edge regions of the fragments tended to have greater diversity and evenness index values than the middle or interior regions. Greater diversity may result from the higher light levels at the edge regions, which might reduce resource competition. More species in small abundances (due to initial dispersal limitations) may be the result of reduced competition. Spatial heterogeneity in the severity of edge effects could also allow the coexistence of many species. Changes in community structure (such as the proportion of native and invasive species) accompany this greater diversity. Smaller fragment areas also tended to have greater diversity and evenness indices. This may result from a less stable community allowing the addition of non-native species. When considering overall diversity there were no significant correlations between index values and fragment area. However, the

diversity and evenness index values for the invasive species community tended to decrease with increasing fragment area. This trend was most accentuated at the edge and middle fragment regions. As both the species richness and abundance of invasive species declines in larger fragments, the diversity and evenness of the non-native species community may be expected to decline. Additionally, increased community stability in the larger fragments could cause only a few, superior competitor invasive species to permeate into the interior of the fragments, leading to decreased diversity and evenness.

Our results suggest that applying diversity indices without supplementary information may yield spurious results. Species diversity indices are frequently used as a means of quantifying the integrity of an ecosystem. However, diversity indices have mathematical weaknesses (see methods section), which may weaken the ability of indices to distinguish patterns in a community. Many of the indices are troublesome to interpret and the large quantity of available indices may compel confusion and difficulties in comparing diversity between studies. The most significant shortcoming of diversity and evenness is that the community structure may change dramatically without altering the value of the index. This can occur if the changes in the abundance and distribution of individuals within different species counterbalance each other. As is the case with invasive species, functional groups can enter a community in the same abundance and distribution as the functional groups they replace. The results of this study provide examples of the weaknesses of diversity indices. The diversity indices for the entire community failed to reflect the changes in community composition that were suggested by examining species richness and number individuals directly. The failure of the diversity indices to distinguish community changes was highlighted by examining the diversity and evenness trends for invasive and native species individually. At a minimum, diversity indices should be supplemented with information regarding the composition of the community (ie. percentage of invasive species, age structure by dominance and abundance, proportion of woody and herbaceous plants). In the case of fragmentation studies such as this, information regarding species richness or abundance trends for native and invasive species individuals is essential (Saunders 1991). The vegetation structure in different fragment regions and fragments of different sizes clearly revealed differences that were not indicated by the diversity indices.

While diversity and evenness indices may not accurately portray forest community structure and dynamics, the concept of diversity is useful for broadly assessing ecological conditions and as a means of conveying the impact of fragmentation. Indeed, the concept of diversity has been an effective catch phrase used to summon public concern over the integrity of ecosystems. The concept of diversity should continue to be applied when appropriate. However, we should also use additional parameters and support the development of an alternative parameter that is more indicative of community conditions. We must not prolong the misconception that a more diverse community necessarily possesses more ecological integrity. As observed in this study, diversity may actually be increased through fragmentation by adding invasive species to the plant community. In cases where a concise parameter is unnecessary, parameters such as species richness, individual abundances, and evenness should be used. In addition, distinguishing between native and non-native species is useful.

A central question relating to diversity in the study of fragmentation, is whether non-native species differentially invade species rich or poor communities (Case 1991, Tilman 1997, Higgins *et al.* 1999, and Wisser *et al.* 1998). Any correlation between species richness or diversity and the abundance of native species may be due to differential invasion in fragments with either high or low species diversity and richness or, alternately, changes in forest composition induced by the presence of invasives. When plotting the transect species diversity against the mean percent invasive species and abundances for each transect observed in this study, a clear positive correlation emerges. However, interpretation of the trend highlights the difficulty in distinguishing whether diverse fragment regions were preferentially invaded or whether the addition of the invasive species results in increasing diversity in the fragment. The trend was plotted against overall diversity, which was observed to remain relatively stable across the spectrum of fragment sizes. This would suggest that the diversity-invasive abundance relationship may be due to differential invasion of high diversity environments. However, the diversity of the invasive species community was observed to increase with decreasing fragment area and, hence, increasing invasive presence. This suggests that some portion of the diversity-invasive abundance trend is due to a greater presence of invasive species in the more diverse, smaller fragments, but does not appear to account for the entirety of the trend.

Due to the lack of stringency in this conclusion, we chose not to explicitly include an analysis of the diversity-invasive abundance relationship in our results section. Our inability to uncouple the two potential causes of the correlation results from the observational nature of our experiment. We lack information regarding the pre-fragmentation species richness and diversities of the study areas. Our study is also somewhat hampered by the coupling of area and edge effects. An experiment in which fragmentation was initiated as an experimental treatment following acquisition of data regarding pre-fragmentation control conditions would remedy these issues. While such studies have proved successful, inducing fragmentation was neither feasible nor desirable in the context of this study.

Community Importance of Dominant Invasive Shrubs

When native and invasive shrubs are considered separately, the species richness and number individuals of native shrubs are not correlated with fragment area. However, the species richness and number individuals of invasive shrubs declines from the edge to interior transects and with increasing fragment area. We attribute the stronger pattern for invasive shrubs (as compared to native shrubs) to the growth and reproductive properties of invasive species. Invasive species are generally opportunistic (Cox 1999). Their ability to disperse widely and rapidly, grow quickly in a variety of conditions, and tolerate disturbance allow them to become abundant along the edges of small fragments (Cox 1999). However, the shade intolerance of invasive species causes them to decline towards to fragment interiors to a greater degree than native species. The limited number of native shrubs present within the fragments suggests that the invasive species are filling a relatively empty niche in the fragments.

The influence of the invasive shrubs is likely dependent upon their time since invasion. A delay of approximately ten years has been observed for the population explosion of some invasive shrubs such as a honeysuckle species (Deering 1999). We lack extensive knowledge of the fragments' disturbance history or the history of invasion in the plots. Hence, an explosion of the invasive shrub population could occur once the invasive communities have existed in the fragments for some minimum duration. Such a population explosion of invasive shrubs may have a detrimental impact on populations of native shrubs. An additional potential future threat to the native shrub communities would be the invasion of non-native species with similar traits to those currently in the fragments, excepting shade-

intolerance. If non-native shrubs are eventually able to invade the shady interiors of the fragments their populations could increase substantially and have significant ramifications for the native species community.

A concern for the integrity of the forest fragment communities involves the ability of native species to propagate. As we primarily examined mature vegetation, we cannot assess the rates of native and invasive seedling recruitment. The somewhat small influences of invasive species perceived in this study may be a product of a time lag associated with the long lifecycles of woody trees and shrubs. The mature tree communities likely preceded the introduction of non-native species. The potential role of invasive species in suppressing germination and growth of native seedling cannot be evaluated with this study's data. Studies of seedling abundance could reveal the potential suppression of native seedlings. A study of the distribution and abundance of shade tolerant tree seedlings in 1, 10, and 100 ha fragments of tropical rainforest observed a decline in seedling density towards the edge of the fragments and as the size of the fragments decreased (Benitez-Malvido 1998). This suppression of native seedlings also extends to the herb communities. In a study conducted among a fragmented Brazilian rainforest, a native herb, *Heliconia acuminata*, was between 3 and 7 times more likely to germinate in continuous forests than in forest fragments of 1 to 10 ha (Bruna 1999).

The population trends for the three dominant invasive shrubs (barberry (*Berberis thunbergii*), honeysuckle (*Lonicera spp.*), and buckthorn (*Rhamnus spp.*)) correspond to those observed for the entirety of invasive shrubs. While these three taxa account for approximately 50% of invasive shrubs in the middle and interior fragment regions, their invasive shrub community importance increases to nearly 70% in the edge region. Thus, if populations of these three shrubs could be controlled, the majority of invasive species would be excluded from the fragments. While resisting fragmentation and preserving large forest areas appears to be sufficient to suppress barberry populations, large fragments are less able to resist invasion by honeysuckle or buckthorn (Figures 30 and 31). The intention of this study was to assess the broad dynamics of fragmentation rather than prescribe management techniques for particular invasive species. However, our results reveal the impact of invasive species on remnant forest patches and lend support to studies evaluating the population dynamics of invasive species with the intent developing management techniques.

Conclusions:

This study examines the theoretical framework that exists for understanding the dynamics of forest fragmentation by considering a case study among ten eastern-deciduous forest remnants. We observed a decrease in species richness, number individuals, and percent invasive species and individuals from the fragment edges to their interiors, suggesting the influence of edge effects. The influence of edge effects declines within 10m of the fragment edge. We also observed a decrease in these parameters with increasing fragment area. This suggests that larger areas are less susceptible to invasion due to factors that may include increased seed sources, greater community stability, or increased resistance to invasion.

Decrease in species richness, number individuals, and percent invasive species and individuals from the fragment edges to their interiors were primarily attributed to patterns of colonization by invasive species, as the native species community was less influenced by fragment region and area. Although the invasive species community did not appear to influence the native species community extensively, the species richness and number individuals did tend to increase in the interior of the fragments with increasing fragment area. The limited presence of native shrubs in the fragments suggests that invasive shrubs may be filling a previously empty community niche. While it does not appear that invasive woody species are substantially displacing native woody species, our study does not address the changes in the community of native herb species or seedling recruitment due to fragmentation. A thorough understanding of the dynamics of forest fragmentation in the study forests cannot be complete without considering the entire vegetation community. However, examining woody invasive species has provided an understanding of the forest framework within which non-woody plants exist.

Non-native species tend to have a greater capacity for dispersal, as non-native species tend to use effective dispersal vectors, such as birds, more often than do native species. This may allow non-native species to colonize edge habitats. Dispersal limitations for the invasive shrubs could be overcome in future years, ultimately allowing the community dominance of the invasive shrubs to increase and prove detrimental to native species communities. Much of the invasive species presence in the fragments was accounted for by three dominant invasive shrubs: barberry (*Berberis thunbergii*), honeysuckle (*Lonicera spp.*), and buckthorn (*Rhamnus spp.*). The ability to manage populations of these three bird

dispersed shrubs may allow for the majority of invasives to be excluded from forest fragments.

Changes in forest community structure were not captured by diversity or evenness indices, questioning the effectiveness of considering responses to forest fragmentation with diversity indices alone. The data also highlight the fact that increases in diversity may be due to the addition of non-native species rather than an increase in forest integrity (associated with factors such as ecosystem health or sustainability). The study generally validates much of the existing body of knowledge regarding the response of forests to fragmentation. We expand the developing collection of case studies that consider the dynamics of fragmentation within particular ecosystems.

Our study reveals the relevance of broad concerns with the loss of species and changes in forest structure to the eastern deciduous forests tracts remaining amongst agricultural lands. We also provide a framework for future research projects in the study region. An important element of this framework is the use of GIS and remote sensing techniques to locate and examine forest fragments. Potential future studies could quantify the microclimate transitions from the edges to interiors of the fragments; compare the physiological response of native and invasive plants to fragmentation; investigate differences in satellite images between fragment regions or fragments of differing area; examine the herbaceous communities of the fragments; or consider the seedling recruitment of native and invasive species in the fragments.

While our study lends some hope that the introduction of invasive species resulting from forest fragmentation may be expanding the community rather than displacing native species, the changes in forest structure resulting from fragmentation are clearly revealed. Our results provide support for conservation efforts dedicated to preserving large tracts of eastern deciduous forests in order to minimize the invasion and dominance by non-native woody plants.

Literature Cited:

- Alatalo RV. 1981. Problems in the measurement of evenness in ecology. *Oikos* 37:199-204.
- Baker HG. 1986. Patterns of plant invasion in North America. In Mooney HA and Drake JA (eds.). *Ecology of Biological Invasions of North America and Hawaii*. New York: Springer-Verlag.
- Bazzaz FA. 1986. Life history of colonizing plants: some demographic, genetic, and physiological features. In Mooney HA and Drake JA (eds.). *Ecology of Biological Invasions of North America and Hawaii*. New York: Springer-Verlag.
- Benitez-Malvido J. 1998. Impact of forest fragmentation on seedling abundance in a tropical rain forest. *Cons. Biol.* 12:380-389.
- Bierregaard RO, Lovejoy TE, Kapos V, dos Santos VK, and Hutchings 1992. The biological dynamics of tropical forest fragmentation. *Bioscience* 42: 859-866.
- Brooks RRR. 1974. *Williamstown, the first two hundred years 1753-1953 and twenty years later, 1953-1973*. Williamstown historical commission. 1974.
- Brothers TS and Spingarn A. 1993. Forest fragmentation and alien plant invasion of central Indiana Old-growth forests. *Con. Biol.* 6:91-99.
- Bruna EM. 1999. Seed germination in rainforest fragments. *Nature* 402: 139.
- Carlquist S. 1974. *Island biology*. New York: Columbia University Press.
- Case TJ. 1991. Invasion resistant species build-up and community collapse in metapopulation models with interspecies competition. *Biological Journal of the Linnean Society* 42: 239- 266.
- Chen J, Franklin JF, and Lowe JS. 1996. Comparison of abiotic and structurally defined patch patterns in a hypothetical forest landscape. *Con. Biol.* 3: 1996.
- Cole BJ. 1981. Colonizing abilities, island size, and the number of species on archipelagoes. *Am. Nat* 117:629-38.
- Cox GW. 1999. *Alien species in North America and Hawaii: impacts on natural ecosystems*. Washington, DC: Island Press
- Deering RH 1999. Forest colonization and developmental growth of the invasive shrub *Lonicera maackii*. *American Midland Naturalist* 141: 43-50.
- Diamond JM. 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation* 7: 129-146.
- Diamond JM. 1976. Island biogeography and conservation: strategy and limitations. *Science* 193: 1027- 1029.
- Diamond JM and May RM. 1981. Island Biogeography and the design of nature reserves. In May RM (ed.). *Theoretical Ecology*. Oxford: Blackwell.
- Doak DF and Mills LS. 1994. A useful role for theory in conservation. *Ecology* 75: 615-616.
- Douglas K. 1998. Hot spots: why are there so many species in the tropics. *New Scientist* 158: 32-36.
- Elton CS. 1958. *The ecology of invasions by animals and plants*. New York: John Wiley & sons.
- Gigord L, Picot F, and Shykoff JA 1999. Effects of habitat fragmentation on *Dombeya acutangula* (*Sterculiaceae*), a native tree on La Reunion (Indian Ocean). *Biological Conservation* 88:43-51.
- Gilfedder L and Kirkpatrick JB 1998. Factors influencing the integrity of remnant bushland in subhumid Tasmania. *Biological Conservation* 84: 89-96.
- Haila Y. 1999. Islands and Fragments. In Hunter ML (ed.). *Maintaining biodiversity in forest ecosystems*. Cambridge: Cambridge University Press
- Hanski I and Kuussaari M. 1995. Butterfly metapopulation dynamics. In Cappuccino N and Price PW, eds. *Population dynamics: new approaches and synthesis*. San Diego: Academic Press.
- Harris LD. 1984. *The fragmented forest: Island biogeography theory and the preservation of biotic diversity*. Chicago: University of Chicago Press.
- Higgins SI, Richardson DM, Cowling RM, and Trinder-Smith TH. 1999. Predicting the landscape-scale distribution of alien plants and their threat to plant diversity. *Conservation Biology* 13: 303-313.
- Hill MO. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology* 54: 427-432.
- Hill JK, Thomas CD, and Lewis OT. 1996. Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: implications for metapopulation structure. *Journal of animal ecology* 65: 725-735.
- Hulbert SH. 1971. The non-concept of species diversity: a critique and alternative parameters. *Ecology* 52:

577-586.

- Huston MA 1997. Hidden treatments in ecological experiments: reevaluating the ecosystem function of biodiversity. *Oecologia* 110: 449-460.
- Hutchinson TF and Vankat JL. 1998. Landscape structure and spread of the exotic shrub *Lonicera maackii* (Amur Honeysuckle) in Southwestern Ohio Forests. *Amer. Midl. Nat.* 139:383-390.
- Kellman M, Tackaberry R, Meave J. 1996. The consequences of prolonged fragmentation: lessons from tropical gallery forests. In Schelhas J and Greenberg R (eds.). *Forest Patches in Tropical Landscapes*. Washington, DC: Island Press.
- Laurence WF, Bierregaard RO, Gascon C, Didham RK, Smith AP, Lynam AJ, Viana VM, Lovejoy TE, Sieving KE, Sites JW, Andersen M, Tocher MD, Kramer EA, Restrepo C, and Mortiz C. 1997 Tropical Forest Fragmentation: synthesis of a diverse and dynamic discipline. In Laurence WF and Bierregaard (eds.). *Tropical forest fragmentation: Ecology, management, and conservation of fragmented communities*. Chicago: University of Chicago Press.
- Laurance WF, Ferreira LV, Rankin-De Merona LM, and Laurance SG. 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology* 79: 2032-2040.
- Levenson JB. 1981. Woodlots as biogeographic islands in Southeastern Wisconsin. In Burgess RL and Sharpe DM (eds.). *Forest island dynamics in man-dominated landscapes*. New York: Springer-Verlag.
- Lovejoy TE and Oren DC. 1981. The minimum critical size of ecosystems. In Burgess RL and Sharpe DM (eds.). *Forest island dynamics in man-dominated landscapes*. New York: Springer-Verlag.
- Lovejoy TE, Bierregaard RO, Rylands AB, Malcom JR, Quintela CE, Harper LH, Brown KS, Powell AH, Powell GVN, Shubart HOR, and Hays MB. 1986. Edge and other effects of isolation on Amazon forest fragments. In Soule ME (ed.). *Conservation Biology: the science of scarcity and diversity*. Sunderland, MA: Sinauer Associates.
- Ludwig JA and Reynolds JF. 1988. *Statistical ecology: a primer on methods and computing*. New York: John Wiley & Sons.
- Luken JO and Goessling M. 1995. Seedling Distribution and potential persistence of the exotic shrub *Lonicera maackii* in fragmented forests. *Amer. Mid. Nat.* 133: 124-130.
- MacArthur RH and Wilson EO. 1967. *The theory of island biogeography*. Princeton: Princeton University Press
- Malcolm JR. 1994. Edge effects in Central Amazonian Forest Fragments. *Ecology* 75: 2438-2445.
- Matlack GR. 1994. Vegetation Dynamics at the Forest Edge- trends in space and successional time. *Journal of Ecology* 82: 113-123
- Matlack G and Litvaitis J. 1999. Forest Edges. In Hunter ML (ed.). *Maintaining biodiversity in forest ecosystems*. Cambridge: Cambridge University Press.
- May RM. 1973. *Stability and Complexity in Model Ecosystems*. Princeton: Princeton University Press.
- Meiners SJ and Pickett STA. 1999. Changes in community structure and population responses across a forest-field gradient. *Ecography* 1999 v22 N3 p261-267
- Murcia C. 1995. Edge effects in fragmented forests: implications for conservation. *TREE* 2: 58- 62.
- Nee S and May RM. 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. *Ecology* 61: 37-40.
- New TR. 1997. *Butterfly Conservation*. Oxford: Oxford university press.
- Palik BJ and Murphy PG. 1990. Disturbance versus edge effects in sugar-maple/beech forest fragments. *Forest Ecology and Management* 32: 187-202.
- Peet RK. 1974. The measurement of species diversity. *Annual review of ecology and systematics* 5:285- 307.
- Peet RK. 1975. Relative diversity indices. *Ecology* 56: 496-498.
- Preston FW. 1962. The canonical distribution of commonness and rarity: part 1. *Ecology* 43: 185- 215.
- Ranney JW. 1977. Forest island edges: their structure, development, and importance to regional forest ecosystem dynamics. Oak Ridge, TN: Oak Ridge National Laboratory.
- Ranney JW, Bruner MC, and Levenson. 1981. The important of edge in the structure and dynamics of forest islands. In Burgess RL and Sharpe DM (eds.). *Forest island dynamics in man-dominated landscapes*. New York: Springer-Verlag.
- Raven PH and McNeely JA. 1998. Biological Extinction: Its scope and meaning for us. In Guruswaour LD and McNeely JA. *Protection of global biodiversity: Converging strategies*. Durham: Duke University Press.

- Roberts MR and Gilliam FS. 1995 Patterns and Mechanisms of Plant Diversity in Forested Ecosystems: implications for forest management. *Ecological Applications* 5:969-977.
- Rose S and Fairweather PG. 1997. Changes in floristic composition of urban bushland invaded by *Pittosporum undulatum* in northern Sydney, Australia. *Australian journal of botany* 45: 123-149.
- Saterson KA. 1977. A vegetation history of Williamstown 1752-1977. Williams College: unpublished thesis.
- Saunders DA, Hobbs RJ, and Margules CR. 1991. Biological consequences of ecosystem fragmentation: a review. *Cons. Biol.* 5:18-32.
- Schulze DE, Bazzaz FA, Nadelhoffer KJ, Koike T, and Takatsuki S. 1996. Biodiversity and Ecosystem Function of temperate deciduous broad-leaved forests. In Mooney HA, Cushman JH, Medina E, Sala OE, and Schulze ED. *Functional Roles of Biodiversity: A global perspective*. England: John Wiley & Sons Ltd.
- Shannon CE and Weaver W. 1949. *The mathematical theory of communication*. Urbana, IL: University Illinois Press.
- Shigesada N and Kawasaki K. 1997. *Biological Invasions: Theory and Practice*. Oxford: Oxford University Press.
- Simberloff DS and Abele LG. 1976. Island biogeography theory and conservation practice. *Science* 191:285-286.
- Simberloff D and Abele LG. 1982. Refuge design and island biogeographic theory: effects of fragmentation. *Am. Nat.* 120:41-50.
- Simberloff D 1988. The contribution of population and community biology to conservation science. *Ann. Rev. Ecol. Syst.* 19:473-511.
- Simpson EH. 1949. Measurement of diversity. *Nature* 163: 688.
- Sullivan AI and Shaffer ML. 1975. Biogeography of the Megazoo. *Science* 189: 13-17.
- Stork NE. 1997. Measuring Global Biodiversity and its decline. In Reaka-Kudla ML, Wilson DE, and Wilson EO. *Biodiversity II: understanding and protecting our biological resources*. Washington, DC: Joseph Henry Press.
- Terborgh J. 1976. Island biogeography and conservation: strategy and limitations. *Science* 193: 1029-1030.
- Thomas CD and Hanski I. 1997. Butterfly Metapopulations. In Hanski IA and Gilpin ME, eds. *Metapopulation Biology: ecology, genetics, and evolution*. San Diego: Academic Press.
- Tilman D. 1997. Community invisibility, recruitment limitation, and grassland biodiversity. *Ecology* 78:81-92
- Wales BA. 1972. Vegetation analysis of north and south edges in a mature oak-hickory forest. *Ecological Monographs* 42: 451-471.
- Weatherbee PB. 1996. *The flora of Berkshire County Massachusetts*. Dalton: the Studley Press.
- Whittaker RJ. 1998. *Island Biogeography: Ecology, evolution, and conservation*. Oxford: Oxford University Press.
- Wilcove DS, McLellan CH, and Dobson AP. 1986. Habitat fragmentation in the temperate zone. In Soule ME (ed.). *Conservation Biology: the science of scarcity and diversity*. Sunderland, MA: Sinauer Associates.
- Wilcox BA and Murphy DD. 1985. Conservation Strategy: the effects of fragmentation on extinction. *American Naturalist* 125:879-87.
- Williams-Linera G, Dominguez-Gastelu V, and Garcia-Zurita ME. 1998. Microenvironment and floristics of different edges in a fragmented tropical rainforest. *Cons. Biol.* 12:1091-1101
- Wiser SK, Allen RB, Clinto PW, and Platt KH. 1998. Community structure and forest invasion by an exotic herb over 23 years. *Ecology* 79: 2071-2081
- Woods KD. 1993. Effects of invasion by *Lonicera tatarica* L. on herbs and Tree Seedlings in Four New England Forests. *Am. Midl. Nat* 130: 62-74
- Yahner RH. 1995. *Eastern Deciduous Forests*. Minneapolis: University of Minnesota Press.
- Zuidema PA, Sayer JA, and Dijkman W. 1996. Forest fragmentation and biodiversity: The case for intermediate sized conservation areas. *Environmental conservation* 23: 290-297.

Appendix A: Study fragment descriptions and directions.

Fragment	Area (ha)	Perimeter (m)	UTM (E m)	* UTM (N m)	Location
Airport Plot	2.1	701	649126	4728118	East of Luce Road, south of Route 2. Immediately south of western edge of the North Adams airport.
Mt. Hope East	3.1	798	646146	4725323	Atop a hill at the eastern edge of Mount Hope Farm. Between Route 43 and Hopper Road.
Chenail South	3.6	723	648696	4726788	South-west of Luce Road, east of Stratton Road. North-west of the initiation of the slope up Mt. Prospect. South of two other forest patches.
Chenail North	5.3	766	648576	4727783	The northern of two forest patches west off of Luce Road and east of Stratton Road.
Luce Road	19.5	2205	649991	4727438	North of Luce Road, once road runs west-east after travelling south from Route 2. Opposite the Williamstown Reservoir.
Mt. Hope West	23.1	2580	645281	4725843	At northwest edge of Mt. Hope Farm. Bordered by Green River Road to north-west.
Hopper Road	37.3	2387	646001	4723758	East of road that continues straight once Hopper Road turns east.
Sloan Road	46.3	4502	642356	4723873	South of Sloan Road and east of Oblong Road. A section of the field farm property managed by the Trustees of Reservations.
Greylock Highschool	60.9	5052	643191	4725443	West of Route 7 and Mt. Greylock Highschool, south of Woodcock Road and north of Sloan Road. A section of the field farm property managed by the Trustees of Reservations.
Deer Ridge	126	9090	644791	4722793	West of Hopper Road, North-east of Route 7. North-east of Green River.

* UTM coordinates based upon the 1983 UTM projection, zone 18N.

Appendix B: Species list of all species observed in study fragments

Common Name	Latin Name	native/non-native *	Tree/Shrub **
Balsam Fir	<i>Abies balsamea</i>	native	tree
Striped Maple	<i>Acer pennsylvanicum</i>	native	tree
Red Maple	<i>Acer rubrum</i>	native	tree
Silver Maple	<i>Acer saccharinum</i>	native	tree
Sugar Maple	<i>Acer saccharum</i>	native	tree
Japanese Barberry	<i>Berberis thunbergii</i>	non-native	shrub
Black Birch	<i>Betula lenta</i>	native	tree
Yellow Birch	<i>Betula lutea</i>	native	tree
Paper Birch	<i>Betula papyrifera</i>	native	tree
Gray Birch	<i>Betula populifolia</i>	native	tree
Iron Wood	<i>Carpinus caroliniana</i>	native	tree
Bitternut Hickory	<i>Carya cordiformis</i>	native	tree
Shagbark Hickory	<i>Carya ovata</i>	native	tree
Alternate leaved dogwood	<i>Cornus alternifolia</i>	native	shrub
Grey Stem Dogwood	<i>Cornus racemosa</i>	native	shrub
Round leaved dogwood	<i>Cornus rugosa</i>	native	shrub
Red Osier Dogwood	<i>Cornus stolonifera</i>	native	shrub
Hawthorn	<i>Crataegus sp.</i>	native	shrub
Winged Euonymus	<i>Euonymus alata</i>	non-native	shrub
Beech	<i>Fagus grandifolia</i>	native	tree
White Ash	<i>Fraxinus americana</i>	native	tree
Black Walnut	<i>Juglan nigra</i>	non-native	tree
Privet	<i>Ligustrum obtusifolium</i>	non-native	shrub
Morrowi Honeysuckle	<i>Lonicera morrowii</i>	non-native	shrub
European Fly Honeysuckle	<i>Lonicera xylosteum</i>	non-native	shrub
Honeysuckle	<i>Lonicera spp.</i>	***	
Apple	<i>Malus pumilla</i>	non-native	tree
Horn Beam	<i>Ostrya virginiana</i>	native	tree
Pitch Pine	<i>Pinus rigida</i>	native	tree
White Pine	<i>Pinus strobus</i>	native	tree
Eastern Sycamore	<i>Platanus occidentalis</i>	native	tree
Quaking Aspen	<i>Populus tremuloides</i>	native	tree
Black Cherry	<i>Prunus serotina</i>	native	tree
Choke cherry	<i>Prunus virginiana</i>	native	tree
White Oak	<i>Quercus alba</i>	native	tree
Red Oak	<i>Quercus borealis</i>	native	tree
Black Oak	<i>Quercus velutina</i>	native	tree
Alder-leaved Buckthorn	<i>Rhamnus alnifolia</i>	native	shrub
Common buckthorn	<i>Rhamnus cathartica</i>	non-native	shrub
European Buckthorn	<i>Rhamnus frangula</i>	non-native	shrub
Smooth Rose	<i>Rosa blanda</i>	native	shrub
Multiflora rose	<i>Rosa multiflora</i>	non-native	shrub
High Bush blackberry	<i>Rubus allegheniensis</i>	native	shrub
Black Raspberry	<i>Rubus occidentalis</i>	native	shrub
Black Willow	<i>Salix nigra</i>	native	tree
Silk Willow	<i>Salix saricea</i>	native	tree
Red-berried elderberry	<i>Sambucus racemosa</i>	native	tree
Night shade	<i>Solanum dulcamara</i>	non-native	shrub
Mountain Ash	<i>Sorbus americana</i>	native	tree
Meadowsweet	<i>Spiraea latifolia</i>	native	shrub
Basswood	<i>Tilia americana</i>	native	tree
Eastern Hemlock	<i>Tsuga canadensis</i>	native	tree
Slippery Elm	<i>Ulmus rubra</i>	native	tree
Maple Leaved Viburnum	<i>Viburnum acerifolium</i>	native	shrub
Arrowwood	<i>Viburnum recognitum</i>	native	tree
Summer Grape	<i>Vitis aestivalis</i>	native	shrub

* native / non-native status as determined by Weatherbee 1996

** some small tree species are categorized as shrubs as distinction was primarily based on spatial dynamics

*** *Lonicera morrowii* and *Lonicera xylosteum* were the *Lonicera* species most frequently observed. Although attempts were made to identify the other *Lonicera* to species, uncertainties result in our differentiating between, but not naming, the other species. Tentative identifications include the following species.

Hybrid Honeysuckle	<i>Lonicera bella</i>	non-native	shrub
Honeysuckle	<i>Lonicera caerulea</i>	non-native	shrub
Amur Honeysuckle	<i>Lonicera maackii</i>	non-native	shrub
Swamp fly honeysuckle	<i>Lonicera oblongifolia</i>	non-native	shrub
Trumpet Honeysuckle	<i>Lonicera sempervirens</i>	non-native	shrub
Tatarian Honeysuckle	<i>Lonicera tatarica</i>	non-native	shrub

Appendix C: Species composition of study fragments

Note that some *Lonicera spp.* identifications are uncertain as noted in Appendix B.

Plots 1-5f are the front row plots of each transect, 1-5b are back row plots

* native (n) or invasive (i) species as defined by Weatherbee (1996).

** tree (t) or shrub (s)

Fragment	Region	Common Name	Latin Name	n/i *	t/s**	1f	2f	3f	4f	5f	1b	2b	3b	4b	5b		
Airport Plots	edge	Sugar Maple	<i>Acer saccharum</i>	n	t	*	*		6	1	1	2	*	12	5		
		Yellow Birch	<i>Betula lutea</i>	n	t	*	*	*	*		2	*	*	*		2	
		Paper Birch	<i>Betula populifolia</i>	n	t	*	*	*	*	*	*		1	3	*	*	
		Iron Wood	<i>Carpinus caroliniana</i>	n	t	*		4	*	1	1	1	9	2	8	1	
		Bitternut Hickory	<i>Carya cordiformis</i>	n	t	*	*	*	*	*	*		3	*	1	*	
		Grey Stem Dogwood	<i>Cornus racemosa</i>	n	s		16	*	15	14	12	2	*	*	*	*	5
		Beech	<i>Fagus grandifolia</i>	n	t		5	2	3	8	4	2	1	7	7	8	
		White Pine	<i>Pinus strobus</i>	n	t	*	*	*	*	*	*	*	*	*	*	*	1
		Quaking Aspen	<i>Populus tremuloides</i>	n	t	*		2	2	*	*	*	*	*	*	*	*
		Black Cherry	<i>Prunus serotina</i>	n	t		1	*	*	*	*	*	*	*	*	*	*
		White Oak	<i>Quercus Alba</i>	n	t	*		1	1	2	*	*	*	*	*	*	1
		Black Raspberry	<i>Rubus occidentalis</i>	n	s		8	8	*	*	*	*	*	*	*	*	*
		Silk Willow	<i>Salix sericea</i>	n	t	*	*	*	*	*	*	*	1	*	*	*	*
		American Basswood	<i>Tilia americana</i>	n	t	*	*	*	*	*	*	3	*	*	*	1	*
		Maple Leaved Viburnum	<i>Viburnum acerifolium</i>	n	s		1	9	3	*		2	*	*	*	*	3
	Japanese Barberry	<i>Berberis thunbergii</i>	i	s		4	1	8	11	30	8	3	11	8	3		
	European Fly Honeysuckle	<i>Lonicera xylosteum</i>	i	s		5	3	4	6	7	13	5	1	2	2		
	Common buckthorn	<i>Rhamnus cathartica</i>	i	s		4	2	3	*		4	3	*	*	*	*	
	European Buckthorn	<i>Rhamnus Frangula</i>	i	s	*	*	*	*	2	4	*	*	*	*	*	*	
	middle	Sugar Maple	<i>Acer saccharum</i>	n	t		33	25	33	11	21	48	2	14	57	17	
		Black Birch	<i>Betula lenta</i>	n	t	*	*	*		1	*	*	*	*	*	*	
		Yellow Birch	<i>Betula lutea</i>	n	t	*	*	*	1	*	*	*	*	*	*	*	
		Gray Birch	<i>Betula papyrifera</i>	n	t		1	*	*	*	*	*	*	*	*	7	
		Paper Birch	<i>Betula populifolia</i>	n	t	*	*	*	*	*	*	*	*	*	*	15	
		Iron Wood	<i>Carpinus caroliniana</i>	n	t		2	1	12	10	11	*		4	3	3	
		Bitternut Hickory	<i>Carya cordiformis</i>	n	t	*	*	*		1	*		2	1	*	*	
		Shagbark Hickory	<i>Carya ovata</i>	n	t	*	*	*	*	*	*	*		5	*	*	
		Red Osier Dogwood	<i>Cornus stolonifera</i>	n	s	*	*	*	*	*	*		3	*	*	*	
		Horn Beam	<i>Ostrya virginiana</i>	n	t	*	*	*	*		1	*			6	*	
		Quaking Aspen	<i>Populus tremuloides</i>	n	t		2	3	*	*	*	*	*	*	*	*	
		Black Cherry	<i>Prunus serotina</i>	n	t	*	*	*	*	*	1	*	*	*	*	*	
		White Oak	<i>Quercus Alba</i>	n	t	*		1	*	*	*	*		3	*	*	
		Maple Leaved Viburnum	<i>Viburnum acerifolium</i>	n	s	*	*	*	*	*	*	*		7	*	*	
		Japanese Barberry	<i>Berberis thunbergii</i>	i	s		1	*	*	*	*		3	3	2	*	1
	Black Walnut	<i>Juglans Nigra</i>	i	t		2	*	*	*	*		2	*	*	*	*	
	Morrow Honeysuckle	<i>Lonicera Morrowii</i>	i	s	*	*	*	*	*	*	*		1	*	*	*	
	European Fly Honeysuckle	<i>Lonicera xylosteum</i>	i	s	*	*	*	*	*	*		6	*	1	*	*	
	interior	Sugar Maple	<i>Acer saccharum</i>	n	t		4	*	*	*	*		3	*	*	*	
		Black Birch	<i>Betula lenta</i>	n	t		3	*	*	*	*	*	*	*	*	*	
		Gray Birch	<i>Betula papyrifera</i>	n	t		2	*	*	*	*		1	*	*	*	
		Paper Birch	<i>Betula populifolia</i>	n	t		1	*	*	*	*	*	*	*	*	*	
		Shagbark Hickory	<i>Carya ovata</i>	n	t		3	*	*	*	*	*	*	*	*	*	
		Grey Stem Dogwood	<i>Cornus racemosa</i>	n	s	*	*	*	*		1	1	1	*	3	*	
		Hawthorn	<i>Crataegus sp.</i>	n	s		5	2	1	8	6	6	1	5	13	2	
		Beech	<i>Fagus grandifolia</i>	n	t		2	*	2	*		1	1	1	*	3	
High Bush blackberry		<i>Rubus allegheniensis</i>	n	s	*	*	*	*	*	*	*		1	*	2		
Black Raspberry		<i>Rubus occidentalis</i>	n	s	*	*	*	*	*	*	*			8	*		
Maple Leaved Viburnum		<i>Viburnum acerifolium</i>	n	s	*	*		1	*	*		2	*		2		
Japanese Barberry		<i>Berberis thunbergii</i>	i	s		4	11	2	*	*		9	5	4	*		
Swamp fly honeysuckle		<i>Lonicera oblongifolia</i>	i	s	*	*	*	*	*	*	*	*	*	*	3		
Trumpet Honeysuckle		<i>Lonicera Sempervirens</i>	i	s	*	*	*	*	*	*	*	*	*	*	2		
European Fly Honeysuckle		<i>Lonicera xylosteum</i>	i	s		21	5	6	4	2	18	5	7	21	4		
Alder-leaved Buckthorn	<i>Rhamnus alnifolia</i>	i	s	*	29	33	2	13	*	18	*	3	20				
European Buckthorn	<i>Rhamnus Frangula</i>	i	s	*		1	30	*	*	*		25	10	5			
Multiflora Rose	<i>Rosa Multiflora</i>	i	s	*	*	*	*	*	*		1	*	*	*			
Night shade	<i>Solanum dulcamara</i>	i	s	*	*	*	*	*	*		1	*	*	*			
Mt. Hope East	edge	Silver Maple	<i>Acer saccharinum</i>	n	t	*		1	*	*	3	*	*	*	*		
		Sugar Maple	<i>Acer saccharum</i>	n	t		1	*	*	3	24		2	*	*	19	
		Iron Wood	<i>Carpinus caroliniana</i>	n	t	*			4	*	*			1	6	*	
		Beech	<i>Fagus grandifolia</i>	n	t	*	*	*	*	*	*	*	*	*	1	*	
		Pitch Pine	<i>Pinus rigida</i>	n	t		1	*	*	*	*	*	*	*	*	*	
		Eastern Sycamore	<i>Platanus occidentalis</i>	n	t	*	*	*	*	*	1	*	*	*	*	*	
		Black Cherry	<i>Prunus serotina</i>	n	t	*		1	3	3	2	4	*	1	*	*	
		White Oak	<i>Quercus Alba</i>	n	t	*		1	*	*	*	*	*	*	*	*	
		High Bush blackberry	<i>Rubus allegheniensis</i>	n	s	*	*		1	4	*	*	*	*	*	4	
		Black Raspberry	<i>Rubus occidentalis</i>	n	s		2	2	2	*		1	*	2	*	*	
		Maple Leaved Viburnum	<i>Viburnum acerifolium</i>	n	s	*	*	*	*		2	*	*	*	*	*	
		Japanese Barberry	<i>Berberis thunbergii</i>	i	s		2	10	14	13	4	6	11	11	5	2	
		Winged Euonymus	<i>Euonymus alata</i>	i	s	*		5	5	17	4	3	1	4	7	3	
		Privet	<i>Ligustrum obtusifolium</i>	i	s	*	*	*	9	*	*	*	*	*	*	*	
		Morrow Honeysuckle	<i>Lonicera Morrowii</i>	i	s	*	*	*	*	1	2	1	*	*	*	1	
European Fly Honeysuckle	<i>Lonicera xylosteum</i>	i	s	*	*	*	*	*	*	*	*	*	1	*			
Common buckthorn	<i>Rhamnus cathartica</i>	i	s		11	1	2	*	*		9	3	*	1			
European Buckthorn	<i>Rhamnus Frangula</i>	i	s		5	18	*	*	*	*	*	*	*	*			

Fragment	Region	Common Name	Latin Name	n/l *	t/s **	1f	2f	3f	4f	5f	1b	2b	3b	4b	5b				
middle		Silver Maple	<i>Acer saccharinum</i>	n	t	*	1	1	*	*	*	*	*	*	*	*			
		Sugar Maple	<i>Acer saccharum</i>	n	t		2	1	4	*	*	2	*	2	1	*	*		
		Black Birch	<i>Betula lenta</i>	n	t		1	*	*	*	*	1	*	*	*	1	*		
		Paper Birch	<i>Betula populifolia</i>	n	t	*	*	*	*	*	*	4	*	*	*	*	*		
		Beech	<i>Fagus grandifolia</i>	n	t		2	*	*	2	*	1	*	*	*	2	*		
		Horn Beam	<i>Ostrya virginiana</i>	n	t	*	*	*	*	*	1	*	*	*	*	*	*		
		Black Cherry	<i>Prunus serotina</i>	n	t	*	*	*	*	*	*	*	*	*	1	*	*		
		White Oak	<i>Quercus Alba</i>	n	t		2	*	*	*	*	*	*	*	*	*	*		
		Black Willow	<i>Salix nigra</i>	n	t	*	*		1	*	*	*	*	*	*	*	*		
		Maple Leaved Viburnum	<i>Viburnum acerifolium</i>	n	s	*	4	*	*	*	*	*	*	*	*	*	*		
		Silk Willow	<i>Salix saricea</i>	n	t	*	*	*	*	*	*	*	*	*	*	1	*		
				Japanese Barberry	<i>Berberis thunbergii</i>	i	s		9	6	7	14	4	4	6	*	10	*	
				Winged Euonymus	<i>Euonymus alata</i>	i	s	*		2	2	1	1	*	1	1	*	*	
				Common buckthorn	<i>Rhamnus cathartica</i>	i	s		1	*	*	*	*	2	*	*	*	*	*
				European Buckthorn	<i>Rhamnus Frangula</i>	i	s	*	*	*		1	*	*	*	*	*	*	*
		interior		Beech	<i>Fagus grandifolia</i>	n	t		1	*	*	*	*	*	*	*	*	*	
				Black Cherry	<i>Prunus serotina</i>	n	t	*	*	*	*	*	*	*	*	*	1	*	
				Red Maple	<i>Acer rubrum</i>	n	t	*	*	*	*	*		2	*	*	1	*	
				Red Oak	<i>Quercus borealis</i>	n	t		2	1	*	5	5	*	3	9	4	1	
Slippery Elm	<i>Ulmus rubra</i>			n	t	*	*	*	*	*	*	*	*	*	1	*			
Sugar Maple	<i>Acer saccharum</i>			n	t		6	5	8	3	*	1	5	4	1	5			
White Oak	<i>Quercus Alba</i>			n	t	*	*	*	*	*	*	*	1	*	*	*			
Common buckthorn	<i>Rhamnus cathartica</i>			i	s	*	*	*	*	*	*	*	*	*	*	3	*		
Japanese Barberry	<i>Berberis thunbergii</i>			i	s		1	1	3	*	*	*	*	*	*	*	*		
Winged Euonymus	<i>Euonymus alata</i>			i	s		1	1	*	*	*	*	*	*	*	*	*		
Chenail South	edge	Red Maple	<i>Acer rubrum</i>	n	t	*	*	*	1	1	*	*	*	*	1	1			
		Sugar Maple	<i>Acer saccharum</i>	n	t		9	8	11	7	13	8	7	15	3	11			
		Black Birch	<i>Betula lenta</i>	n	t		7	1	*	*	1	4	*	*	*	*			
		Gray Birch	<i>Betula papyrifera</i>	n	t	*	*	*	1	*	*	*	*	*	6	*			
		Bitternut Hickory	<i>Carya cordiformis</i>	n	t	*	*	*	*	*	*	1	*	*	*	*			
		Beech	<i>Fagus grandifolia</i>	n	t	*		1	2	*	12	*	3	*	*	11			
		Horn Beam	<i>Ostrya virginiana</i>	n	t		1	*	*	1	*	2	*	*	*	*			
		Quaking Aspen	<i>Populus tremuloides</i>	n	t		3	*	3	*	*	*	*	*	*	*			
		White Oak	<i>Quercus Alba</i>	n	t		1	4	4	9	1	*	*	*	*	1			
		Black Oak	<i>Quercus velutina</i>	n	t		1	*	*	*	*	2	*	1	*	*			
		High Bush blackberry	<i>Rubus allegheniensis</i>	n	s		1	*	*	10	6	*	*	*	*	*			
		Black Raspberry	<i>Rubus occidentalis</i>	n	s		7	1	*	1	*	*	*	*	*	*			
		Mountain Ash	<i>Sorbus Americana</i>	n	t	*		1	*	*	*	*	*	*	*	*			
		Maple Leaved Viburnum	<i>Viburnum acerifolium</i>	n	s	*	*	*		1	*	*	*	*	*	*			
		Japanese Barberry	<i>Berberis thunbergii</i>	i	s	*	*	*	1	1	*	*	*	*	*	*			
		European Fly Honeysuckle	<i>Lonicera xylosteum</i>	i	s		1	4	*	*	*	*	*	*	*	*			
		Common buckthorn	<i>Rhamnus cathartica</i>	i	s		3	1	1	2	*	*	*	*	*	*			
		Multiflora rose	<i>Rosa Multiflora</i>	i	s	*	2	*	4	2	*	*	*	*	*	*			
		middle		Red Maple	<i>Acer rubrum</i>	n	t	*	2	*	*	*	*	*	*	*	1	*	
				Sugar Maple	<i>Acer saccharum</i>	n	t	*	2	5	8	9	*	4	4	2	13		
				Bitternut Hickory	<i>Carya cordiformis</i>	n	t		1	*	*	*	*	*	*	*	*		
				Beech	<i>Fagus grandifolia</i>	n	t		7	*	*	*	*	4	*	2	*		
White Ash	<i>Fraxinus americana</i>			n	t	*	*	*	2	2	1	4	*	3	*				
Black Cherry	<i>Prunus serotina</i>			n	t	*	*	*	1	*	*	*	2	*	*				
Black Oak	<i>Quercus velutina</i>			n	t	*	*	*	*	*	*	*	1	*	1				
High Bush blackberry	<i>Rubus allegheniensis</i>			n	s	*	*	2	*	*	2	*	4	2	*				
Black Raspberry	<i>Rubus occidentalis</i>			n	s	*	*	*	2	*	*	*	*	3	*				
European Fly Honeysuckle	<i>Lonicera xylosteum</i>			i	s	*		1	*	3	*	3	2	*	*				
Common buckthorn	<i>Rhamnus cathartica</i>	i	s	*		1	*	1	*	*	*	1	*						
interior		Beech	<i>Fagus grandifolia</i>	n	t	*	4	*	*	*	1	*	*	*	*				
		Gray Birch	<i>Betula papyrifera</i>	n	t		1	1	*	*	1	4	4	*	*				
		Horn Beam	<i>Ostrya virginiana</i>	n	t		1	3	*	1	1	4	*	4	1				
		Paper Birch	<i>Betula populifolia</i>	n	t	*		1	*	*	*	1	*	*	*				
		Red Maple	<i>Acer rubrum</i>	n	t	*	*	*	*	1	*	*	*	*	*				
		Sugar Maple	<i>Acer saccharum</i>	n	t		11	8	5	9	8	5	8	2	10	4			
		White Ash	<i>Fraxinus americana</i>	n	t	*	*	1	*	*	*	*	*	*	1				
		High Bush blackberry	<i>Rubus allegheniensis</i>	n	s	*	*	16	*	*	*	*	*	*	3				
		European Fly Honeysuckle	<i>Lonicera xylosteum</i>	i	s	*	*	*	3	*	*	*	*	*	1				
		Japanese Barberry	<i>Berberis thunbergii</i>	i	s		1	*	*	1	1	*	*	*	1				

Fragment	Region	Common Name	Latin Name	n/l *	t/s **	1f	2f	3f	4f	5f	1b	2b	3b	4b	5b				
Chenal North	edge	Red Maple	<i>Acer rubrum</i>	n	t	*	*	*	1	*	*	1	1	*	*				
		Sugar Maple	<i>Acer saccharum</i>	n	t	*	*	*	*	*	1	*	*	1	*	2			
		Bitternut Hickory	<i>Carya cordiformis</i>	n	t	*		3	2	1	2	1	6	*	*	*			
		Shagbark Hickory	<i>Carya ovata</i>	n	t	*	*	*	*	*	*	1	*	*	*	*			
		Grey Stem Dogwood	<i>Cornus racemosa</i>	n	s	*		7	12	24	23	*	*	*	*	*			
		Red Osier Dogwood	<i>Cornus stolonifera</i>	n	s	*	*	4	6	*	*	*	*	*	*	*			
		Beech	<i>Fagus grandifolia</i>	n	t	*	*	1	*	4	3	1	6	5	4	4			
		Choke cherry	<i>Prunus virginiana</i>	n	t	*	*	*	*	*	*	*	1	*	*	2			
		Maple Leaved Viburnum	<i>Viburnum acerifolium</i>	n	s			4	4	*	5	6	*	*		4	2		
				Japanese Barberry	<i>Berberis thunbergii</i>	i	s		4	5	15	3	1	10	11	1	3	7	
Amur Honeysuckle	<i>Lonicera maackii</i>			i	s	*	*	*	*	*	*	1	*	*	*	*			
European Fly Honeysuckle	<i>Lonicera xylosteum</i>			i	s		1	*	12	1	1	2	3	*	1	3			
Apple	<i>Malus Pumilla</i>			i	t	*	*	1	*	1	*	*	1	*	*	*			
Common buckthorn	<i>Rhamnus cathartica</i>			i	s		10	6	4	3	2	4	7	*	1	3			
Multiflora rose	<i>Rosa Multiflora</i>			i	s		2	15	1	6	2	3	4	*	1	4			
middle				Red Maple	<i>Acer rubrum</i>	n	t	*	*	*	*	1	*	*	*	*	1		
				Sugar Maple	<i>Acer saccharum</i>	n	t		3	10	*	*	3	4	1	2	1	*	
				Gray Birch	<i>Betula papyrifera</i>	n	t	*		1	2	1	*	*	*	2	1	*	
				Paper Birch	<i>Betula populifolia</i>	n	t	*	*	*	*	*	*	*	*	*	2	*	
		Bitternut Hickory	<i>Carya cordiformis</i>	n	t		1	1	3	2	3	1	1	2	1	*			
		Shagbark Hickory	<i>Carya ovata</i>	n	t	*	*	*	*	*	2	*	*	2	*	*			
		Beech	<i>Fagus grandifolia</i>	n	t		2	2	18	28	4	8	6	10	10	*			
		Slippery Elm	<i>Ulmus rubra</i>	n	t	*	*	*	*	*	1	*	*	*	2	*			
		Maple Leaved Viburnum	<i>Viburnum acerifolium</i>	n	s	*	*	*	*	*	1	1	*	*	*	1			
				Japanese Barberry	<i>Berberis thunbergii</i>	i	s		8	*	*	1	15	5	1	*	2	3	
European Fly Honeysuckle	<i>Lonicera xylosteum</i>			i	s	*	*	*	*	*	6	*	*	*	2	7			
Apple	<i>Malus Pumilla</i>			i	s		4	*	1	*	*	*	*	*	1	*			
Common buckthorn	<i>Rhamnus cathartica</i>			i	s	*		3	*	*	2	*	3	1	*	1			
Multiflora Rose	<i>Rosa multi</i>			i	s	*	*	*	*	*	*	*	*	*	*	1			
interior				Sugar Maple	<i>Acer saccharum</i>	n	t	*		2	1	1	7	*	1	*	12		
				Yellow birch	<i>Betula lutea</i>	n	t	*	*	*	*	*	1	*	*	*	*		
				Bitternut Hickory	<i>Carya cordiformis</i>	n	t	*	*	*	*	*	1	*	*	*	1		
				Beech	<i>Fagus grandifolia</i>	n	t		15	6	18	16	2	20	11	23	15	13	
				European Fly Honeysuckle	<i>Lonicera xylostem</i>	n	s	*		1	*	*	*	*	*	*	*		
		Maple Leaved Viburnum	<i>Viburnum acerifolium</i>	n	s	*	*	*	*	*	*	*	*	1	*				
				Japanese Barberry	<i>Berberis thunbergii</i>	i	s		2	*	*	*	*	3	*	1	*	2	
				Luce Road	edge	Sugar Maple	<i>Acer saccharum</i>	n	t	*	*	*	*	1	*	*	*	1	*
						Yellow Birch	<i>Betula lutea</i>	n	t	*		2	2	*	4	*	*	*	1
						Gray Birch	<i>Betula papyrifera</i>	n	t	*		1	*	*	*	*	*	*	*
Iron Wood	<i>Carpinus caroliniana</i>					n	t	*		2	*	*	*	1	*	*	*		
Bitternut Hickory	<i>Carya cordiformis</i>					n	t	*	*	*	*	*	*	1	1	*	*		
Grey Stem Dogwood	<i>Cornus racemosa</i>					n	s		1	2	*	*	*	*	*	*	*		
Round-leaved dogwood	<i>Cornus rugosa</i>					n	s	*	*	1	*	*	*	*	*	*	*		
Beech	<i>Fagus grandifolia</i>					n	t		38	4	*	*	1	29	4	1	1	*	
Horn Beam	<i>Ostrya virgininiana</i>					n	t	*		4	*	*	*	*	*	*	*		
Black Raspberry	<i>Rubus occidentalis</i>	n	s				1	*	*	*	*	*	*	*	*				
		Japanese Barberry	<i>Berberis thunbergii</i>	i	s		3	20	43	55	40	2	12	46	43	21			
		Morrowi Honeysuckle	<i>Lonicera Morrowii</i>	i	s	*	*	*	*	*	1	*	1	*	*				
		European Fly Honeysuckle	<i>Lonicera xylosteum</i>	i	s		1	6	17	22	14	3	6	6	4	6			
		Common buckthorn	<i>Rhamnus cathartica</i>	i	s		5	16	19	28	22	2	6	5	6	19			
		European Buckthorn	<i>Rhamnus Frangula</i>	i	s		1	1	*	*	*	*	4	10	2	*			
		Multiflora rose	<i>Rosa Multiflora</i>	i	s	*		3	*	*	1	*	*	*	*				
		middle		Red Maple	<i>Acer rubrum</i>	n	t	*	*	*	*	1	*	*	*	1	*		
				Sugar Maple	<i>Acer saccharum</i>	n	t		1	*	*	1	3	*	2	1	*	5	
				Iron Wood	<i>Carpinus caroliniana</i>	n	t	*	*	*	*	*	*	*	*	*	1	*	
				Bitternut Hickory	<i>Carya cordiformis</i>	n	t		4	1	3	2	2	4	*	1	*		
Shagbark Hickory	<i>Carya ovata</i>			n	t	*	*	*	3	*	1	*	*	*	*				
Alternate leafed dogwood	<i>Cornus alternifolia</i>			n	s	*	*	*	*	1	*	*	*	1	*				
Grey Stem Dogwood	<i>Cornus racemosa</i>			n	s	*	*	1	*	*	*	*	*	1	*				
Beech	<i>Fagus grandifolia</i>			n	t		2	1	1	3	*	*	1	2	*				
High Bush blackberry	<i>Rubus allegheniensis</i>			n	s	*	*	*	1	*	10	*	4	*	*				
Black Raspberry	<i>Rubus occidentalis</i>			n	s		3	*	*	1	*	*	4	3	*				
		Maple Leaved Viburnum	<i>Viburnum acerifolium</i>	n	s	*	*	*	*	*	1	*	*	*					
				Japanese Barberry	<i>Berberis thunbergii</i>	i	s		7	5	2	6	2	6	3	3	5	4	
				European Fly Honeysuckle	<i>Lonicera xylosteum</i>	i	s		2	*	*	5	*	3	2	*	1	*	
				Common buckthorn	<i>Rhamnus cathartica</i>	i	s	*	*	*	1	*	1	*	*	1	*		
				European Buckthorn	<i>Rhamnus Frangula</i>	i	s		1	*	*	*	*	*	*	*	*		
				Multiflora rose	<i>Rosa Multiflora</i>	i	s		4	6	*	*	*	1	1	*	*		
				interior		Sugar Maple	<i>Acer saccharum</i>	n	t		3	2	1	*	*	3	2	1	*
						Yellow Birch	<i>Betula lutea</i>	n	t	*	*	2	2	2	*	1	*	*	*
						Bitternut Hickory	<i>Carya cordiformis</i>	n	t	*	*	*	1	4	*	*	*	1	1
						Beech	<i>Fagus grandifolia</i>	n	t		7	7	4	*	*	10	4	10	*
Horn Beam	<i>Ostrya virgininiana</i>					n	t	*	*	*	*	*	1	*	*	*	1		
High Bush blackberry	<i>Rubus allegheniensis</i>	n	s			*	*	*	6	4	9	*	1	5	*				
Black Raspberry	<i>Rubus occidentalis</i>	n	s			*	*	1	7	3	4	*	4	2	6				
		Japanese Barberry	<i>Berberis thunbergii</i>			i	s	*	*	*	10	2	4	*	3	2	2		
		Honeysuckle	<i>Lonicera Caerulea</i>			i	s	*	*	*	*	3	*	*	*	*	2		
		European Fly Honeysuckle	<i>Lonicera xylosteum</i>			i	s		1	*	*	1	2	1	*	*	*		

Fragment	Region	Common Name	Latin Name	n/1 *	t/s **	1f	2f	3f	4f	5f	1b	2b	3b	4b	5b			
interior		Sugar Maple	<i>Acer saccharum</i>	n	t		7	3	1	1	3	7	5	6	3	1		
		Gray Birch	<i>Betula papyrifera</i>	n	t	*	*	*	*	*	*	*	*	*	1	*	*	
		Iron Wood	<i>Carpinus caroliniana</i>	n	t	*	*	2	2	2	2	*	*	*	1	2	3	
		Grey Stem Dogwood	<i>Cornus racemosa</i>	n	s	*	*	*	*	*	*	*	*	*	*	1	*	
		Hawthorn	<i>Crataegus sp.</i>	n	s	*	*	*	*	2	*	*	*	*	*	1	*	
		Beech	<i>Fagus grandifolia</i>	n	t		7	15	9	11	6	2	4	9	3	10		
		Quaking Aspen	<i>Populus tremuloides</i>	n	t		4	1*	*	*	1*	*	*	1	1*			
		Black Cherry	<i>Prunus serotina</i>	n	t	*	3*	*	*	*	*	*	*	1*	1*			
		White Oak	<i>Quercus Alba</i>	n	t		2	1*	*	*	*	*	*	1	2*			
		High Bush blackberry	<i>Rubus allegheniensis</i>	n	s	*	*	*	3*	*	1*	*	*	*	*	1*		
		Black Raspberry	<i>Rubus occidentalis</i>	n	s	*	*	*	*	*	*	*	*	*	*	2*		
		Meadowsweet	<i>Spirea latifolia</i>	n	s	*	*	*	1*	*	*	*	*	*	*	*		
		Arrowwood	<i>Viburnum recognitum</i>	n	t	*	*	*	*	*	*	*	*	1*	*	*		
		Japanese Barberry	<i>Berberis thunbergii</i>	i	s		1*	*	1*	*	*	*	*	*	*	*		
		Privet	<i>Ligustrum obtusifolium</i>	i	s	*	*	*	1*	*	*	*	*	*	*	*		
		Morrowi Honeysuckle	<i>Lonicera Morrowii</i>	i	s	*	*	*	*	*	2	3*	*	*	1	1		
		Common buckthorn	<i>Rhamnus cathartica</i>	i	s	*	*	*	*	2*	*	*	*	3*	*	*		
		Sloan Road	edge	Sugar Maple	<i>Acer saccharum</i>	n	t	*	1*	*	*	1	4	2*	1	1		
				Black Birch	<i>Betula lenta</i>	n	t	*	*	*	*	*	*	1*	*	*	*	
				Gray Birch	<i>Betula papyrifera</i>	n	t		1*	*	*	1	3*	*	*	*	*	
				Iron Wood	<i>Carpinus caroliniana</i>	n	t	*	*	*	1*	*	1*	*	*	*	*	
				Bitternut Hickory	<i>Carya cordiformis</i>	n	t	*	*	*	*	*	*	*	*	*	1	
				Hawthorn	<i>Crataegus sp.</i>	n	s	*	1*	*	*	*	2*	*	1	1*		
				Beech	<i>Fagus grandifolia</i>	n	s	*	*	*	*	2	3	1*	*	*	*	
				Black Cherry	<i>Prunus serotina</i>	n	t	*	*	*	1	3	1*	*	3	5	2	
High Bush blackberry	<i>Rubus allegheniensis</i>			n	s	*	*	7*	*	*	5*	*	*	*	4			
Black Raspberry	<i>Rubus occidentalis</i>			n	s		2*	3*	*	2*	*	*	1*	*	*			
Silk Willow	<i>Salix sericea</i>			n	t		1*	*	*	1*	*	*	*	*	1			
Maple Leaved Viburnum	<i>Viburnum acerifolium</i>			n	s		1*	*	*	*	*	*	*	*	*			
Arrowwood	<i>Viburnum recognitum</i>			n	t		1	1*	1	1*	*	*	*	1*	*			
Hybrid Honeysuckle	<i>Lonicera bella</i>			i	s	*	*	*	1*	*	*	*	*	*	*			
Morrowi Honeysuckle	<i>Lonicera Morrowii</i>			i	s		2*	2	3	3*	*	*	*	1	1			
European Fly Honeysuckle	<i>Lonicera xylosteum</i>			i	s		15	34	14	17	6	22	18	23	6	3		
Common buckthorn	<i>Rhamnus cathartica</i>			i	s	*	*	7	1	5	2*	*	10	1*	*	4		
European Buckthorn	<i>Rhamnus Frangula</i>			i	s	*	*	*	*	*	*	*	6*	*	*			
Multiflora rose	<i>Rosa Multiflora</i>			i	s		2*	*	*	*	*	*	*	*	*			
middle				Sugar Maple	<i>Acer saccharum</i>	n	t	*	1	5	4	4	2	5	7	5	3	
				Black Birch	<i>Betula lenta</i>	n	t		1*	*	*	*	4*	*	3*	*		
				Yellow Birch	<i>Betula lutea</i>	n	t		2*	*	*	*	*	*	*	*		
				Gray Birch	<i>Betula papyrifera</i>	n	t	*	1	1	3	2*	*	*	*	2*		
				Paper Birch	<i>Betula populifolia</i>	n	t	*	*	*	1*	*	*	1*	*	*		
				Iron Wood	<i>Carpinus caroliniana</i>	n	t		2	4	1	2	1*	*	3	1	1*	
		Shagbark Hickory	<i>Carya ovata</i>	n	t		2	1*	*	*	2*	*	*	*				
		Beech	<i>Fagus grandifolia</i>	n	t		4	3	2*	*	1*	*	8	2	1	3		
		Horn Beam	<i>Ostrya virgininiana</i>	n	t	*	*	1	2*	*	*	*	1	1*	*			
		Quaking Aspen	<i>Populus tremuloides</i>	n	t	*	*	*	*	*	*	*	*	*	3*			
		European Fly Honeysuckle	<i>Lonicera xylosteum</i>	i	s	*	*	*	2	1*	*	*	*	1*				
		interior		Sugar Maple	<i>Acer saccharum</i>	n	t		34	8	2	1	1	3	12	3*	1	
				Gray Birch	<i>Betula papyrifera</i>	n	t	*	*	*	*	8*	*	*	*	2*		
				Paper Birch	<i>Betula populifolia</i>	n	t	*	*	*	*	12*	*	*	*	*		
				Beech	<i>Fagus grandifolia</i>	n	t	*	20	26	12	3	6	19	45	22	6	
				Horn Beam	<i>Ostrya virgininiana</i>	n	t	*	1	2	1	2	2*	*	3*	2*		
				Greylock High School	edge	Sugar Maple	<i>Acer saccharum</i>	n	t		7	19	17	12	19	8	5	5
		Gray Birch	<i>Betula papyrifera</i>	n	t		2*	*	*	*	*	*	*	*	*			
		Shagbark Hickory	<i>Carya ovata</i>	n	t	*	*	*	1*	*	*	*	*	*	*			
		Beech	<i>Fagus grandifolia</i>	n	t		1*	1*	*	*	*	*	*	*	*			
		Quaking Aspen	<i>Populus tremuloides</i>	n	t	*	3*	*	1*	*	*	*	*	*	*			
		Black Cherry	<i>Prunus serotina</i>	n	t	*	*	*	*	1*	*	*	*	1	1			
		Smooth Rose	<i>Rosa Blanda</i>	n	s	*	*	*	*	*	1*	*	*	*	*			
		Black Raspberry	<i>Rubus occidentalis</i>	n	s		5*	*	*	6*	*	*	*	*	3			
		Silk Willow	<i>Salix saricea</i>	n	t		2*	*	1*	*	*	*	*	*	*			
Japanese Barberry	<i>Berberis thunbergii</i>	i	s	*	*	*	*	1	1*	*	*	*	*					
European Fly Honeysuckle	<i>Lonicera xylosteum</i>	i	s	*	*	*	*	*	*	*	*	*	1					
Common buckthorn	<i>Rhamnus cathartica</i>	i	s		7*	1	1*	*	*	*	*	*	*					
Multiflora rose	<i>Rosa Multiflora</i>	i	s		1*	*	1*	*	*	*	*	*	*					
middle		Sugar Maple	<i>Acer saccharum</i>	n	t		4	2	17	4	3	7	4	7	1	4		
		Black Birch	<i>Betula lenta</i>	n	t	*	*	*	*	*	1*	*	*	*				
		Iron Wood	<i>Carpinus caroliniana</i>	n	t		1*	*	*	*	*	*	*	*				
		Beech	<i>Fagus grandifolia</i>	n	t		4	5*	3	5	4	8	2	5	4			
		Horn Beam	<i>Ostrya virgininiana</i>	n	t		3	3	1	1*	1	1	3*	*				
		Japanese Barberry	<i>Berberis thunbergii</i>	i	s	*	*	4*	*	*	*	*	1*	1				
		interior		Sugar Maple	<i>Acer saccharum</i>	n	t		1	2*	*	*	3	1	1	1*		
				Iron Wood	<i>Carpinus caroliniana</i>	n	t		1*	*	1*	*	2*	*	*	*		
				Beech	<i>Fagus grandifolia</i>	n	t		16	27	28	9	9	16	15	21	9	6
				Horn Beam	<i>Ostrya virgininiana</i>	n	t	*	*	*	1*	*	1*	*	1*	1*		
Red Oak	<i>Quercus borealis</i>			n	t	*	*	*	2*	*	*	*	*	2*				
Black Raspberry	<i>Rubus occidentalis</i>			n	s	*	*	*	*	2*	*	*	*	*				
European Fly Honeysuckle	<i>Lonicera xylosteum</i>			i	s	*	*	*	*	*	*	*	*	1*				
Multiflora rose	<i>Rosa Multiflora</i>			i	s	*	*	*	*	*	*	*	*	*				

Fragment	Region	Common Name	Latin Name	n/l *	t/s **	1f	2f	3f	4f	5f	1b	2b	3b	4b	5b				
Deer Ridge	edge	Sugar Maple	<i>Acer saccharum</i>	n	t	*	*	*	2	*	*	*	*	*	*	*			
		Black Birch	<i>Betula lenta</i>	n	t	*	*	*	*	*	1	*	*	*	*	*	*		
		Yellow Birch	<i>Betula lutea</i>	n	t	*	*	*	*	2	*	*	*	*	*	*	*		
		Iron Wood	<i>Carpinus caroliniana</i>	n	t	*	*	*	*	3	4	*	*	*	3	*	*		
		Beech	<i>Fagus grandifolia</i>	n	t	*		1	3	*	5	*	2	2	4	4			
		White Ash	<i>Fraxinus americana</i>	n	t		2	1	*	*	*	5	*	*	*	*	*		
		Horn Beam	<i>Ostrya virginiana</i>	n	t		2	2	4	4	4	*	*	*	*	*	*		
		Black Cherry	<i>Prunus serotina</i>	n	t	*	*		6	4	2	3	2	2	*	*	*		
		White Oak	<i>Quercus Alba</i>	n	t		3	*	1	*	*	*	*	*	*	*	*		
		High Bush blackberry	<i>Rubus allegheniensis</i>	n	s	*		11	24	26	*	*	*	*	*	10	*		
		Black Raspberry	<i>Rubus occidentalis</i>	n	s		14	*	1	*	*	5	*	*	*	*	*		
		Mountain Ash	<i>Sorbus Americana</i>	n	t	*	*		7	2	*	*	*	2	*	*	*		
		Basswood	<i>Tilia Americana</i>	n	t	*		1	*		2	*	*	*	*	*	*		
		Maple Leaved Viburnum	<i>Viburnum acerifolium</i>	n	s		2	6	3	*	1	*	2	*	2	*	*		
		Morrowi Honeysuckle	<i>Lonicera Morrowii</i>	i	s	*	*	*	*	*	*	*	*	*	*	*	1		
		Common buckthorn	<i>Rhamnus cathartica</i>	i	s	*		4	*	*	3	*	*	*	*	*	1		
		middle		Sugar Maple	<i>Acer saccharum</i>	n	t		2	1	4	2	2	1	2	*	*	4	
				Black Birch	<i>Betula lenta</i>	n	t	*	*	*	*	4	*	*	*	*	*	*	2
				Iron Wood	<i>Carpinus caroliniana</i>	n	t	*		3	*	*	1	*	*	*	*	*	*
				Beech	<i>Fagus grandifolia</i>	n	t	*		7	1	1	13	*	2	*	2	13	
				Horn Beam	<i>Ostrya virginiana</i>	n	t	*		1	*	*	*	*	*	*	*	*	1
				Black Cherry	<i>Prunus serotina</i>	n	t	*	*		1	1	1	*	*	*	*	*	*
White Oak	<i>Quercus Alba</i>			n	t		1	1	1	*	2	*	1	1	*	1			
High Bush blackberry	<i>Rubus allegheniensis</i>			n	s	*	*	*	*	*	11	*	*	*	*	*	3		
Red-berried elderberry	<i>Sambucus racemosa</i>			n	t	*		3	1	*	1	*	*	*	*	*	*		
Japanese Barberry	<i>Berberis thunbergii</i>			i	s	*	*	*	*	*	*	*	*	*	1	*	*		
interior		Balsam Fir	<i>Abies balsamea</i>	n	t	*	*	*	*	*	*	1	*	*	*	*			
		Sugar Maple	<i>Acer saccharum</i>	n	t	*		4	1	5	6	1	8	7	14	6			
		Black Birch	<i>Betula lenta</i>	n	t	2	*	*	*	*	*	*	*	*	*	*			
		Yellow Birch	<i>Betula lutea</i>	n	t	1	*	*	*	1	1	*	*	*	*	*			
		Gray Birch	<i>Betula papyrifera</i>	n	t	11	5	13	1	5	14	7	8	4	5				
		Paper Birch	<i>Betula populifolia</i>	n	t	*	*	*	*	*	1	*	1	*	*	1			
		Iron Wood	<i>Carpinus caroliniana</i>	n	t	*		1	*	*	*	*	1	*	*	*			
		Shagbark Hickory	<i>Carya ovata</i>	n	t	*	*	*	*	*	*	1	*	*	*	*			
		Beech	<i>Fagus grandifolia</i>	n	t	23	10	7	11	16	11	9	11	5	16				
		Horn Beam	<i>Ostrya virginiana</i>	n	t	*	*	*	*	*	*	2	*	*	*	*			
Black Cherry	<i>Prunus serotina</i>	n	t	*	*	*	*	*	*	1	*	*	*	*					

