PRESENCE OF NON-NATIVE VASCULAR FLORA IN PRINCE EDWARD ISLAND'S REMNANT ACADIAN FOREST

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ABSTRACT

Biological invasion is ranked second only to habitat loss as the greatest threat to biodiversity on both a local and global scale. The upland hardwood component of Prince Edward Island's Acadian forest is among the best remaining examples of PEI's pre-colonial landscape, but there has been no assessment of the presence of exotic species in these areas. Three 300 metre long edge to interior transects were established in each of six Acadian forest study areas. Nine 100 m^2 circular plots were sampled along each transect at distances from 5.7 to 300 metres; one external plot was established at each transect to sample species in adjacent (non forest) habitats. In each plot, all vascular plants were identified, a visual estimate of percent cover was made, and soil temperature, canopy cover and tree diameters were measured. The results show that there is an edge-to-interior plant community gradient within these forests, and suggest that interior conditions are not reached until a distance of more than 120 metres from an edge. This suggests that upland hardwood Acadian forest protected areas smaller than 240 metres on a side (5.75 hectares) are unlikely to include interior habitat, and sites should be at least 320 metres on all sides (10.24 hectares) to ensure interior habitat is present.

Invasion by exotic vascular plants was found to be more extensive than that reported from other jurisdictions, and innermost (300 metre) plots were not free from exotics. This suggests that PEI's remnant upland hardwood forests have been subjected to greater anthropogenic influences than those elsewhere in eastern North America, including areas with historical land use comparable to or more intensive than that of Prince Edward Island.

Fifteen exotic species were found within upland hardwood study sites, with *Veronica officinalis* (Common Speedwell) and *Hieracium lachenalii* (Hawkweed) being the most invasive species both in terms of distance penetrated and area covered. Seeds from each species were collected from edge and interior conditions and weights and viability were compared. *V. officinalis* seeds from interior conditions were lighter, due at least in part to environmental conditions including light. This species has developed increased shade tolerance in eastern North America as compared to that found in its native Eurasian range, and North American individuals may represent a separate ecotype. No differences in seed weights were found for *H. lachenalii* and viability was not significantly different for either species in edge or interior conditions. Both species were found to have morphological traits that confer a competitive advantage over native species.

Because of the extent of infestation in the Acadian forest study sites, active control of exotic species is not recommended unless their potential to out-compete or hybridize with native species is realized. Management within these sites should be designed to minimize the spread of exotic species and prevent new introductions.

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1.0 INTRODUCTION

1.1 The problem of non-native and invasive species: an overview

For thousands of years, humans have moved plants and animals around the world accidentally as well as intentionally for agricultural, medical, ceremonial and ornamental purposes (Godwin, 1975; Mack and Lonsdale, 2001). While intentional movements of species beyond their native ranges have been essential to the development of agriculture and industrialized society, the scope and scale of biological introductions have increased exponentially since pre-colonial times. Mack *et al.* (2000) suggest that the dramatic change in global species distribution observed over the past 500 years is comparable to that brought about by continental glaciation cycles, even though it has occurred in a fraction of the time.

A species that has been introduced beyond its native range is considered non-native in its new land. Within this category of non-native species are three sub-categories - introduced, naturalized and invasive - each of increasing severity from a biological perspective. Introduced species persist in their new range only though cultivation or frequent re-introduction. Prince Edward Island (PEI), Canada, has species such as *Solanum tuberosum* (Irish potato) or *Populus nigra* (black cottonwood) which do not invade habitats beyond those in which they are cultivated. Naturalized species are able to persist without cultivation or re-immigration (Mack *et al.*, 2000). Former crop species such as *Lotus corniculatus* (bird's-foot trefoil) or ornamentals such as *Saponaria officinalis* (soapwort) are examples. Naturalized plants or animals which have the potential to cause environmental or economic harm, or harm to human health are classified as invasive (Office of Technology Assessment, 1993). In many regions, the well-known *Lythrum salicaria* (purple loosestrife) or dense-growing *Vinca minor* (periwinkle) extend into natural areas and have the potential to cause harm and thus become invasive.

Biological invasion by non-native plants and animals has been recognized as a significant ecological problem, ranking second only to habitat loss as the greatest threat to biodiversity on both a local and global scale (Cronk and Fuller, 1980; Center, Frank and Dray, 1995; Vitousek *et al.*, 1996; Baker, 2001). Although high-profile problematic introductions such as zebra mussel (*Dreissena polymorpha*) in the Great Lakes or brown spruce and Asian longhorn beetles (*Tetropium fuscum* and *Anoplophora glabripennis*) in northeastern North America have focussed attention on non-native animals over the past decade, both the general public and (to a lesser extent) the scientific community remain largely unaware of the biological and economic impact of non-native plant species (Vitousek *et al.*, 1996; Colton and Alpert, 1998; Reichard and White, 2001).

Numbers and extent of non-native species are recognized as stressors which affect ecological integrity of an area (Parks Canada, 1998). In the United States, non-native plants are considered serious problems in 50% of National Parks and 60% of lands managed by The Nature Conservancy (Campbell, 1997). In Canada, the numbers are comparable: 21 of 36 National Parks - including remote wilderness parks such as Kluane and Pacific Rim - have reported non-native vegetation as responsible for significant ecological impacts (Parks Canada, 1998).

Non-native plants displace native plant communities in more than 437,000 km^2 of native grasslands and wetlands in the U.S. (Campbell, 1997); to put this into perspective, this represents an area 77 times the size of Prince Edward Island, or nearly as large as the Yukon Territory. In Britain, *Rhododendron ponticum* has invaded a variety of habitats, often forming impenetrable stands that prevent growth of native species (Cronk and Fuller, 1980). In New England, non-native honeysuckles (*Lonicera* spp.) have invaded forest interiors, in some cases becoming the dominant forest vegetation (Woods, 1993). In Canada, purple loosestrife (*Lythum salicaria*) is a dramatic example of displacement of native species and communities: in many areas, native marsh vegetation has been replaced by a sea of non-native loosestrife.

In addition to displacing native species, non-native plants can put indigenous populations at risk of extinction. Nearly one-fifth of plants considered endangered or threatened by the U.S. Fish and Wildlife Service are imperilled because of non-native flora (Haber, 1998) and half of these at-risk species are vulnerable to non-native predation or competition (Baker, 2001). In Canada, non-native species are listed as contributing threats to 16% of plants listed as endangered or threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (Haber, 1998).

Similarly, non-native species can be vectors of disease that infect native species. Imported ornamental nursery stock was responsible for introducing such devastating diseases as chestnut blight (caused by the fungus *Cryphonectria parasitica*) in the late 1890s and white pine blister rust (caused by the fungus *Cronartium ribicola*) in the early 1900s (von Broembsen, 1989). Ornamental stock was also the pathway of introduction for beech canker (caused by the fungus *Nectria coccinea* var *faginata* facilitated by the beech scale insect *Cryptococcus fagisuga*) which had spread throughout the Maritimes by 1932 (Canadian Forest Service, 2001). von Broembsen (1989) reports that all known plant pathogens that have successfully invaded natural ecosystems have been introduced by humans, and suggests that it is probable that many such invasions have not yet been recognized.

While displacement of native species or communities and spread of disease are often a highly visible impact of non-native species, less obvious impacts include alteration of fire regimes (Cronk and Fuller, 1980) and ecosystem-level changes such as alteration of productivity and energy flow (Ramakrishnan and Vitousek, 1989; Vitousek *et al.*, 1996), and changes in nitrogen fixation, hydrologic cycles and sedimentation (Reichard and White, 2001). Hybridization between native and non-native species can also be a problem. For example, in Ontario, red mulberry (*Morus rubra*) is being threatened by hybridization with the non-native white mulberry (*Morus alba*) (Haber, 1998). In eastern Canada, the taxonomy of species such as field mint (*Mentha arvensis*) and reed canary grass (*Phalaris arundinacea*) is made more difficult because these taxa are a blend of native and non-native genotypes (Zinck, 1998).

In addition to these biological costs, non-native species have the potential to incur huge economic costs. It has been estimated that costs directly attributable to invasive species in the United States alone exceed $125 billion annually (Baker, 2001). Individual non-native species can be responsible for large expenditures. For example, the U.S. allocates $25 million annually for control of hydrilla (*Hydrilla verticillata*); Florida budgets $3 million per year for control of water hyacinth (*Eichhornia crassipes*) (Mullin *et al.*, 2000).

Despite these biological and economic costs, non-native species continue to be introduced at an alarming rate: in 1993, some 456 million non-native plant individuals were imported to the United States alone (Center, Frank and Dray, 1995). In general, the public fails to appreciate the threat posed by non-native species. In their California survey, Colton and Alpert (1998) found that fewer than 20% of respondents considered non-native plants to be a threat to natural systems. As Cronk and Fuller (1980) note, botanists and ecologists tend to study native flora, often disregarding non-native species.

1.2 Invasions

Traditionally, it was predicted that complex and diverse communities would be resistant to invasion (Elton, 1958); more recently, there have been many examples of species-rich habitats being more susceptible to invasion than their comparatively depauperate counterparts (Center, Frank and Dray, 1995; Stohlgren *et al.*, 1999; Lonsdale, 1999). For example, botanically diverse riparian zones have been repeatedly shown to be vulnerable to invasion (Stohlgren *et al.*, 1999), as have relatively undisturbed and species-rich habitats in tropical and subtropical Australia (Center, Frank and Dray, 1995). Furthermore, Stohlgren *et al.* (1999) found increased invasions with increased species richness in the Colorado Rockies and suggest that species-rich habitats are susceptible to invasion and that invasion may be more closely linked to available resources than diversity. Lonsdale (1999) also concluded that richer communities had greater numbers of non-native species.

While anthropogenic habitats often have a higher proportion of non-native species than natural areas (Hobbs and Huenneke, 1992; Williamson, 1996), it is difficult to separate cause and effect. There is debate between those who view disturbed habitats as being more easily invaded (*e.g.* Hobbs and Huenneke, 1992) and those who suggest that, because of human use, such habitats have simply had contact with greater numbers of non-native species (*e.g.* Mooney and Drake, 1989; Lonsdale, 1999). There is also debate between those who view all habitats as roughly equally susceptible to invasion (Williamson, 1996) and those who suggest that there are factors which make some communities more vulnerable (Mack *et al.*, 2000).

For example, islands are often reported as being more vulnerable to invasions than mainland areas (Cronk and Fuller, 1980; Saunders, Hobbs and Margules, 1991; Meffe and Carroll, 1994; Kupfer, 1995; Walker and Steffen, 1997). A common generalization is that island communities are relatively simple as compared to mainland systems and thus have vacant niches - functional roles within the community waiting to be filled (Simberloff, 1995; Lonsdale, 1999; Mack *et al.*, 2000). This suggests that such communities have lower internal competition and decreased resistance to non-native species (Simberloff, 1995; Lonsdale, 1999; Mack *et al.*, 2000). Testing of this generalization by Lonsdale (1999) found that while islands are more invaded, they did not have significantly simpler communities with fewer native species. Clear evidence in support of the vacant niche hypothesis has proven elusive, and there are very few examples of introductions leading to increased competition (Simberloff, 1995).

Additionally, the fact that islands are more invaded does not immediately lead to the conclusion that they are more vulnerable to invasion (Lonsdale, 1999). Alternative explanations include the possibility that islands are subject to greater numbers of introductions (greater propagule pressure) (Lonsdale, 1999). Only those introductions that persist in their new habitat are known and assessed; information on the total immigration rate would be needed to accurately test this explanation (Simberloff, 1995; Lonsdale, 1999). Another explanation is that islands may not have refuges which remain free from invaders (Simberloff, 1995). For example, a non-native species can spread through a 500 km^2 island but the same geographical coverage on the mainland would be considered a localized invasion (Cronk and Fuller, 1980).

Although it is difficult to make valid generalizations about invasive species (Blossey and Nötzold, 1995) and there are insufficient data to predict which communities will be more or less resistant to invasion (Simberloff, 1995; Williamson, 1996), one can say that natural areas are not immune. As previously noted, the majority of National Parks in both Canada and the United States cite the introduction of non-native plants as a serious problem (Campbell, 1997; Parks Canada, 1998).

Not all non-native species will successfully invade natural communities. The proliferation of a non-native species depends not only on characteristics of the invaded habitat, but of the invader itself (Pimm, 1989). It is impossible to determine exactly how many species have been moved from their native ranges because many do not survive the trip. Those that do often face a host of biological, physical and climatic obstacles and many perish shortly after arrival in the new land (Mack *et al.*, 2000). Of those that make the transition, few will become successfully naturalized and fewer still will invade natural communities.

The "tens rule" has been shown to apply to many groups of organisms, including species introduced to North America (Williamson and Fitter, 1996). In its simplest form, the tens rule predicts that 10% of introduced species will escape, 10% of these escapes will become naturalized, and 10% of naturalized species will become problems. As with most rules, this should be treated as a relative guide rather than a firm number, and some authors prefer to think of the tens rule as meaning "a small proportion", between 5% and 20% (Williamson and Fitter, 1996).

Characteristics of an "ideal" invader include high seed production, fast growth, early flowering, vegetative reproduction and broad germination and habitat requirements (Baker, 1965; Parendes and Jones, 2000). For example, production of large numbers of seeds can ensure rapid expansion of a population, even if seed viability is low. Additionally, high seed production is correlated with small seed mass, and small seeds have been shown to have a greater dispersal capacity than their larger counterparts (Guo *et al.*, 2000). A short life cycle, with early germination, fast growth and early reproduction gives an invader the ability to use available resources (especially light and moisture) before other vegetation in the community (Reichard and Hamilton, 1997; Parendes and Jones, 2000). Broad habitat and germination requirements increase the probability of an invader finding suitable habitat in its new community (Reichard and Hamilton, 1997; Parendes and Jones, 2000).

Other morphological features that contribute to the success of invasive species include size (Cronk and Fuller, 1980), seed adaptations that aid in dispersal (Heywood, 1989), and rhizomatous or vine-link growth (Haber, 1998). For example, more than 50% of the invasive plants in New Zealand protected areas are over 3 metres (m) in height; size may allow the invader to reach for limited resources such as light (Cronk and Fuller, 1980). Seed adaptations such as wings, hooks, spines, or fruit help the invader to disperse its seed, often via native animals such as birds, mammals or ants (Baskin and Baskin, 1998; Morales and Heithaus, 1998). Finally, rhizomatous or vine-like growth allows rapid expansion of the population and confers an ability to spread rapidly and densely though a community (Haber, 1998). While this list may be more useful as a key to potential warning signs rather than as a predictor of what species will become problematic in a given community (Noble, 1989), Reichard and Hamilton (1997) were able to predict successful invasions with greater than 85% accuracy based on morphological traits and global distribution.

It has been suggested that some non-native plants, when freed from the natural pressures of their home environments, will tend to grow faster, produce more and larger seeds, have greater fitness and live longer than in their native habitats (Blossey and Nötzold, 1995). Such escape from predation, competition and disease may in this way give non-native species a major advantage over native species (Mack *et al.*, 2000). There is also evidence that some species exhibit "positive feedback" (Whisenant, 1990). For example, *Bromus japonicus* (Japanese Chess) has been shown to alter microhabitat features such as soil moisture and litter buildup in a way that favours its germination and establishment (Whisenant, 1990).

Added to these characteristics are the less predictable variables of chance and timing (Crawley, 1989). For example, even an ideal invader may not succeed if the community is subjected by chance to an unusual meteorological or geological event to which native species have adapted but the invader has not. Similarly, should the same invader arrive in the community too early in the season, its required resources may not be present; too late, and native competitors or predators may be too abundant to allow establishment (Crawley, 1989).

1.3 Fragmentation and edge effect

In many landscapes, once-contiguous forests have been reduced to smaller and smaller patches surrounded by anthropogenic habitats (the matrix). This process is fragmentation, and the resulting patches of habitat are referred to as fragments, remnants or islands (Saunders, Hobbs and Margules, 1990; Murcia, 1995). Unlike true islands, fragments are surrounded by a sea of potential non-native invaders (Brothers and Spingarn, 1992; Meffe and Carroll, 1994). Fragment and matrix meet at the edge, a zone with structural and functional distinctions from both the interior and the matrix (Matlack, 1993). Air temperature, light intensity, soil temperature, soil moisture, wind effects, and species richness, composition and density are all factors that vary over the matrix → edge → interior continuum (*e.g.* Saunders, Hobbs, and Margules, 1991; Brothers and Spingarn 1992; Matlack, 1993; Fraver, 1994; Adkison and Jackson, 1996; Burke and Nol, 1998). The edge is thus a transition zone between matrix and fragment (*i.e.* an ecotone). The edge ecotone has width (sometimes called depth-of-edge [Chen, Franklin and Spies, 1992]), which is a measure of how far into a fragment the edge-associated physical, environmental and biological factors persist. This width is an important consideration in fragmented landscapes because smaller fragments with their higher edge-to-interior ratios are more likely to be influenced by edge environments (Matlack, 1993). This width also varies depending upon the variable considered.

While wildlife managers have traditionally viewed edge habitat as beneficial because species richness is often higher near edges (Yahner, 1988; Kupfer, 1995), conservation biologists generally recognize problems that can be associated with edges and habitat fragmentation (*e.g.* Noss, 1983). For example, Wilcove, McLellan and Dobson (1986) found that edge-related predation of quail eggs by mammalian and avian predators extended up to 600 m from a forest edge. Nest parasitism by cowbirds (*Molothrus ater*), a species associated with ruderal habitats and edges (Peterson, 1980), has been found to be four times greater within 100 m of a forest edge as compared to the interior (Brittingham and Temple, 1983).

Unlike edge effects on animals, significant microenvironmental and botanical changes such as soil temperature and community composition are reportedly restricted to a narrower zone. Brothers and Spingarn (1992) found that microenvironmental changes were restricted to within a few metres of the edge in Indiana old-growth forests. Their study found that the mean richness of non-native species dropped within eight metres of an edge and remained low beyond that point, although 50 m from an edge roughly 10% of sample points included non-native species. Matlack (1993) examined parameters including air temperature, light, throughfall precipitation, humidity, canopy closure, litter moisture and litter depth and suggested that a buffer of 50 m around interior habitat would eliminate most of the microenvironmental edge effects. Fraver (1994) studied changes in vegetation and determined that edge effects penetrate from 30 to 60 m into forests, with aspect being an important consideration. Burke and Nol (1998) concluded that beyond 20 m from an edge, microenvironmental and plant community features were more characteristic of interior than edge habitats. These and examples of other variables that have been examined are summarized in Table 1.1.

While significant microenvironmental and botanical edge effects may be restricted to within 50 m of an edge, seed dispersal can bring edge-adapted plant species well into forest interiors. With the exception of Chen *et al.*'s (1990, 1992) work in Douglas Fir forests, the studies cited in Table 1.1 were not designed to detect changes beyond 100 m from an edge. Janzen (1986) found invasion by plants at least five kilometres into a forest community and has also suggested that forest blocks smaller than 30,000 to 50,000 hectares (ha) could be subject to considerable edge effect.

1.4 The Prince Edward Island Situation

Prior to the beginning of European settlement (circa 1720) virtually all of Prince Edward Island's 576,000 ha land mass was forested (Stewart, 1806; Johnstone, 1820; McAskill, 1987). Upland areas were dominated with such species as *Fagus grandifolia* (American beech), *Acer saccharum* (sugar maple) and *Betula alleghaniensis* (yellow birch), with scattered *Picea rubens* (red spruce), *Tsuga canadensis* (eastern hemlock) and *Quercus rubra* (red oak), as well as *Abies balsamea* (balsam fir) and *Pinus strobus* (white

Table 1.1: A summary of examples of edge effect studies in North American Forests.

Reference	Habitat	Variable(s) Studied	Depth-of-Edge (m)
Brothers & Spingarn, 1992	Indiana old-growth hardwood	Microenvironmental and botanical changes	<50
Bruner, 1997 (in Fraver, 1994)	Wisconsin hardwood	Botanical changes and tree density	15
Burke & Nol, 1998	Ontario hardwood	Microenvironmental and botanical changes	<20
Chen, Franklin & Spies, 1992	Washington and Oregon old-growth Douglas fir	Tree density, growth, mortality and regeneration	16 to 137
Chen, Franklin & Spies, 1990	Washington and Oregon old-growth Douglas fir	Microenvironmental	240
Fraver, 1994	North Carolina mixed hardwood	Botanical changes	30 to 60
Gysel, 1951	Michigan hardwood	Stem counts of woody plants	2 to 11
Matlack, 1993	Pennsylvania and Delaware hardwood	Microenvironmental	50
Miller & Lin, 1985	Connecticut red maple	Leaf density gradients	15
Palik & Murphy, 1990	Michigan hardwood	Botanical changes and tree density	5 to 45
Ranney, Bruner & Levenson, 1981	Wisconsin hardwood	Stem counts of woody plants	10 to 30

pine) in places. Lowland areas featured *Acer rubrum* (red maple), *Picea mariana* (black spruce), *Thuja occidentalis* (eastern white cedar) and - less frequently - *Ulmus americana* (American elm) and *Fraxinus nigra* and *F. americana* (black ash and white ash) (Erskine, 1960; McAskill, 1987). This is a generalized summary of pre-colonial forest distribution; detail is provided in Sobey and Glen (1999).

Little mention Prince Edward Island's ground flora was made until the late 1800s, and this was restricted to brief notes on the most conspicuous species (Catling, Erskine and MacLaren, 1985). By 1933, the list of plants of Prince Edward Island totalled only 594 species (Hurst, 1933) compared with more than 1,000 species known today (Blaney, MacQuarrie and Curley, 2000). It is difficult to describe with accuracy the abundance and distribution of PEI's pre-colonial ground flora, and it is virtually impossible to know with any certainty which (if any) species have been extirpated.

Between 1798 and 1901, Prince Edward Island's population grew from approximately 5,000 individuals to over 100,000 (Clark, 1959). Throughout this time land clearing accelerated and the once-contiguous forest became increasingly fragmented. Clark (1959) estimated that approximately 4,050 ha of land was cleared in 1805; by 1900 this had grown to nearly 399,000 ha, some 70% of the entire province (PEI Department of Agriculture and Forestry, Forestry Division, 1997a). The remaining forest was not only severely fragmented, but it had been extensively disturbed through a combination of harvest of trees for shipbuilding, construction, fuel and wood export, and from past cycles of human-caused fires (Johnstone, 1820; Clark, 1959; McAskill, 1987). Today, approximately 50% of PEI is forested (PEI Department of Agriculture and Forestry,

Forestry Division, 1997b), but virtually none of this area has escaped anthropogenic disturbance.

Extensive habitat loss and fragmentation inspired biologists both around the world and on Prince Edward Island to identify and protect examples of undisturbed natural ecosystems (Taschereau, 1974). This early work lead to the identification of 15 areas of natural importance on Prince Edward Island, including four small forest stands considered relatively undisturbed examples of PEI's original tolerant hardwood forest community. Nearly a decade later, a province-wide survey of natural areas (University of Prince Edward Island [UPEI], 1982) added three additional tolerant upland hardwood areas to this list of relatively undisturbed examples of PEI's original forest community, noting that "*...there are probably no* [forest] *stands which have remained completely untouched since the arrival of the European settlers*". Both Taschereau (1974) and UPEI (1982) included site visits and floral inventories, but neither considered or examined the presence of non-native vascular floral species.

More recently, it has been recognized by both Island Nature Trust (a non-governmental conservation group) and the Government of Prince Edward Island (through the Natural Areas Protection Act Technical Advisory Committee) that the tolerant hardwood forest community is seriously under-represented in PEI's protected areas system (Arsenault, 1997). This community is thought to most closely resemble PEI's original upland hardwood covertype that was one component of the Acadian forest, and these forest types have been identified as priorities for protection by both Island Nature Trust and the Government of Prince Edward Island. From 1998 to 2000, Island Nature

Trust coordinated a program to clearly define which forests are highest priorities for protection and where these forests are located. This work resulted in the identification of 547 ha of Class I and 5,747 ha of Class II forests, defined as follows (Natural Areas Protection Act Technical Advisory Committee, meeting minutes, March 01, 2000):

> Class I: any forest stand with a minimum 30% presence of climax tree species (*e.g. Betula alleghaniensis*, *Acer saccharum*, *Fagus grandifolia*) with heights greater than 18 m in 1990 and ages greater than 80 years.
>
> Class II: any forest stand with a minimum 30% presence of climax tree species with heights greater than 14 m (but less than 18 m) in 1990 and ages greater than 80 years.

Forests meeting these criteria are believed to be the best remnants of Prince Edward Island's original upland hardwood component of the Acadian forest. Sobey (1995) found that lands on which the tolerant hardwood species noted above occur are significantly associated with lands that were forested before 1935, and - by extrapolation - at the turn of the last century. Although it is recognized that these are not "virgin" forests that have escaped the influence of human settlement patterns, these areas are considered to be among the least disturbed of Prince Edward Island's forest communities.

In addition to habitat loss and severe forest fragmentation, Prince Edward Island has also been subject to extensive intentional and accidental introductions of non-native species. While PEI's original aboriginal inhabitants may have moved species from the mainland to the Island (McAskill, 1987) the first large-scale invasion of non-native species accompanied the early Acadian settlers who brought agricultural crops previously unknown to Prince Edward Island (Clark, 1959). Subsequent immigrants brought additional non-native plants for economic or aesthetic reasons (*e.g.* agricultural and other commercial crops, garden ornamentals), while other species arrived accidentally, for example in shipments of grain from Western Canada (Catling, Erskine and MacLaren, 1985). Today, 332 (33%) of PEI's 1,005 known vascular plants species are classified as non-native (Blaney, MacQuarrie and Curley, 2000), a proportion slightly higher than that for Canada as a whole (27%) (Scoggan, 1979). New non-native species are being found on PEI on an annual basis. For example, field work during the summer of 2001 (unrelated to this study) uncovered species such as *Lonicera xylosteum* (European Fly Honeysuckle), *Lonicera x bella* (Pink Honeysuckle), and *Sorbus thuringiaca* (Oak-leaved Mountain Ash) among others (personal observation).

A number of studies have looked at the flora of selected Prince Edward Island woodlands: Taschereau, 1974; UPEI, 1982; Parks Canada, 1984; the 1990/92 PEI Forest Inventory; Sobey, 1993, 1995a, and 1995b; Hovingh, 1995; MacQuarrie, Schaefer and Schoenrank, 1999 and 2000; and Island Nature Trust, unpublished data. Of these studies, only three considered anthropogenic effects or disturbance (Hovingh, 1995, MacQuarrie, Schaefer and Schoenrank, 1999 and 2000). Hovingh (1995) examined variables including tree age and diameter distributions, vertical stratification, as well as species composition and arrangement, to assess the level of anthropogenic disturbance of the Townshend Woodland Natural Area, a forest considered to be among the best examples of old-growth hardwood on Prince Edward Island (Taschereau, 1974; UPEI, 1982). Hovingh's results suggested a history of extensive anthropogenic activity at Townshend Woodland. MacQuarrie, Schaefer and Schoenrank (1999, 2000) examined all habitats, including forest, within Greenwich, Prince Edward Island National Park and commented on the anthropogenic impacts as indicated by the presence of non-native vascular plant species. In these latter two studies, old field habitats revealed the highest proportion of non-natives (54%) and wetlands the lowest (7%); 24% of forest flora were found to be non-native. The 1991 PEI Forest Inventory undoubtably identified non-native plants, but the data have not been considered from that perspective (W. Glen, Manager of Resource Inventory and Monitoring, PEI Department of Natural Resources, personal communication).

Although Class I and II forest areas are being considered priorities for conservation by Island Nature Trust and the Government of Prince Edward Island because they are believed to be the best representatives of PEI's original upland hardwood component of the Acadian forest, to date there has been no assessment of the presence and impacts of non-native vascular plant species in these areas. While we can make some assumptions about a few species that are likely to be present and problematic (*e.g.* Stapleton *et al.*, 1998), we do not have sufficient information to answer fundamental questions such as which non-native species are present in older upland hardwood forests on Prince Edward Island, and to what extent they have invaded these habitats. Answering these questions will have practical implications in the selection and management of tolerant hardwood forest natural areas on Prince Edward Island, leading to identification of whether an optimum size for old-growth hardwood protected areas and/or a minimum buffer around such areas can be prescribed for Prince Edward Island.

1.5 Objectives:

The primary goal of this research is to improve our knowledge the remnant upland hardwood component of the Acadian forest, leading to optimal conservation of this habitat. The specific objectives of this study are to:

(1) Identify which non-native plant species are present in PEI's Acadian forest, and which have become invasive;

(2) Identify the extent to which non-native species have penetrated natural areas (*e.g.* distance from edge, proportion of ground cover);

(3) Identify whether those non-native species that do invade natural areas have morphological and developmental features (*e.g.* size, weight and appearance of seed, seed viability, growth form) that give them an advantage over native species; and

(4) Identify whether a minimum buffer through which non-native species are unlikely to invade can be prescribed for Acadian forest protected areas on PEI.

1.6 Sampling protocol - theoretical considerations

A review of the literature reveals an enormous diversity in sampling protocol among studies looking at forests in North America (examples, Table 1.2). At one end of the spectrum is the 1990/92 Forest Biomass Inventory for Prince Edward Island, which assessed timber quality and biomass of commercial tree species, as well as collecting information on ground vegetation. To survey ground vegetation, twelve hundred 4 m^2 circular plots were used to survey Prince Edward Island's 253,409 ha of forests (W. Glen, personal communication), giving a sample effort of 0.019 m^2/ha. The protocol for the

Table 1.2: Examples of sampling protocols (plot size, shape and number) for recent field studies in North American forest communities.

Reference	Habitat	Sample size & shape	Sample effort (m^2/ha)
Alaback and Juday, 1989	Old-growth forests in Alaska	10 - 20 plots/site for understorey vegetation sites = 600 to 5,391 ha plots = 4 m^2, square	0.067 to 0.13
PEI Forest Biomass Inventory, 1990-92	All forest types on PEI	1,200 plots total study area = 253,409 ha plots = $4m^2$, circular	0.019
Brothers & Spingarn, 1992	Old-growth hardwood	five 50m belt transects/site sites = 8 to 23 ha 1 transect = ten $20m^2$ quadrats plots = $20m^2$, rectangular (4X5)	43.5 to 125
Cain & Shelton, 1994	Old-growth Pine-hardwood	60 plots study area = 32 ha plots = 8 m^2, circular	15
Hovingh, 1995	Townshend, PEI old-growth hardwood	40 plots study area = 90 ha plots = $1m^2$, square	0.44
Hardt & Swank, 1997	Southern Appalachian old-growth hardwood	20 plots/site 6 sites, areas unknown plots = $100m^2$, square	N/A
Burke & Nol, 1998	Ontario hardwood (maple, beech, ash, oak)	6 plots/site study sites = 0.25 to 163 ha plots = $100m^2$, rectangular (5X20)	3.7 to 2,400
Haney & Lydic, 1999	old-growth oak-pine forest in Tennessee	14 plots study site = 13.25 ha plots = $400m^2$, circular	422.6
Francis *et al.*, 2000	Ontario hardwood	1 plot/ "patch" (<1 ha to >1,000 ha) plots = $3,900m^2$, circular	3.9 to 3,900
MacQuarrie, 2002	PEI Class I and Class II Forest	27 plots/site study sites = 40 ha to 70 ha plots = $100m^2$, circular	38 to 68

inventory, which was repeated in the 2000/01 fields seasons, was originally developed for the 1980/82 Forest Biomass Inventory through joint Federal/Provincial field research by the Canadian Forest Service and PEI Natural Resources Division. A similar protocol has been adopted by both Alberta and British Columbia (W. Glen, personal communication).

At the other end of the spectrum is recent work by Burke and Nol (1998) and Frances *et al.* (2000) which reveal sample efforts ranging from 3,900 m^2/ha for the smallest sites (<1 ha) to 3.9 m^2/ha for the largest sites (163 to >1000 ha) (Table 1.2). Burke and Nol's (1998) actual sample plot size was 100 m^2 while that of Francis *et al.* (2000) was 3,900 m^2; for comparison, sample effort has been converted to unit per area. Neither study commented on the efficiency of their sampling effort. Consequences of undersampling can include increased variance in the data, use of less powerful statistics and increased probability of committing a Type I or II error (rejecting a true null hypothesis or accepting a false null hypothesis) (Dytham, 1999). Oversampling increases the cost and labour required for data collection and analysis.

A similar examination of plot shape and size suggests that circular quadrats are most commonly used because they are easy to establish and minimize edge influences on sampling. In the literature reviewed, plot size varies from 4 m^2 (PEI Forest Biomass Inventory, W. Glen, personal communication) to 3,900 m^2 (Francis *et al.*, 2000). Obviously, one must weigh available time for sampling and feasibility of vegetation assessment when determining plot size.

Sobey (1993), in a test of the 4 m^2 plot size, found that the 4 m^2 circular plots used by the PEI Forest Biomass Inventory picked up an average of 8.6 species per plot at each sampling point. His tests found that by increasing the plot size to 100 m^2, species number per plot was increased to 21.7. For this reason, he recommended that if time and finances allowed, future forest inventories that assess ground vegetation should have a plot size of at least 100 m^2 (Sobey, 1993). In preparation for this study, field trials with circular sample plots beginning at 1 m^2 and increasing in size exponentially to 200 m^2 were conducted in two forest fragments which were comprised of a combination of Class I and II forest. Species/area curves created with those data supported 100 m^2 as the optimum plot size (Figure 1.1).

This study thus used circular plots with an area of 100 m^2 (radius=5.64 m). In each study area, there were 27 sample plots, giving a sample size in the range of 38 m^2/ha to 68 m^2/ha depending on the area of each study site (Table 1.2). The sample effort of this study is within the range of literature values, and well above that of previous work on Prince Edward Island.

1.7 Data Analysis: General Background

For comparison of microenvironmental and botanical variables among sample plots, standard parametric or non-parametric analyses of variance are among the most commonly used tests (Chen, Franklin and Spies, 1992; Fraver, 1994; Adkison and Jackson, 1996; Burke and Nol, 1998; Lonsdale, 1999; Stohlgren *et al.*, 1999). Such tests are not appropriate when data matrices have many 0 values, replicates have a high degree of variance (even when sample sizes are large), the number of factors influencing species composition and distribution is very large, or the species themselves are not independent

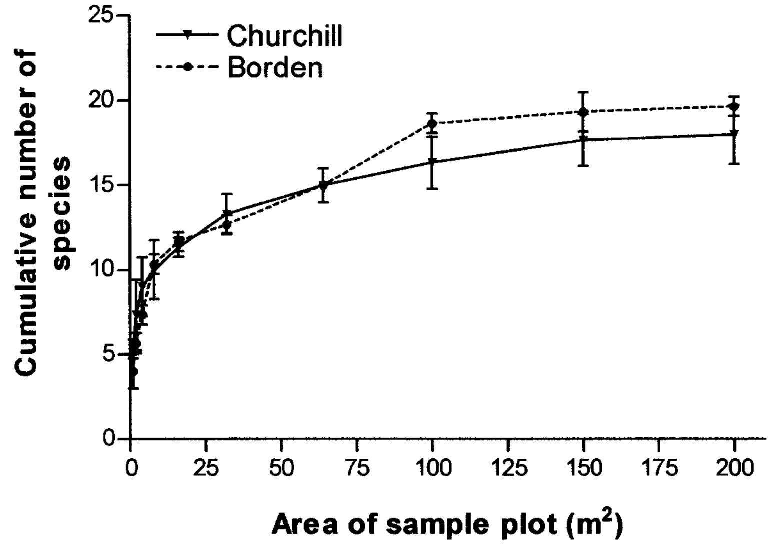

Figure 1.1: Species-area curves from field trials in two Class I and II forest fragments at Churchill and Borden, PEI. Trials began with circular plots of 1 m^2, increasing exponentially to 200 m^2. Curves represent the average of three trials (a total of 30 plots) at each site.

of each other (such as *Epifagus virginiana* [Beech Drops] which is parasitic on the roots of *Fagus grandifolia* [American Beech]) (Palmer, undated). These are common characteristics of plant community datasets. Consequently, data exploration techniques such as seriation and ordination are often used to reveal patterns among the taxa or sample plots, or to answer questions such as how community composition changes along a gradient such as a transect (Palik and Murphy, 1990; Fraver, 1994; Sobey, 1995; Parendes and Jones, 2000).

Seriation arranges species and/or plot locations in a data matrix to achieve the best diagonal of symbols indicating presence. When columns are used to represent plot locations and the seriation is constrained so that these locations cannot move, this technique sorts the rows (taxa) such that strict edge species appear at the top of the matrix, strict interior species at the bottom, and intermediates in between (Hammer, Harper and Ryan, 2001). This is useful in providing a visual representation of the arrangement of taxa along a presumed gradient, such as an edge-to-interior transect. If no clear diagonal arrangement of taxa is achieved with a constrained seriation, the assumption of a gradient is rejected.

Ordination is a general term for a variety of multivariate techniques that find associations between site factors and species distribution (Palmer, undated). Unlike other types of statistics, these are data exploration techniques that are used to generate, rather than test, hypotheses about the communities being studied (Dytham, 1999). Species and samples are assigned ordination scores based on how similar they are to each other. These scores are coordinates along an ordination axis, and when the data are plotted, similar species or samples are closer together, dissimilar ones far apart (Gauch, 1982; Sobey, 1995). Axes may reflect gradients of one or more environmental variables or site factors (*e.g.* distance from edge, elevation, grazing intensity, light intensity) that influence distribution of species or sample plots (Palmer, undated). Through correlation or consideration of the eigenvalues (a measure of variation along and strength of an axis, generally interpreted as the importance of the ecological gradient it represents), one can determine the contribution each axis makes to the distribution of points on the ordination scatterplot. The higher the eigenvalue, the stronger the contribution. Generally, eigenvalues less than 0.25 are not considered meaningful, and values in the range of 0.5 or higher are better indicators; the optimal range is 0.65 to 0.95 (Walker, 1998). Most ordination techniques (except non-metric multidimensional scaling) place the variable with the highest eigenvalue on axis 1, and so the order of axes is important to interpretation with axis 1 having more influence over distribution on the scatterplot than axis 2. Many axes may be generated by the analysis, but often only the first few are meaningful.

While locations on the scatterplot tell you how similar species or samples are, and eigenvalues tell you the degree to which an axis contributes to this similarity, identification of exactly what variable each axis represents can be difficult (Gauch, 1982). For example, although Parendes and Jones (2000) found that 65% of the variation in botanical communities along roads and streams could be attributed to ordination axis 2, the underlying factor responsible for this relationship was not immediately apparent (note that the fact that axis 2 was most important reveals that non-metric multidimensional scaling was the technique used). Overlaying the ordination results with the variables of light intensity and level of human use suggested that axis 2 was a gradient of increasing disturbance intensity and light levels: communities with higher light and more human use (as measured during the fieldwork) were placed higher on axis 2 by the ordination. If environmental data have been collected, one can test the correlation between the location on an axis and the magnitude of the environmental factor for all points on the ordination scatterplot to determine the degree to which that factor contributes to the ordination (Sobey, 1995). Thus, the ordering of the samples on the ordination scatterplot is used to interpret the axes, rather than the other way around. Or, put more elegantly by Palmer (undated), ordination essentially asks the species what the most important gradients are.

Detrended correspondence analysis (DCA) and non-metric multidimensional scaling (NMDS) are the two most common ordination techniques (Palmer, undated). The main distinction between the two is that DCA assumes a unimodal rather than linear relationship among variables - that each species has a single set of optimal conditions at which abundance will be maximized (Gauch, 1982). The assumption of a linear relationship can be a problem in communities with high beta diversity (species turnover) in which species composition blends from one community to another along a gradient. Because of this underlying model of species distribution, DCA is said to be closer to theories of community ecology than other techniques (Palmer, undated).

Another advantage of DCA over other techniques is that the axes are in units of beta diversity (Gauch, 1982). Each unit represents one standard deviation of beta diversity, or roughly one-quarter turnover in species; four units are roughly 100%

turnover (Walker, 1998). This not only assists with interpretation, but can suggest whether DCA is the appropriate technique for the data. If an axis is less than two units long, another ordination technique would be more appropriate; greater than four units and DCA is appropriate (Walker, 1998).

For datasets with high beta diversity, correspondence analysis can result in second and subsequent axes being related to or dependant on the first axis (Gauch, 1982). This causes a pattern called the arch effect which, as its name implies, results in a curved arrangement of points on the ordination plot. Some see this as a fault of the technique and an impediment to data interpretation (Hill and Gauch, 1980; Palmer, undated), although others maintain the arch is an accurate representation of the data and integral to interpretation (Wartenberg, Ferson and Rohlf, 1987). Additionally, the data at either end of a correspondence analysis axis tend to be compressed, or more closely arranged than one would expect based on differences in sample taxa (Gauch, 1982). This compression means that a pair of samples will be plotted more closely together if they occur at either end of an axis than if they occur in the middle, which makes interpretation along the length of the axis difficult (Gauch, 1982). Wartenberg *et al.* (1987) suggest that compression is not necessarily a distortion of the data, and could indicate that species turnover may not be constant along a gradient, or for all species in a community.

DCA addresses both arch effect and compression. In a controversial process that has been called “inelegant” by some (Gauch, 1982) and “brute force” by others (Walker, 1998), DCA removes the arch effect by arbitrarily segmenting axis 1, and moving each up or down until the scores within each segment have a mean of 0 in relation to axis 2

(Gauch, 1982). The position of each point in relation to others in the segment is maintained, but the relationship between points which are placed in different segments is not (Walker, 1998). For example, two species or sample plots placed closely together on the plot before detrending may be placed in different segments when the arbitrary divisions are made and end up apart from each other. Compression is eliminated via rescaling each axis so that the variance of the species scores is the same in each sample (Gauch, 1982; Wartenberg *et al.*, 1987). This assumes that each species completes its unimodal distribution - it appears, reaches maximum abundance and disappears - at the same rate everywhere in the sample: four standard deviations of beta diversity, which is four divisions of the DCA axis (Gauch, 1982; Walker, 1998). Despite the controversy surrounding detrending, DCA remains an important multivariate tool in plant community ecology.

2.0 ALIENS IN THE ACADIAN FOREST

2.1 Introduction

Nearly three centuries of European settlement have dramatically altered Prince Edward Island's landscape. Early writers such as Stewart (1806) and Johnstone (1822) describe the extensive Acadian forest that once covered PEI. When accounts of these and other explorers and travellers are taken into account, we can build an image of pre-colonial Prince Edward Island: old-growth Acadian forest, with *Pinus strobus* and *P. resinosa* (white and red pine) 1.5 m in diameter and towering 48 m, *Tsuga canadensis* (hemlock) of more than one metre in diameter and 27 m tall, and *Betula alleghaniensis* (yellow birch) 1.8 m across with canopies more than 18 m above the forest floor (McAskill, 1987). More specifically, we know that PEI's upland areas were dominated by species such as *Fagus grandifolia* (American beech), *Acer saccharum* (sugar maple), and *B. alleghaniensis* with scattered *Picea rubens* (red spruce), *Tsuga canadensis* and *Quercus rubra* (red oak), as well as *Abies balsamea* (balsam fir) and *P. strobus* in places. Lowland areas featured *Acer rubrum* (red maple), *Picea mariana* (black spruce), *Thuja occidentalis* (eastern white cedar) and - less frequently - *Ulmus americana* (American elm) and *Fraxinus nigra* and *F. americana* (black and white ash) (Erskine, 1960; McAskill, 1987). Within this forest wandered mammals such as woodland caribou, black bear, lynx and marten (Cameron, 1958), none of which exist on PEI today.

By 1900, approximately 70% of this original forest had been cleared for agriculture and settlement (PEI Department of Agriculture and Forestry, Forestry Division, 1997a). The remaining 30% was not only severely fragmented, but had also been extensively disturbed through a combination of tree harvest for shipbuilding, construction, fuel and wood export, and from past cycles of human-caused fires (Johnstone, 1820; Clark, 1959; McAskill, 1987). Today, approximately 50% of PEI is forested (PEI Department of Agriculture and Forestry, Forestry Division, 1997b), but virtually none of this area has escaped anthropogenic disturbance. As the University of Prince Edward Island's 1982 Natural Areas Survey noted: "*...there are probably no* [forest] ***stands which have remained completely untouched since the arrival of the*** *European settlers*".

This history of land use has resulted in a fragmented landscape, with patches of remnant forest surrounded by a matrix of developed land. The fragment/matrix ecotone is the edge, a zone with structural and functional distinctions from both matrix and interior (Matlack, 1993). Microclimatic and biological factors such as air temperature, light intensity, soil temperature, soil moisture, wind, species richness, community composition and structure, and biomass are among the factors that have been shown to vary over the matrix-edge-interior continuum (Saunders, Hobbs, and Margules, 1991; Brothers and Spingarn 1992; Matlack, 1993; Fraver, 1994; Adkison and Jackson, 1996; Burke and Nol, 1998). Typically, edges are characterized by warmer air and soil temperatures, drier soils, greater light intensity, greater wind velocities, greater species richness, greater numbers of non-native species and greater vegetation density (Saunders, Hobbs, and Margules, 1991; Brothers and Spingarn 1992; Matlack, 1993; Fraver, 1994; Adkison and Jackson, 1996; Burke and Nol, 1998). This can create conditions that are inhospitable to shade-tolerant forest species such as *Fagus grandifolia* (Palik and

Murphy, 1990), are conducive to the establishment of non-native species (Parendes and Jones, 2000) and result in a community ecologically and statistically distinct from interior forest (Matlack, 1993). As a result, a small Acadian forest natural area may not be large enough to escape the influences of edge. Understanding the width of the edge ecotone is thus critical to conservation of interior habitat.

To a certain extent, this edge width may depend upon the variable considered, with botanical effects generally reported as being restricted to a narrower zone than zoological effects. However even within comparable sets of parameters, researchers have found a range of edge widths. For example, increased nest predation has been reported 600 m to 800 m from a forest edge in some studies (*e.g.* Meffe and Carroll, 1994; Wilcove, McLellan and Dobson, 1986), while others suggest no relationship between predation and proximity to an edge (Ibarzabal and Desrochers, 2001). Similarly, significant botanical changes have been both reported as being restricted to within 50 m of an edge (Gysel, 1951; Ranney, Bruner and Levenson, 1981; Miller and Lin, 1985; Brothers and Spingarn, 1992; Matlack, 1993; Bruner, 1994; Burke and Nol, 1998) and as extending well beyond 100 m (Chen, Franklin and Spies, 1990; Chen *et al.*, 1992), with invasion by non-native plants recorded as much as five kilometres into forest communities (Janzen, 1986).

Fragmentation not only increases edge, it also results in habitat loss - the greatest threat to native biodiversity; invasion by non-native species is ranked as the second most significant ecological problem on both a local and global scale (Noss, 1987; Center, Frank and Dray, 1995; Vitousek *et al.*, 1996; Baker, 2001). In both Canada and the

United States, non-native species are considered serious problems in National Parks and other protected areas (Campbell, 1997; Parks Canada, 1998). Such species can displace native plant communities (Woods, 1993; Campbell, 1997), put indigenous species at risk of extinction (Haber, 1998), serve as vectors of disease that infect native species (von Broembsen, 1989), alter fire regimes (Cronk and Fuller, 1980) and cause ecosystem-level changes such as alteration of productivity and energy flow (Ramakrishnan and Vitousek, 1989; Vitousek *et al.*, 1996), and changes in nitrogen fixation, hydrologic cycles and sedimentation (Reichard and White, 2001). Invasive species - non-native species that have the potential to cause environmental or economic harm (Office of Technology Assessment, 1993) - are estimated to incur costs in the order of $125 billion each year in the US alone (Baker, 2001).

In spite of this, the general public remains largely unaware of the biological and economic impacts of invasive species (Vitousek *et al.*, 1996; Colton and Alpert, 1998) and studies tend to focus on native flora. For example of 10 studies that considered the forests of Prince Edward Island (Taschereau, 1974; UPEI, 1982; Parks Canada, 1984; the 1990/92 PEI Forest Inventory; Sobey, 1993, 1995a, 1995b; Hovingh, 1995; MacQuarrie, Schaefer and Schoenrank, 1999, 2000), only the latter two specifically commented on the presence and potential impacts of non-native plants.

Recently, there have been efforts on Prince Edward Island to identify, map and conserve remnant pockets of upland Acadian forest, areas with American beech, sugar maple and yellow birch at least 16 m tall and 100 years old (Island Nature Trust, 2000). Although these areas are thought to be the best representatives of PEI's original forest cover, there has been no assessment of the presence of non-native plants in these areas. While regional research allows assumptions to be made about the species likely to be present and problematic (Stapleton *et al.*, 1998), this is not specific to Acadian forest or Prince Edward Island. Additionally, much of the botanical research in northern beech-maple forests has not been designed to detect changes beyond 100 m from an edge.

The objectives of this study are to identify which invasive vascular plants are present in Prince Edward Island's Acadian forest, the extent to which these plants and typical edge environmental factors have penetrated these forests (maximum 300 m detectable) and whether a minimum buffer through which invasive plants are unlikely to extend can be prescribed. Answering these questions has practical implications for selection and management of Acadian forest protected areas.

2.2 Materials and Methods

2.2.1 Study Sites

Through its Forest Conservation Program, Island Nature Trust used MapInfo (version 5.0) and the 1990 Prince Edward Island Forest Inventory Geographical Information System layer (used with permission of the PEI Department of Agriculture and Forestry, Natural Resources Division) to identify all forest stands on Prince Edward Island meeting the following criteria:

> Class I: any forest stand with a minimum 30% presence of climax tree species (*e.g. Betula alleghaniensis*, *Acer saccharum*, *Fagus grandifolia*) with heights greater than 18 m in 1990 and ages greater than 80 years.
>
> Class II: any forest stand with a minimum 30% presence of climax tree species

with heights greater than 14 m (but less than 18 m) in 1990 and ages greater than 80 years.

To identify potential study sites for this project, this information was reviewed and all Class I and II forest stands with at least one straight, well-defined edge and interior habitat not less than 300 m from an edge in any direction were identified. Candidate sites were examined on 1958 aerial photographs to ensure that edges were not newly-created (*e.g.* a recent clear-cut) and were known to have been present for at least 40 years. Before being incorporated into this study, candidate sites were visited to verify that they met Class I and II criteria, were not interrupted by significant disturbance (*e.g.* transmission corridor, forestry road) and did not cross major changes in terrain, topography or soil type. Only eight Class I and II forest stands - ranging in size from 40 to 70 ha - were found to meet these criteria. These were selected for the study and permission to access these lands was secured from the owners. Two of the eight sites were partially harvested before they could be surveyed and so were dropped from the study, leaving six forest areas (Figure 2.1). Attempts to find alternate sites were unsuccessful; no other Class I and II forests with uninterrupted habitat at least 300 m from an edge could be found.

As Class I and II forests, all study sites had comparable overstory vegetation (*F. grandifolia*, *A. saccharum*, *A. rubrum*, *B. alleghaniensis*) of comparable age (all greater than 80 years). Five of the study sites had straight, well-defined hard edges; the sixth (Townshend) is considered to be one of the best remaining examples of Acadian forest on PEI (Taschereau, 1974; UPEI, 1982) and had what has been referred to as an embedded

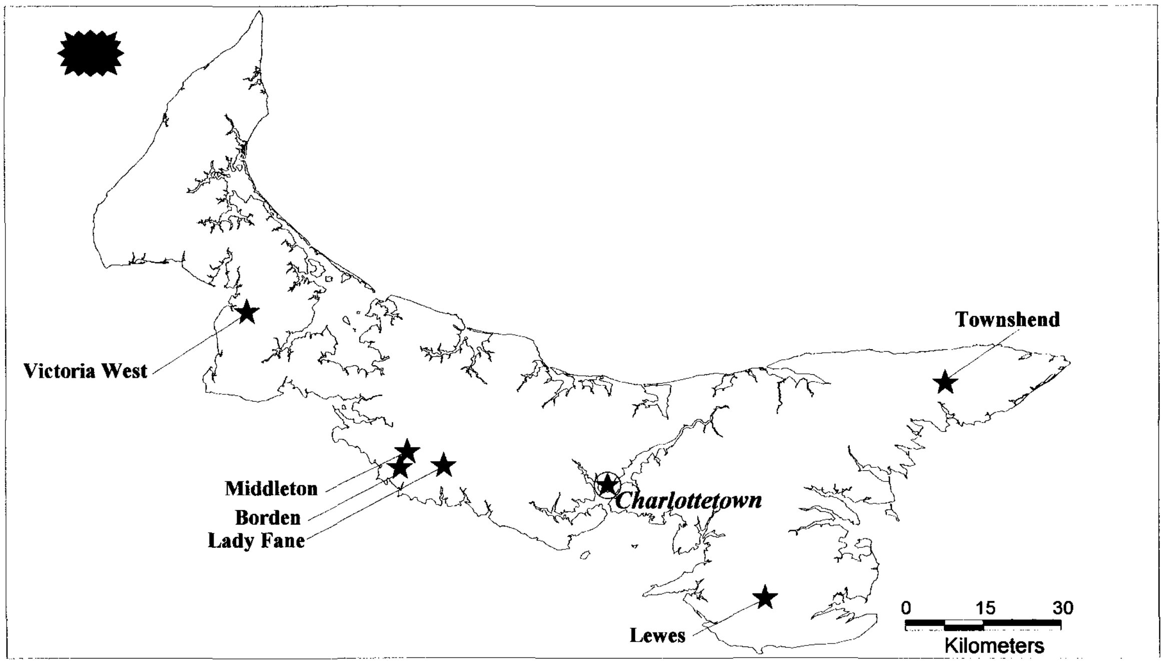

Figure 2.1: Locations of the six Acadian forest study sites.

edge, abutting younger successional forest rather than field (Matlack, 1993) A summary of the attributes of the six study sites is given in Table 2.1.

2.2.2 Sampling protocol

Three equidistant transects on an azimuth perpendicular to the forest edge were established in each study area. The starting point for the first transect in each area was randomly selected prior to visiting the site, and the distance between transects was preselected to provide optimum coverage of the Class I and II forest.

At the start of each transect, the centre of the outermost line of tree trunks was taken to be the forest edge. The centre of the first sample plot was established at −5.7 m (to record species present in the adjacent habitat; sensu Burke and Nol, 1998), with subsequent plot centres located at 5.7 m, 20 m, 40 m, 80 m, 120 m, 160 m, 200 m, 250 m and 300 m along the transect. A 60 m benchmark measuring tape and Suunto MC-1 standard compass were used to locate plot centres along the prescribed azimuth. In the few cases where plot centres coincided with an obstacle such as a tree, they were offset the minimum distance required to avoid the obstacle. Sample plots were established by placing an agricultural field marker at the centre point, using the tape to measure the 5.65 m radius and placing a number of agricultural field markers around the circumference of the sample plot. Upon completion of data collection in each plot, all field markers were removed except for the one in the centre of each 100 m^2 circular sample plot which was labelled in indelible ink with a unique plot identification code. At the end of each field

Table 2.1: Attributes of the six study sites. Size refers to the Class I and II forest comprising the study area, and the specific areas of each forest class are given. The nature of the edge is what maintains the boundary of the Acadian forest. Latitude and longitude were obtained from MapInfo ver. 5.0 using provincial base layer information.

Location	Latitude (⁰) Longitude (⁰)	Size (ha)	Class I ha [%]	Class II ha [%]	Nature of Edge
Borden	-63.6510 46.2720	46	12 [26]	34 [74]	Hard edge: shale pit
Lady Fane	-63.5380 46.2770	54	22 [41]	32 [59]	Hard edge: agriculture
Lewes	-63.7340 46.0480	64	22 [34]	42 [66]	Hard edge: agriculture
Middleton	-63.6280 46.2990	62	24 [39]	38 [61]	Hard edge: agriculture
Victoria West	-64.0310 46.5420	40	10 [25]	30 [75]	Hard edge: agriculture
Townshend	-62.2870 46.4200	70	32 [46]	38 [54]	Embedded edge: forestry road and successional forest

season, the locations of these plot centres were recorded via real-time differential Geographic Information System with sub-metre accuracy (Trimble GeoExplorer II with Phase Processor Software option and differential correction) and all remaining flagging was removed from the study sites. In total, this protocol resulted in thirty 100 m^2 circular sample plots per study area: 27 forest plots and three plots in the adjacent habitat (Figure 2.2).

In each plot, all vascular plants - including trees, shrubs, forbs, ferns, club mosses, horsetails and graminoids - were identified to the species level and a visual estimate of percent cover to the nearest percent was made (1 m^2 = 1% of the sample plot). When field identification was not possible, specimens were collected and labelled for later examination using standard floral keys, primarily Zinck (1999), Hinds (2000) and Scoggan (1979). For reporting purposes, taxonomy and nomenclature follow Kartesz (1999). Species status on Prince Edward Island (native, non-native, common, rare, *etc.*) was assigned based on the provincial vascular plant tracking list (Blaney, MacQuarrie and Curley, 2000).

In addition to data on species composition and cover, overstory density was measured using a Model C spherical densiometer (Forest Densiometers, Bartiesville, OK; Lemmon, 1957), soil temperature was measured once at the centre of each sample plot at 15cm depth with a Traceable® digital thermometer accurate to ±1°C (Control Company, Friendswood, TX) and the diameter at breast height (DBH) of all woody vegetation with a diameter greater than 2.5 cm was measured with a standard diameter tape. Seeds were collected from non-native species found in interior plots to allow an examination of

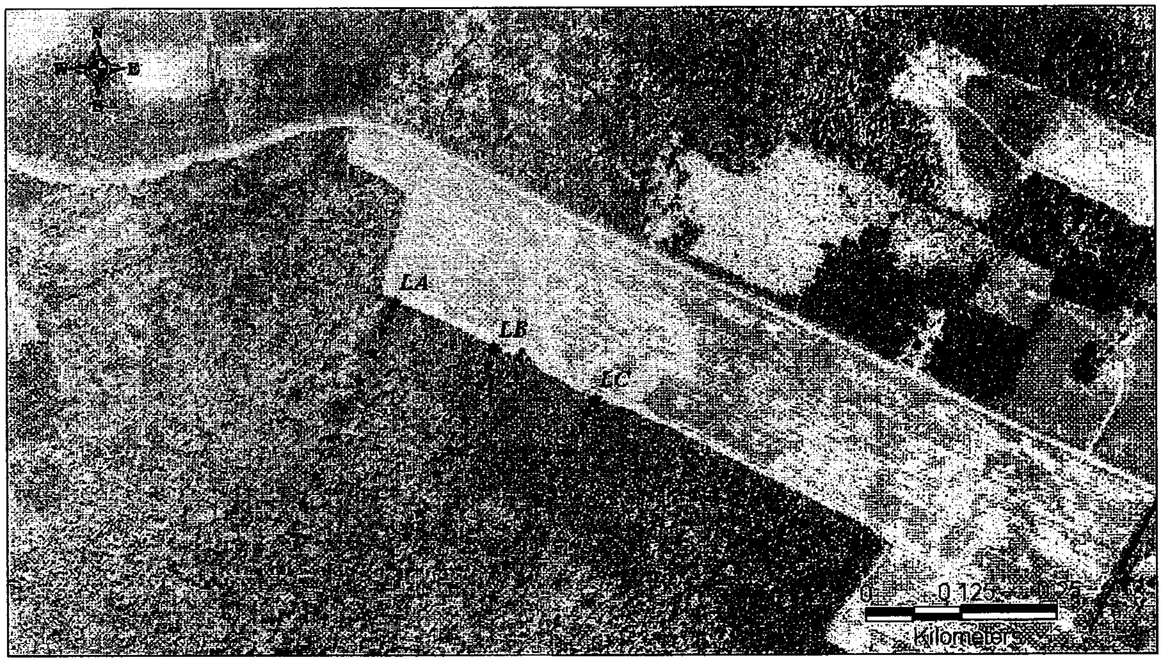

Figure 2.2: A 2000 aerial photograph of the Lewes study area, showing three parallel transects (LA, LB and LC) running perpendicular to the forest edge. Stars represent 100 m^2 sample plots.

morphological and developmental aspects. Seeds of these non-native species were also collected from edge habitat to allow a comparison of morphological and developmental aspects between edge and interior individuals.

Field work was conducted between June and August in 2000 and 2001, with one sampling session (three field days) per study area. While the flowering times for early spring species (*e.g. Viola* spp.) were missed, field work captured the vast majority of PEI's flora and every effort was made to identify remnants of spring ephemerals. For some species, flowers or mature seed were required for positive identification and specific plots were re-visited later in the year to confirm identification of such species (*e.g. Aster* spp.; *Rumex* spp.) and to collect seeds of non-native species.

Collection followed Island Nature Trust's sampling protocol which specifies that no more than one in 20 individuals be removed. Additionally, seeds of non-native species were collected from the study sites, although not from within study plots. This was to ensure that such collection would not affect species richness or mean percent cover, should these plots be used for replication of this study or for future research. In all cases, mature seed heads were clipped from the plant with scissors, placed in a labelled plastic bag, air dried and frozen at -7°C.

2.2.3 Data analysis

Similarity among the six study sites was compared using the Baroni-Urbani and Buser similarity coefficient. This uses a two-by-two contingency table to provide an assessment of how botanically similar areas are using the following equation:

$$S_B = \frac{\sqrt{ad} + a}{a + b + c + \sqrt{ad}}$$

in which S_B is the Baroni-Urbani and Buser similarity coefficient, a is the number of species present in both areas, b is the number of species present only in area 1, c is the number of species present only in area 2 and d is the number of species absent from both areas, but present in one of the other study sites (Krebs, 1989). The result ranges from 0 (totally dissimilar sites) to 1 (identical sites). Although most similarity coefficients ignore species that are absent in both samples, it is useful to include in a study where the species array is well-sampled and the absence of a species is relevant (Krebs, 1989). Such is the case with this study.

Temperature, canopy, and species richness data were pooled for each distance (*e.g.* 5.7 m, 20 m, 40 m, *etc.*) and tested for conformity to assumptions of normality and equal variance. For variables that met these assumptions, one-way Analysis of Variance (ANOVA) with Tukey's post-hoc test was used to determine if there were differences among various distances from the edge and identify which pairs were significantly different. For variables that did not conform to assumptions, Kruskall-Wallis Analysis of Variance was used to determine whether significant differences existed at various distances, and Dunn's multiple comparison test was used to identify significantly different pairs. Pearson (parametric) or Spearman (non-parametric) correlation was used to measure the strength of the relationship between percent cover of non-native species persisting beyond 5.7 m from the edge with canopy cover and distance.

Constrained seriation is a matrix re-arrangement that keeps columns (plot locations) fixed while allowing rows (species) to move until the best diagonal of symbols representing presence is achieved. When plot locations (columns) are arranged from edge to interior, this provides a visual representation of the change in species along a presumed gradient. Constrained seriation with a Monte Carlo simulation (30 random matrices) was performed on the full dataset to identify edge, interior and ubiquitous species, provide a visual representation of the edge-to-interior arrangement of taxa, identify the extent to which non-native species are present in the study area and assess the probability of the arrangement being random rather than representative of a gradient.

To examine species similarity among sample plots in each site and for the dataset as whole and to identify any patterns along environmental gradients, Detrended Correspondence Analysis (DCA) plots were prepared. The resulting eigenvalues were used to measure the relative importance of the ecological gradient represented by each axis. DCA is one of a variety of ordination techniques that seeks to find associations between site factors and species distribution (Palmer, undated). Species and samples are assigned ordination scores based on how similar they are to each other. These scores are coordinates along an ordination axis, and when the data are plotted, similar species or samples are closer together, dissimilar ones farther apart (Gauch, 1982; Sobey, 1995). Axes are likely to be determined by one environmental variable or site factor (*e.g.* distance from edge, soil temperature, light) that influence distribution of species or sample plots (Palmer, undated). Through correlation or consideration of the eigenvalues (a measure of variation along and strength of an axis, generally interpreted as the importance of the ecological gradient it represents), one can determine the contribution each axis makes to the distribution of points on the ordination scatterplot. The higher the eigenvalue, the stronger the contribution. Generally, eigenvalues less than 0.25 are not considered meaningful, and values in the range of 0.5 or higher are better indicators; the optimal range is 0.65 to 0.95 (Walker, 1998). DCA places the variable with the highest eigenvalue on axis 1, and so the order of axes is important to interpretation; axis 1 has more influence over distribution on the ordination plot than axis 2. Many axes may be generated by the analysis, but often only the first few are meaningful. The ordering of the samples on the ordination plot thus is used to interpret the axes, rather than the axes being used to interpret the plot, and this can suggest important gradients within the community.

Because it assumes a unimodal, rather than linear, relationship among variables, DCA is said to be closer to theories of community ecology than other methods (Palmer, undated). Additionally, for datasets with high beta diversity (four or more units on the axes) DCA eliminates the arch effect which results in scores towards the ends of the axes being compressed relative to the middle, making interpretation difficult. (Whether this arch is a real attribute of the data or an artifact of the analysis is debated [eg. Wartenberg, Ferson and Rohlf, 1987]).

Cluster analysis (Ward's method) was used to assess which sample plots were most similar or dissimilar when data for each distance were pooled for each site, and for the dataset as a whole. Ward's method uses Euclidian distance and is generally considered a very efficient algorithm (Hammer, Harper and Ryan, 2001; StatSoft, 2002).

Analysis of variance and correlation were performed with Systat version 8.0. Data exploration was performed with PAST version 0.72.

2.3 Results

2.3.1 Site similarity

The botanical similarity among the study sites as assessed by the Baroni-Urbani and Buser similarity coefficient is given in Table 2.2. Similarity coefficients among study sites were not significantly different (ANOVA, p=0.88).

2.3.2 Environmental and composite variables

Variation in soil temperature, canopy, total species number, number of native species, number of non-native species, proportion of native species, proportion of non-native species and tree diameter were analysed along edge-to-interior transects in the five sites with a hard edge (Table 2.3) and in the one site with an embedded edge (Townshend, Table 2.4). Analysis of variance showed that external (−5.7 m) and first forest (5.7 m) plots of the Townshend study site were significantly different from those of other sites, supporting this separation. Among external plots, soil temperature, non-native species richness and proportion of non-native species were lower (p<0.001 for each) and canopy, native species richness and proportion of native species were greater (p=0.006 for native species richness, p<0.001 for the others) at Townshend as compared to the other sites. Townshend's first forest plots had lower non-native species richness and proportion non-native species and greater proportion of native species than the same locations at other study sites (p=0.042 for each). Plots 20 m and further from the edge showed no differences in these variables between hard and embedded edge sites or among each other at each type of site (Figure 2.3).

Table 2.2. Comparison of six PEI Acadian forest study sites using the Baroni-Urbani and Buser similarity coefficient. Values range from 0 (totally dissimilar sites) to 1.0 (identical sites). Similarity coefficients were not significantly different among sample sites (ANOVA, p=0.88).

	Borden	Lady Fane	Lewes	Middleton	Townshend	Victoria West
Borden		0.72	0.77	0.75	0.66	0.61
Lady Fane	0.72		0.79	0.71	0.70	0.76
Lewes	0.77	0.79		0.79	0.69	0.70
Middleton	0.75	0.71	0.79		0.75	0.68
Townshend	0.66	0.70	0.69	0.75		0.61
Victoria West	0.61	0.76	0.70	0.68	0.61	

Table 2.3: Results of environmental and composite variables from five Acadian forest study sites with a hard edge. Columns are distance from an edge in metres, values are mean ± standard deviation and n=15 at each distance for all variables except tree diameter.

Variable	**-5.7**	**5.7**	**20**	**40**	**80**	**120**	**160**	**200**	**250**	**300**
Temperature (°C)	16.9 ±1.0	13.5 ±1.5	13.7 ±1.1	13.7 ±1.2	13.6 ±1.1	13.7 ±1.4	13.6 ±1.3	13.9 ±1.2	13.9 ±1.0	13.4 ±0.7
Canopy (% closure)	0 ±0	93.9 ±1.8	94.3 ±1.8	93.9 ±2.9	94.1 ±2.8	91.5 ±8.1	94.8 ±1.2	92.7 ±5.0	94.8 ±1.7	94.7 ±3.2
Tree diameter (cm)	n=0	6.0 ±2.9 n=45	6.4 ±3.0 n=38	6.8 ±3.2 n=40	7.2 ±3.4 n=33	6.4 ±2.5 n=42	5.7 ±1.9 n=41	4.8 ±2.0 n=34	8.1 ±3.9 n=30	8.1 ±6.3 n=29
Number of species	22.9 ±6.5	25.6 ±6.4	22.2 ±3.3	22.4 ±5.2	19.5 ±3.6	20.6 ±5.2	20.9 ±3.1	20.9 ±4.3	20.9 ±6.0	19.5 ±5.0
Number native	13.9 ±3.1	20.4 ±3.4	21.0 ±2.7	21.1 ±4.7	19.1 ±3.4	20.1 ±5.2	20.1 ±3.2	20.1 ±4.1	20.5 ±5.6	19.3 ±4.8
Proportion native	60.7 ±9.9	79.7 ±9.6	94.6 ±6.1	94.2 ±6.6	97.3 ±4.2	97.6 ±4.2	96.2 ±5.8	96.2 ±6.2	98.1 ±3.4	99.0 ±3.1
Number non-native	9.0 ±3.4	5.2 ±2.7	1.2 ±1.1	1.3 ±1.5	0.5 ±0.8	0.5 ±0.7	0.7 ±1.0	0.8 ±1.1	0.4 ±0.8	0.3 ±0.6
Proportion non-native	39.3 ±9.9	20.3 ±9.6	5.4 ±6.1	5.8 ±6.6	2.6 ±4.2	2.4 ±4.2	3.3 ±5.8	3.8 ±6.2	1.9 ±3.4	1.5 ±3.1

Table 2.4: Results of environmental and composite variables from the Acadian forest study site with an embedded edge. Columns are distance from an edge in metres, values are median ± standard deviation and n=3 at each distance for all variables except tree diameter. Tree diameter values are mean ± standard deviation and n is given for each distance.

Variable	**-5.7**	**5.7**	**20**	**40**	**80**	**120**	**160**	**200**	**250**	**300**
Temperature (°C)	14.1 ±0.1	14.5 ±0.4	13.8 ±0.1	14.1 ±0.8	14.2 ±0.7	14.0 ±0.4	12.7 ±1.1	13.1 ±0.7	13.9 ±0.3	13.1 ±0.3
Canopy (% closure)	96.8 ±1.1	94.5 ±1.9	94.0 ±1.0	95.6 ±1.1	95.3 ±0.9	92.7 ±1.3	95.1 ±1.2	95.6 ±0.9	96.1 ±1.1	93.8 ±4.8
Tree diameter (cm)	8.0 ±4.1 n=8	9.7 ±6.5 n=11	11.1 ±7.1 n=8	8.7 ±3.6 n=7	10.4 ±4.7 n=6	8.2 ±4.8 n=8	7.4 ±3.5 n=7	9.6 ±5.3 n=9	7.8 ±4.1 n=9	8.2 ±4.3 n=9
Number of species	24. 0±3.5	23.0 ±4.5	18.0 ±3.5	20.0 ±3.8	19.0 ±7.8	23.0 ±7.5	20.0 ±6.2	21.0 ±2.6	18.0 ±4.9	23.0 ±3.6
Number native	20.0 ±2.3	20.0 ±3.1	18.0 ±3.5	20.0 ±3.8	19.0 ±7.8	23.0 ±7.5	20.0 ±6.2	21.0 ±2.6	18.0 ±4.9	23.0 ±3.6
Proportion native	88.9 ±8.5	87.2 ±7.2	100 ±0	100 ±0	100 ±2.2	100 ±0	100 ±2.1	100 ±0	100 ±0	100 ±0
Number non-native	3.0 ±2.1	3.0 ±1.7	0.0 ±0	0.0 ±0	0.0 ±0.6	0.0 ±0	0.0 ±0.6	0.0 ±0	0.0 ±0	0.0 ±0
Proportion non-native	11.1 ±8.5	12.8 ±7.2	0.0 ±0	0.0 ±0	0.0 ±2.2	0.0 ±0	0.0 ±2.1	0.0 ±0	0.0 ±0	0.0 ±0

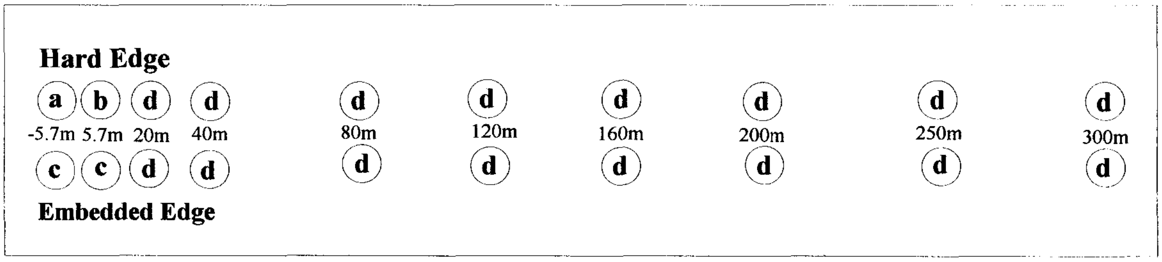

Figure 2.3: A comparison of edge-to-interior transects in sites with hard edges versus one with an embedded edge. Different letters represent sample plots with significantly different environmental or composite variables. Soil temperature: a > b = c = d; number of non-native species: a > b > c > d; proportion of non-native species: a > b > c > d; canopy: a < b = c = d; number of native species: a < b = c = d; proportion of native species: a < b < c < d. Explanation of symbols: = no significant difference between plot locations; > variable is significantly greater at the first location; < variable is significantly lower at the first location. For example, soil temperature was significantly greater in plot a than at all other plot locations, and there were no significant difference among other plot locations.

For the five sites with a hard edge, all environmental and composite variables other than total species richness showed significant differences along edge-to-interior transects ($p<0.001$ in all cases). External (−5.7 m) plots had greater soil temperature, non-native species richness and proportion of non-native species, and lower canopy, native species richness and proportion of native species than all other sample plots along the transects. The first forest plots (5.7 m) had greater richness and proportions of non-native species and lower proportions of native species than all subsequent plots along the transect (Figure 2.3, Table 2.5). Total number of species did not vary significantly along the transects (Table 2.5).

In the study site with an embedded edge, no significant differences along edge-to-interior transects were detected in four of the variables (temperature $p=0.461$; canopy $p=0.068$; species richness $p=0.738$; and native species richness $p=0.784$). Of the remaining variables, non-native species richness and proportion non-native species were higher and proportion native species was lower in the external (−5.7 m) and first forest (5.7 m) plots than at all other points along the transect, although these two points were not significantly different from each other (Figure 2.3). In the study site with an embedded edge, tree diameter did not vary significantly along edge-to-interior transects ($p=0.956$). In those sites with a hard edge, external plots had no woody vegetation greater than 2.5 centimetres in diameter and so were excluded from tree diameter analysis. Within the remaining plots, tree diameters 200 m from an edge were significantly lower than those at 250 m ($p=0.003$) or 300 m ($p=0.004$). One *Tsuga canadensis* in the innermost plot of the Lewes study area had a diameter of 88.6 cm and was determined to

Table 2.5: Differences in eight environmental and composite variables along edge-to-interior transects in five PEI Acadian forest study sites with a hard edge. Row and column titles represent distance from the edge in metres. One-way ANOVA with Tukey's post-hoc was used for all variables except those in ***italics*** (e, f and g) which did not conform to assumptions and were tested with Kruskall-Wallis and Dunn's post-hoc. a-soil temperature, b-canopy, c-species richness, d-native species richness, e-non-native species richness, f-proportion native species, g-proportion non-native species, h-tree diameter. ns-not significant ($p>0.05$), *$p=0.011$ to 0.05, **$p=0.001$ to 0.01, ***.$p<0.001$, n/a - not applicable (external plots were not treed). External (−5.7 m) and edge (5.7 m) plots differed significantly from each other and from other locations along edge-to-interior transects.

	5.7	**20**	**40**	**80**	**120**	**160**	**200**	**250**	**300**
-5.7	a,b,d*** _e,f,g_* c^{ns} h$^{n/a}$	a,b*** d,_e,f,g_** c^{ns} h$^{n/a}$	a,b*** d,_e,f,g_** c^{ns} h$^{n/a}$	a,b,_e_*** d,_f,g_* c^{ns} h$^{n/a}$	a,b,_e_*** d,_f,g_* c^{ns} h$^{n/a}$	a,b,_e_*** d,_f,g_* c^{ns} h$^{n/a}$	a,b,_e_*** d,_f,g_* c^{ns} h$^{n/a}$	a,b,_e_*** d,_f,g_* c^{ns} h$^{n/a}$	a,b,_e_*** d,_f,g_* c^{ns} h$^{n/a}$
5.7	-	_e,f,g_* a,b^{ns} c,d,h^{ns}	_e,f,g_* a,b^{ns} c,d,h^{ns}	_e,f,g_* a,b^{ns} c,d,h^{ns}	_e,f,g_* a,b^{ns} c,d,h^{ns}	_e,f,g_* a,b^{ns} c,d,h^{ns}	_e,f,g_* a,b^{ns} c,d,h^{ns}	_e,f,g_* a,b^{ns} c,d,h^{ns}	_e,f,g_* a,b^{ns} c,d,h^{ns}
20	-	-	a,b,c,d^{ns} _e,f,g_,h^{ns}	a,b,c,d^{ns} _e,f,g_,h^{ns}	a,b,c,d^{ns} _e,f,g_,h^{ns}	a,b,c,d^{ns} _e,f,g_,h^{ns}	a,b,c,d^{ns} _e,f,g_,h^{ns}	a,b,c,d^{ns} _e,f,g_,h^{ns}	a,b,c,d^{ns} _e,f,g_,h^{ns}
40	-	-	-	a,b,c,d^{ns} _e,f,g_,h^{ns}	a,b,c,d^{ns} _e,f,g_,h^{ns}	a,b,c,d^{ns} _e,f,g_,h^{ns}	a,b,c,d^{ns} _e,f,g_,h^{ns}	a,b,c,d^{ns} _e,f,g_,h^{ns}	a,b,c,d^{ns} _e,f,g_,h^{ns}
80	-	-	-	-	a,b,c,d^{ns} _e,f,g_,h^{ns}	a,b,c,d^{ns} _e,f,g_,h^{ns}	a,b,c,d^{ns} _e,f,g_,h^{ns}	a,b,c,d^{ns} _e,f,g_,h^{ns}	a,b,c,d^{ns} _e,f,g_,h^{ns}
120	-	-	-	-	-	a,b,c,d^{ns} _e,f,g_,h^{ns}	a,b,c,d^{ns} _e,f,g_,h^{ns}	a,b,c,d^{ns} _e,f,g_,h^{ns}	a,b,c,d^{ns} _e,f,g_,h^{ns}
160	-	-	-	-	-	-	a,b,c,d^{ns} _e,f,g_,h^{ns}	a,b,c,d^{ns} _e,f,g_,h^{ns}	a,b,c,d^{ns} _e,f,g_,h^{ns}
200	-	-	-	-	-	-	-	h** a,b,c^{ns} d,_e,f,g_^{ns}	h* a,b,c^{ns} d,_e,f,g_^{ns}
250	-	-	-	-	-	-	-	-	a,b,c,d^{ns} _e,f,g_,h^{ns}

be an outlier ($n=29$, $\alpha=0.635$, $p<0.01$). The analysis of variance remained significant following removal of this outlier, but the Tukey's pairwise comparison p-value for 200 m and 300 m was increased to 0.047. Mean tree diameter in the 200 m plots of sites with a hard edge was significantly lower than Townshend's 5.7 m, 20 m and 200 m plots ($p<0.001$, $p=0.009$ and $p=0.011$, respectively).

2.3.3 Non-native species

Of 170 species found in all six study sites, one-quarter (43 species) were not native to Prince Edward Island. The number of non-native species per study area ranged from seven at Victoria West to 21 at Borden (Table 2.6). There was no correlation between site size and species richness ($r_p = 0.4720$, $p=0.3446$, $n=6$), number of non-native species ($r_p = -0.1388$, $p=0.7931$, $n=6$), or proportion of non-native species ($r_p = -0.2776$, $p=0.5944$, $n=6$). The site-specific lists of species and the plot locations in which each was found are given in Appendix 2.

The majority of non-native taxa (28 species, 65%) were restricted to the adjacent non-forested habitat and classed non-invasive (Table 2.7); nine native species were found only in the adjacent habitat. Additional species found along edge-to-interior transects within the forests were almost exclusively native: of fifteen non-native species that invaded forest, only two - *Hieracium lachenalii* (Hawkweed) and *Ranunculus repens* (Creeping Buttercup) - were absent from the external plots (Table 2.8). Once transects moved from adjacent habitat into the forest, the proportion of the total species array that was non-native declined rapidly (Figure 2.4).

Table 2.6. A summary of the species richness, number of non-native species and proportion of non-native species found in each of the six Acadian forest study areas. There was no correlation between any of these variables and the size of the sites.

Site Name	Total Number of Species	Number of Non-native Species	Proportion Non-native Species (%)	Size of Site (ha)
Borden	93	21	22.6	46
Lady Fane	80	19	23.8	54
Lewes	78	16	20.5	64
Middleton	69	10	14.5	62
Townshend	95	9	9.5	70
Victoria West	55	7	12.7	40

Table 2.7. Non-native plant species found adjacent to but not within Acadian Forest study areas in Prince Edward Island.

Scientific Name	**Common Name**	**Scientific Name**	**Common Name**
Agrostis stolonifera	Spreading Bentgrass	*Potentilla recta*	Sulphur Cinquefoil
Avena sativa	Oat	*Rumex acetosella*	Sheep Sorrel
Cirsium arvense	Canada Thistle	*Rumex crispus*	Curled Dock
Elymus repens	Quack Grass	*Solanum tuberosum*	Potato
Galium mollugo	Wild Madder	*Sonchus arvensis*	Sow Thistle
Hieracium floribundum	King Devil	*Stellaria graminea*	Grass-leaved Stitchwort
Hieracium piloselloides	Mouse-eared Hawkweed	*Stellaria media*	Common Stitchwort
Hypericum perforatum	Common St. John's Wort	*Spergularia rubra*	Purple Sandspurry
Leontodon autumnalis	Fall Dandelion	*Trifolium aureum*	Yellow Clover
Linaria vulgaris	Toadflax	*Trifolium campestre*	Low Hop Clover
Lotus corniculatus	Bird's-foot Trefoil	*Trifolium pratense*	Red Clover
Matricaria discoidea	Pineapple Weed	*Trifolium repens*	White Clover
Phleum pratense	Timothy	*Tussilago farfara*	Colt's Foot
Polygonum persicaria	Lady's Thumb	*Verbascum thapsus*	Common Mullein

Table 2.8. Non-native plant species that invaded Acadian Forest study sites in Prince Edward Island and the distance to which each species penetrated. Maximum detectable distance is 300 m. Mean % cover at the maximum distance includes only those plots in which the species occurred. Total number of species found within forests was 133.

Scientific Name	**Common Name**	**Distance from Edge (m)**	**Mean % Cover at Max. Distance**
Leucanthemum vulgare	Ox-eye Daisy	5.7	3
Malus pumila	Apple	5.7	20
Plantago major	Common Plantain	5.7	3
Poa pratensis	Kentucky Bluegrass	5.7	2
Vicia cracca	Tufted Vetch	5.7	2
Hieracium caespitosum	Yellow Hawkweed	40	4
Ribes rubrum	European Red Currant	40	<1
Hieracium aurantiacum	Orange Hawkweed	160	5
*Ranunculus repens**	Creeping Buttercup	160	3
Galeopsis tetrahit	Hemp Nettle	200	3
Ranunculus acris	Tall Buttercup	200	5
Taraxacum officinale	Dandelion	200	<1
Veronica officinalis	Common Speedwell	250	16
*Hieracium lachenalii**	Hawkweed	300	13
Sorbus aucuparia	European Mountain Ash	300	3

* indicates species that did not occur in external (-5.7 m) sample plots.

A similar pattern was found in the number of sampling units having non-native species. Although all but one of the 18 external plots had non-natives, this dropped to 10 of the 18 first forest plots. The number of sampling units with non-natives declined along edge-to-interior transects but did not reach zero; at the innermost distance of 300 m, two plots (11%) were found to have non-natives (Figure 2.5).

There was a significant negative relationship between the number of sampling units having non-native species and both distance (Spearman correlation (r_s) =-0.8292, p=0.003, n=10), and canopy (r_s=-0.7987, p=0.0056, n=10). Canopy and distance are uncorrelated variables (r_s=0.4075, p=0.2425).

Consistent with the greater frequency of non-native species found in edge plots, greater percent cover of non-natives was also found in these areas. More than 50% of the total cover of nine of the ten non-native species persisting beyond 5.7 m was found within the first 40 m of the edge-to-interior transects, and three of these species had reached their maximum cover by this distance (Figures 2.6 and 2.7). Similarly, when the total cover of all non-native species is considered, the highest cover captured to transect distance ratio appears at 40 m (13% of the transect); beyond this, increases in the transect do not capture a proportional increase in non-native species cover (Figure 2.8).

Of the ten species persisting beyond 5.7 m, total cover of both *Veronica officinalis* (Common Speedwell) and *Ribes sativum* (European Red Currant) was negatively correlated with distance. Cover of an additional five non-native species were negatively correlated with canopy, while the remaining three non-native species showed no significant correlation with either variable (Table 2.9).

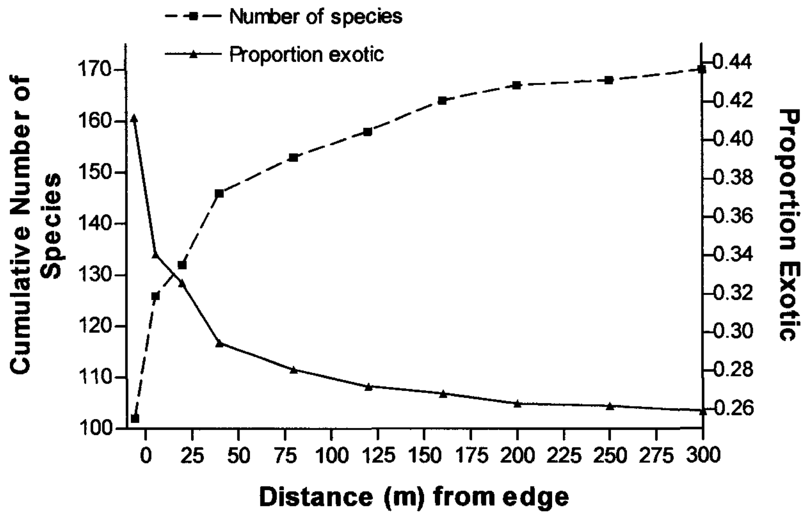

Figure 2.4: The cumulative number of species and proportion of those that are non-native along edge-to-interior transects in six Prince Edward Island Acadian forest study sites.

Figure 2.5: Non-native species occurrence in 100 m^2 sample plots along edge-to-interior transects in six Prince Edward Island Acadian forests study sites. Total number of plots at each distance was 18 (six sites with three plots at each distance); total area surveyed at each distance was 1,800 m^2 (18 plots of 100 m^2 each).

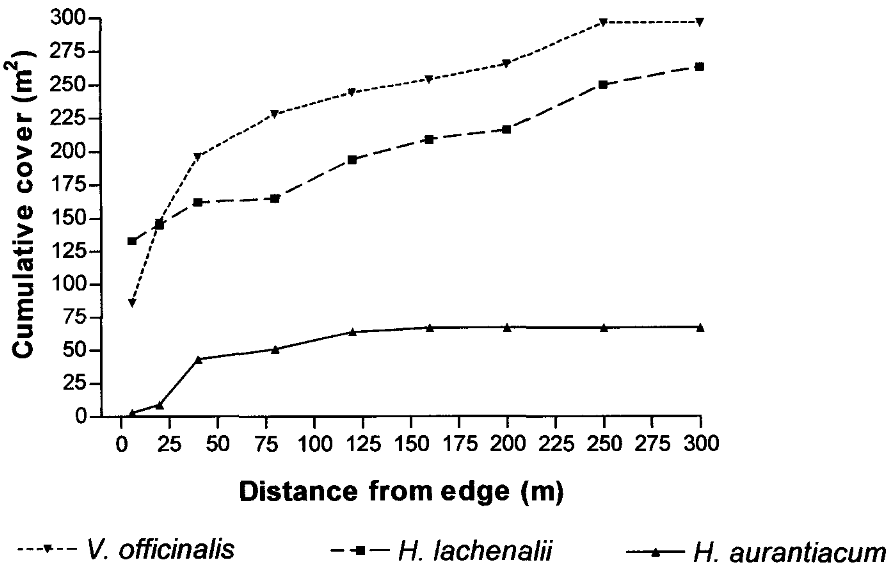

Figure 2.6: Cumulative cover (m^2) for three non-native species that each comprised more than 50 m^2 of sample plots along edge-to-interior transects in six Prince Edward Island Acadian forest study sites. More than 50% of the total cover of each species was found within the first 40 m of the transects. Total area surveyed was 16,200 m^2 (six sites, three transects per site, nine 100 m^2 plots per transect).

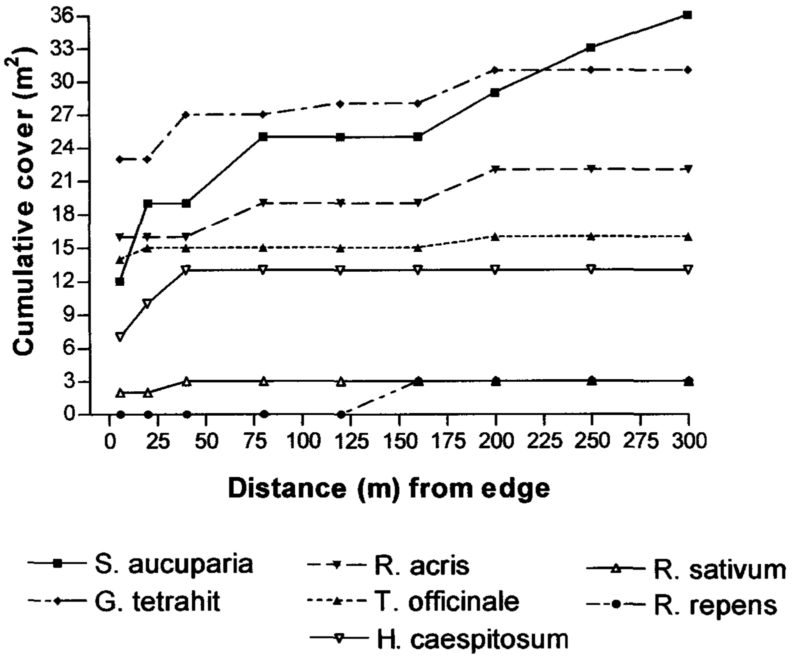

Figure 2.7: Cumulative cover (m^2) for seven non-native species that each comprised less than 50 m^2 of sample plots along edge-to-interior transects in six Prince Edward Island Acadian forest study sites. More than 50% of the total cover of six of these seven species was found within the first 40 m of the transects. Total area surveyed was 16,200 m^2 (six sites, three transects per site, nine 100 m^2 plots per transect).

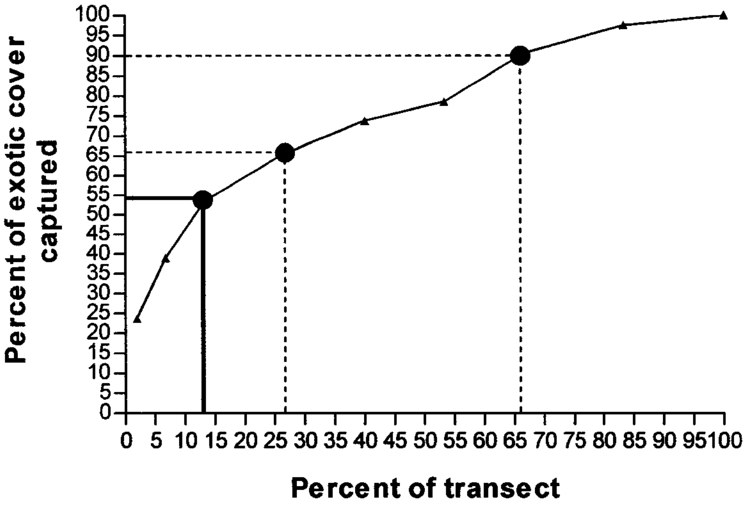

Figure 2.8: The increase in percent of non-native cover captured per percent of transect. The most efficient cost per unit effort appears at 13% of the transect (40 m), by which point half of the total non-native cover has been captured (solid lines). Beyond this point, increases in the transect do not result in proportional increases in non-natives captured, although there may be ecological reasons for setting the preferred non-native capture rate at 66% or 90%, for example (dashed lines).

Table 2.9: Correlations between total percent cover of ten non-native species persisting more than 5.7 from the edge of six PEI Acadian forest study sites, and the uncorrelated variables of canopy and distance. r_p = Pearson (parametric) correlation; r_s = Spearman rank (nonparametric) correlation. ns-not significant ($p>0.05$).

Total Cover of:	Correlation with Distance	Correlation with Canopy
Galeopsis tetrahit	ns	$r_p = -0.9869$, $p<0.001$ $n=10$
Hieracium aurantiacum	ns	$r_p = -0.6781$, $p=0.031$ $n=10$
Hieracium caespitosum	ns	$r_p = -0.8455$, $p=0.002$ $n=10$
Ranunculus acris	ns	$r_p = -0.9076$, $p<0.001$ $n=10$
Taraxacum officinale	ns	$r_p = -0.7701$, $p<0.009$ $n=10$
Ribes sativum	$r_s = -0.7218$, $p=0.002$ $n=10$	ns
Veronica officinalis	$r_p = -0.8065$, $p=0.0048$ $n=10$	ns
Hieracium lachenalii	ns	ns
Ranunculus repens	ns	ns
Sorbus aucuparia	ns	ns

2.3.4 Distribution of taxa

A constrained seriation with columns as plot locations along the edge-to-interior transects was performed both on the entire data matrix and separately for each site (Appendix 2). In all cases the probability of the column order being random was $p<0.001$; the assumption of a community gradient through the columns, and therefore along the transects, is supported.

2.3.5 Community Structure

To examine similarity among sample plots within hard and embedded edge sites, detrended correspondence analysis (DCA) ordination was prepared using the cover of all taxa. (Because external plots were similar to first forest plots for the embedded edge site but significantly different at sites with a hard edge (Figure 2.3, Table 2.5), external plots were included in the ordination for Townshend but excluded for others). DCA for the Townshend study area resulted in an axis 1 eigenvalue of 0.4096; this is less than the optimal value of 0.65 or greater, but well above the minimum threshold of 0.25. The axis 2 eigenvalue was 0.2183 and thus not significant. Plots TA0 to TC3 (-5.7 m to 40 m along the edge-to-interior transects) grouped together at or below position 1 on DCA axis 1 (Figure 2.9). Ordination scores were not found to be associated with environmental or composite variables, but plotting taxa on the ordination suggested a possible moisture gradient. Xerotolerant species such as *Plantago major* (Common Plantain), *Osmunda claytoniana* (Interrupted Fern) and *Fragaria virginiana* (Strawberry) grouped at the lower end of axis 1, with hydrophilous plants such as *Impatiens capensis* (Spotted Touch-me-

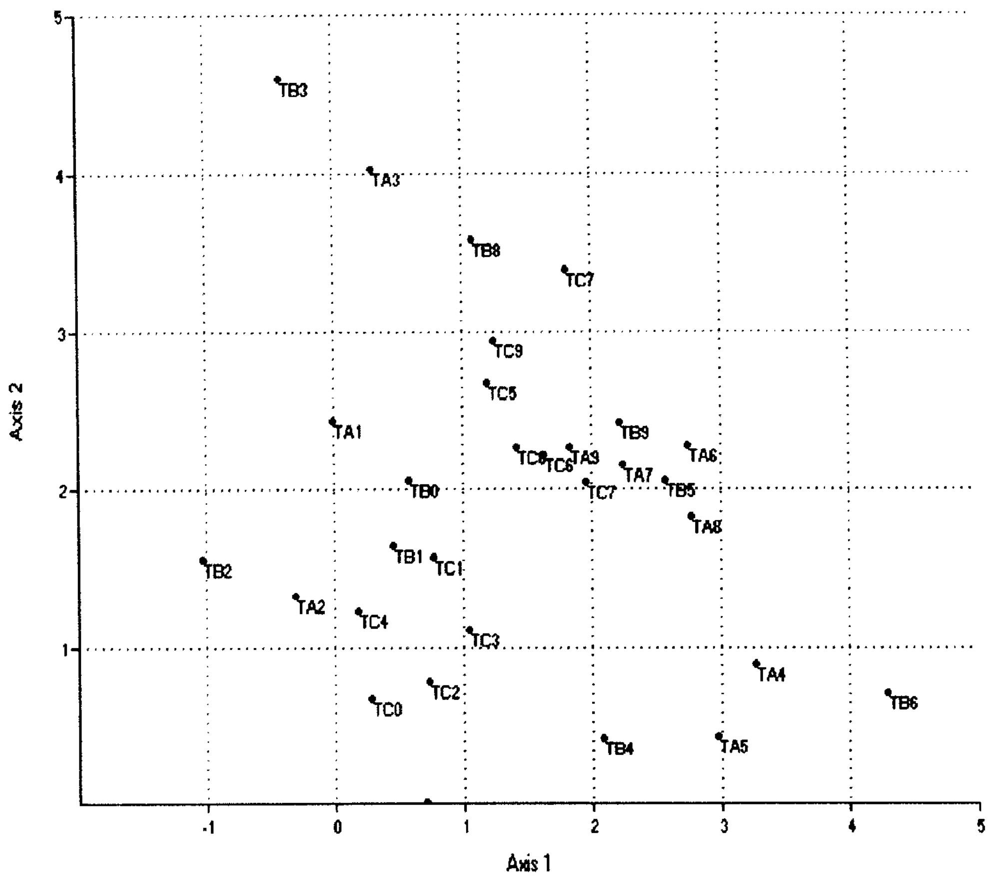

Figure 2.9: Detrended correspondence analysis ordinaton of plot locations from plant community data (taxa and cover) from edge-to-interior transects in Townshend woodlot, the study site with an embedded edge. Axis 1 eigenvalue is 0.4096; axis 2 is 0.2183. Each plot has a unique code indicating the site (Townshend, T), transect (A, B or C) and distance from the edge (0 through 9, corresponding with distances −5.7 m to 300 m). Edge plots 0 to 3 (−5.7 m to 40 m from an edge) group at or below position 1 on axis 1, which may represent a moisture gradient (refer to Figure 2.10).

not), *Matteuccia struthiopteris* (Ostrich Fern) and *Ranunculus acris* (Common Buttercup) at the upper end and generalists such as *Abies balsamea* (Balsam Fir) and *Cornus canadensis* (Bunchberry) in between (Figure 2.10). Because moisture data were not collected, this hypothesized gradient cannot be confirmed.

Cluster analysis was also performed using cover data from the Townshend study site. As illustrated by Figure 2.11, the first split separated plots 160 m and greater along edge-to-interior transects from those within 120 m of the edge. The second split separated plots within 20 m of the edge from those between 40 m and 120 m. Results of cluster analysis suggest a depth-of-edge of at least 20 m at the Townshend study site.

DCA with species cover for the five sites with a hard edge did not result in strong eigenvalues (axis 1= 0.2938; axis 2 = 0.1978), but did show that interior sample plots were more similar than those at the edges, particularly for the Borden, Lady Fane, Lewes and Middleton study sites (Figure 2.12). The first division of the cluster analysis for hard edge sites was similar to that of Townshend, separating plots 160 m and further along edge-to-interior transects from those nearer the edge (Figure 2.13). However, unlike Townshend, the edge cluster includes the 40 m plots, suggesting a wider edge zone.

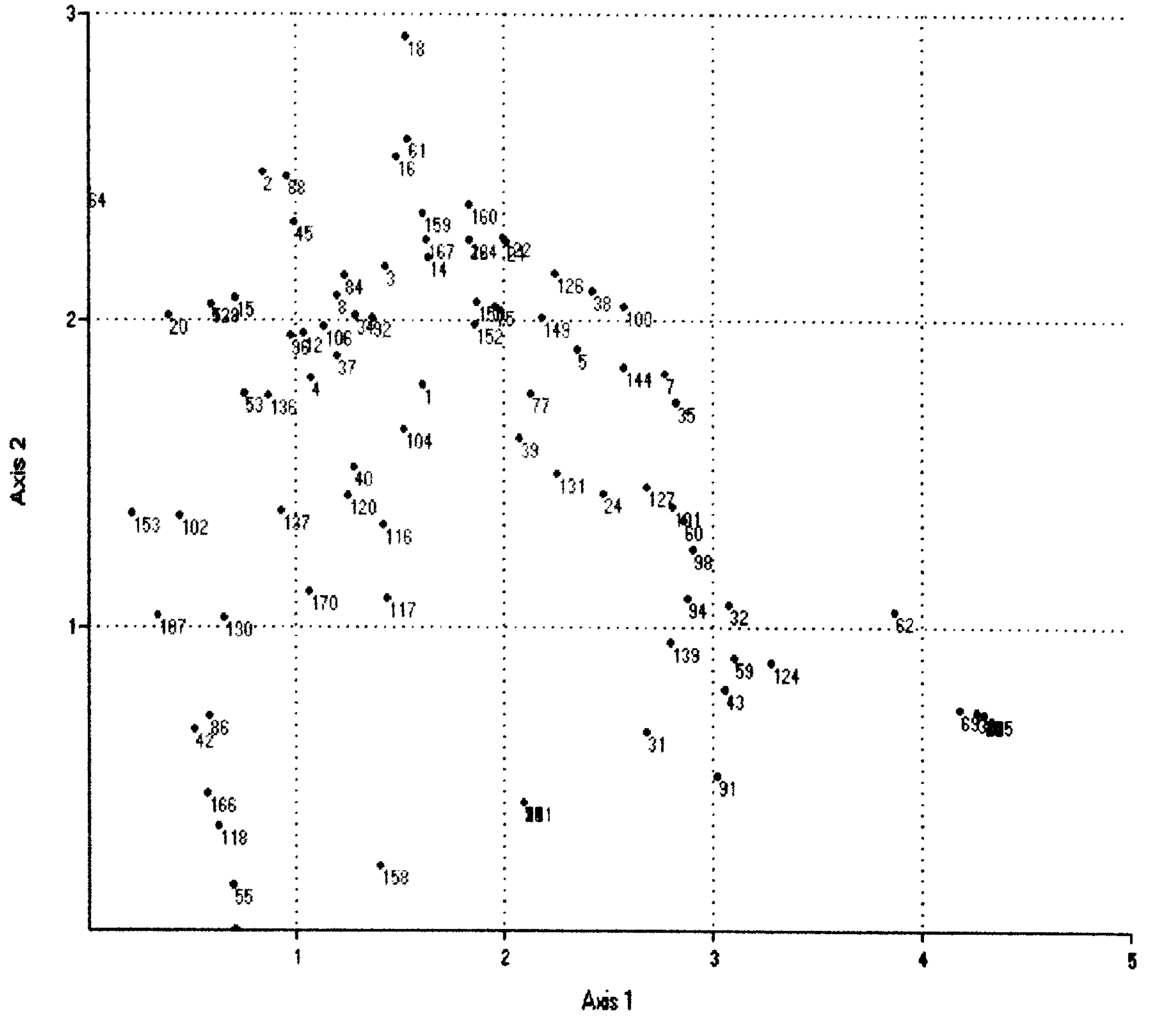

Figure 2.10. Detrended correspondence analysis ordination of taxa from plant community data from edge-to-interior transects in Townshend woodlot, the study site with an embedded edge. Numbers refer to species, and the key is given in Appendix 1. Although ordination scores were not found to be associated with any of the environmental or composite variables for which data were collected, axis 1 may represent a moisture gradient, with xerotolerant species at the lower end and hydrophilous species at the upper end. For example, *Fragaria virginiana* (55), *Dennstaedia punctilobula* (42) and *Plantago major* (107) are at the lower end of axis 1 while *Impatiens capensis* (69), *Matteuccia struthiopteris* (91) and *Ranunculus acris* (124) are at the upper end.

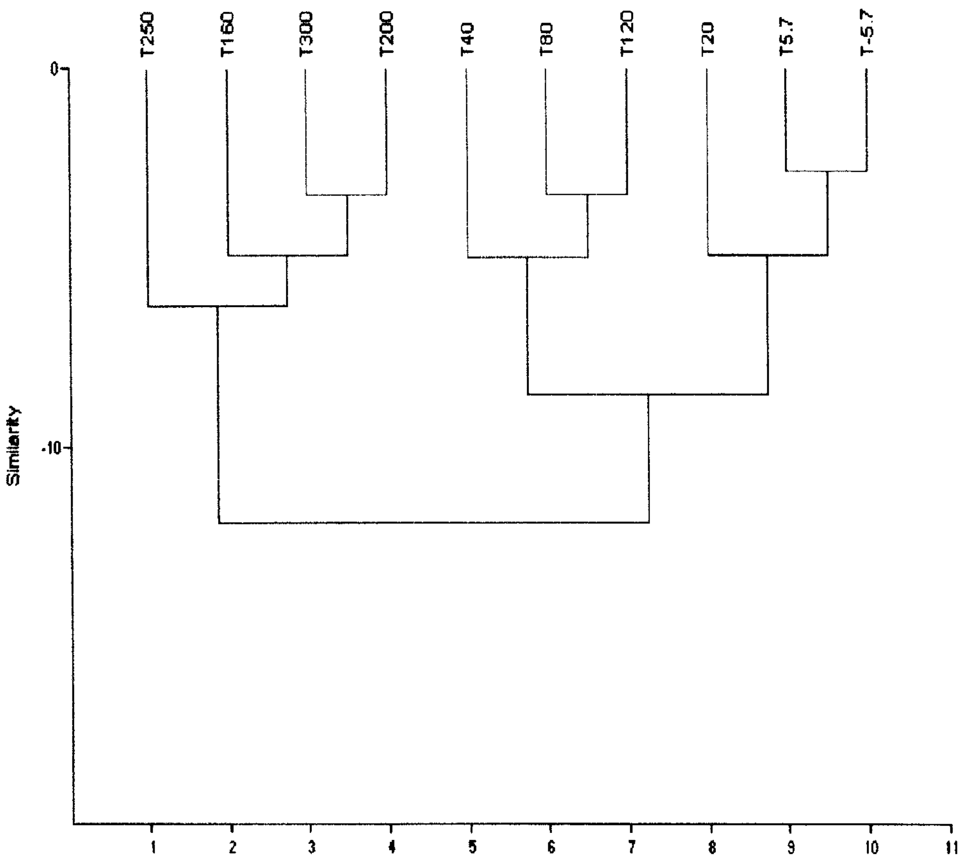

Figure 2.11: Cluster analysis (Ward's method) using plant community data (taxa and cover) from edge-to-interior transects in Townshend woodlot, the study site with an embedded edge. Plots 160 metres and more from an edge cluster separately from plots within 120 metres of an edge. Within the latter group, external (T-5.7) and the first two forest plots (T5.7 and T20) cluster together as edge.

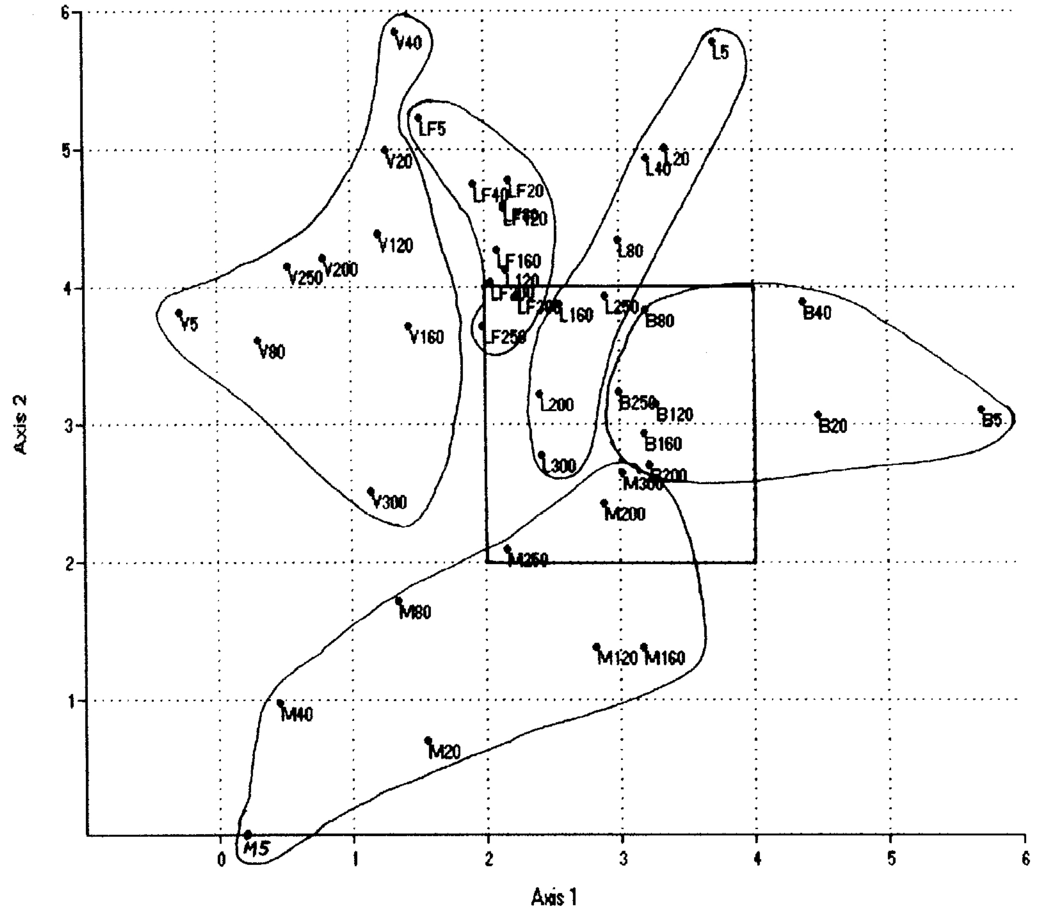

Figure 2.12: Detrended correspondence analysis ordination of plant community data (taxa and cover) from five study sites with a hard edge. Axis 1 eigenvalue is 0.2938 and axis 2 eigenvalue is 0.1978. Although plots nearer the forest edge differ markedly among study sites, four of the five areas show increased similarity beyond 200 metres (centre box). V=Victoria West, LF=Lady Fane, L=Lewes, B=Borden and M=Middleton.

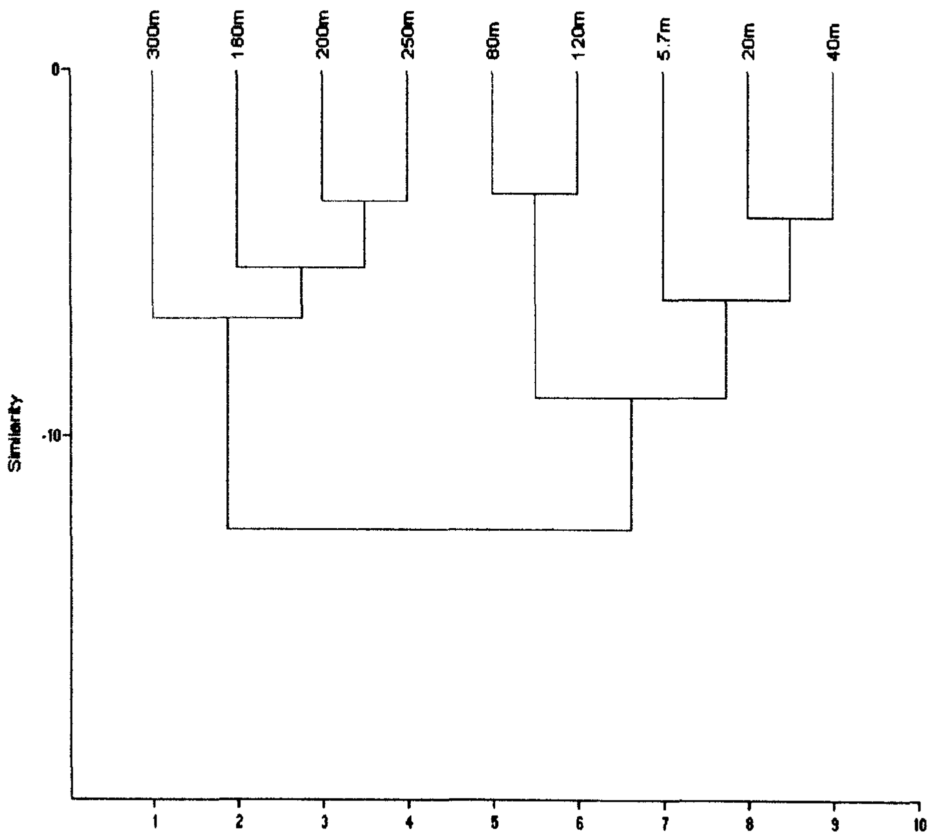

Figure 2.13: Cluster analysis (Ward's method) using plant community data (taxa and cover) from the five study sites with a hard edge. As with the Townshend study site (Figure 2.11), plots 160 metres and greater from an edge cluster separately from those within 120 metres, however within the latter group the first three forest plots (5.7 m, 20 m, and 40 m) cluster together as edge.

2.4 Discussion

The results of this study show that there is an edge-to-interior plant community gradient in older hardwood forests and that invasion of these areas by non-native species can be more extensive than previously reported. Although differences in environmental and plant community variables between edge and interior plots are consistent with other work in eastern North American forests (*i.e.* Palik and Murphy, 1990; Brothers and Spingarn, 1992; Fraver, 1994; Bruner, 1997; Burke and Nol, 1998), the depth-of-edge influences suggested by these results is an important difference.

Consideration of environmental and composite variables such as soil temperature or canopy cover in the absence of information on the plant community can lead to the conclusion that edge effects are restricted to within a few metres of an edge. For example, this study found that soil temperature and canopy cover suggest depth of edge influences extend at least 5.7 m into the forest but not beyond 20 m (Figure 2.3, Table 2.5). Additional sampling between these distances would be required to pinpoint the extent of edge influences more precisely. Similarly, Burke and Nol (1998) reported soil temperature and light reaching interior conditions within five metres of an edge, and Fraver (1994) found similar variables had equilibrated within eight metres. However, consideration of non-native species combined with analysis of changes in species composition within the entire plant community suggests a broader edge zone.

2.4.1 Non-native Taxa

The number of non-native species in Prince Edward Island's upland hardwood forests (15) is in the lower end of the range (12 to 21 species) found in other eastern North American studies (Brothers and Spingarn, 1992; Fraver, 1994; Burke and Nol, 1998), but the frequency of occurrence, percent cover and distance penetrated were markedly higher in the PEI study sites. For example, Brothers and Spingarn (1992) found non-native species in only 10% of quadrats 50 m from an edge. The PEI study found non-native species in 50% of quadrats 40 m from an edge (the nearest sample point to 50 m); the proportion of plots with non-native species did not approach 10% until a distance of 300 m (Figure 2.5). This is six times further than that reported by Brothers and Spingarn (1992), although it is noted that their sample plots were 20 m^2, smaller than the 100 m^2 plots used in the PEI study.

Similarly, Fraver (1994) reported only two non-native species extending more than 20 m from an edge in the hardwood forests of North Carolina, while the PEI study found 10 species beyond this distance (Table 2.8). Although Burke and Nol (1998) found eight non-native species persisting to 100 m (the maximum detectable in their study), all but one of these occupied less than 1% of the interior sample plot. The PEI study also found eight non-native species extending to (and beyond) 100 m, but all except one had cover greater than 1%. *Veronica officinalis* and *Hieracium lachenalii* each had mean percent cover greater than 10% in the innermost plots in which they occurred (Table 2.8). Additional study of the morphology and seed weight and viability of these two species is detailed in Section 3.

Although the number of non-native species found in this study is within the range of those reported in other studies, it is worth noting that its position in the lower end of this range is not attributable to the notion that islands have fewer species than comparable mainland habitats. All of the non-native species found in the Ontario study (Burke and Nol, 1998) are present on Prince Edward Island (Blaney, MacQuarrie and Curley, 2000). Although half of Burke and Nol's (1998) invading species were not found in the PEI study sites, all have been seen in other forest types on the Island (*e.g.* MacQuarrie, Schaefer and Schonerank, 1999 and 2000; personal observation). Similarly, eight of the 15 invasive species found in this PEI study were not reported by Burke and Nol (1998), although all are present in that province (Kartesz, 1999). A few of the non-native species found in the Indiana (Brothers and Spingarn, 1992) and North Carolina (Fraver, 1994) studies have not been recorded on PEI, because they are more southern species [eg. *Campsis radicans* (Trumpet Creeper)] that are absent from the Maritime region (Zinck, 1998; Kartesz, 1999; Hinds, 2000).

The higher percent cover and greater distance penetrated may be a legacy of the history of forest use and disturbance on Prince Edward Island. Each of the comparable studies was located within a fragmented, primarily agricultural landscape. For example, it is estimated that 90% of pre-colonial Indiana (the focal area for Brothers and Spingarn, 1992) was forested, but by 1920 this had dropped to barely 6%; today, forest covers roughly 19% of that state (Nelson, Indiana Division of Forestry, undated). Burke and Nol's (1998) work was done in southern Ontario, which was also almost entirely forested before the arrival of European settlers. By the 1880s, forest cover in this region had been reduced to less than one-third of the land area; today it is estimated that forests cover roughly 38% of the landmass of this region (Landowner Resource Centre, 1997).

These historical patterns of forest conversion mirror those of PEI. More than 90% of this province was forested before European settlement (McAskill, 1987), but this had dropped to 30% by 1900 (PEI Department of Agriculture and Forestry, Forestry Division, 1997a). Today, approximately 50% of PEI is forested (PEI Department of Agriculture and Forestry, Forestry Division, 1997b).

While historical anthropogenic use of the surrounding landscape in PEI is comparable to that of Ontario and perhaps less severe than that of Indiana, this does not provide direct information about the level of disturbance within remnant forests. Authors of comparable studies note that their sites were not free from past human use, although evidence of recent disturbance such as logging, livestock grazing or fire was absent (Brothers and Spingarn, 1992; Fraver, 1994; Burke and Nol, 1998). While the same is true of the PEI sites, remnant upland hardwood stands in this province are acknowledged as "heavily modified descendants" of the pre-colonial forest (Sobey, 1999) and it has long been recognized that there are likely no forests on PEI that have escaped human disturbance (UPEI, 1982).

For example, Townshend Woodlot is among the best remaining examples of Acadian forest on Prince Edward Island (Taschereau, 1974; UPEI, 1982; Griffin, Baglole and Baglole, 1986), but Hovingh (1995) found ample evidence of historical anthropogenic activity within this site. While it is not known how the levels of historical disturbance within the PEI study sites compare to those of the other areas, the greater cover and distance penetrated by non-natives suggests PEI's forests may have experienced a greater level of human use, even though forest conversion in the larger landscape is similar to or less than that of other study areas. Detailed information about the historical uses of forest study sites both on PEI and elsewhere would be required to confirm this suggestion. This may be an important variable that has not been adequately emphasized in studies of forest ecology.

While human disturbance is clearly a factor in Island forests, natural events should not be overlooked. Glen (1997) suggested that recurring catastrophic weather events such as ice storms have left their mark on Island forests, and noted that hardwood trees are more susceptible to damage from such events than are conifers. While such meteorological events can open up relatively large areas of canopy, natural forest processes including tree death and windfall create smaller gaps. As with anthropogenic disturbance such as select harvest of trees for fuel wood, such natural disturbances create openings in the canopy that allow more light to reach the forest floor. As noted in Table 2.9, more non-native species showed a negative correlation with canopy than distance from edge. Disturbance that creates openings in the canopy, regardless of whether it is natural or anthropogenic, may facilitate the spread of non-native species.

The only information from the comparable studies that relates (albeit indirectly) to the suggestion that PEI's forests may be more disturbed than those in other areas are the mean tree diameter data presented by Burke and Nol (1998). While caution must be used in this comparison because the sample sizes and distances from edge differ and tree diameter is not necessarily an accurate indicator of age (Hovingh, 1995), it is interesting to note that tree diameters in the Ontario study are larger than those in the PEI study (Table 2.10).

A second factor that could contribute to the distribution and abundance of non-native species is time. European settlement began circa 1720 in this province. Subsequent land clearing led to major forest fires as early as 1736 (Sobey, 2002), and non-native agricultural plants were under cultivation by the time of the 1751 De la Roque census (Clark, 1959). In addition to crop plants, accidental introductions likely accompanied these early settlers. Palynological studies suggest that the first major influx of pollen from weedy and non-native species appears about 150 years ago (Anderson, 1980; MacQuarrie, 2001), which was during a period of rapid expansion of settlement and land clearing (Clark, 1959). This is consistent with the pollen record of southern Ontario (Landowner Resource Centre, 1997) and Indiana (Cole, National Biological Service, undated). While the increased cover and distribution of non-native species recorded in PEI forests may be a result of increased historical human use of remnant woodlands, it does not appear to be attributable to an earlier arrival of such species.

A third potential explanation for non-natives' increased frequency of occurrence, cover and distance penetrated in the PEI study is the invasiveness of the taxa that were recorded here. Species common among studies were most often those that persisted to interior plots (*e.g. Veronica officinalis*, *Taraxacum officinale*, *Ranunculus acris*) while those that were found only in the PEI study were often cited by other sources as being invasive. For example, *Ranunculus repens* persisted to 160 m from an edge in this study and is listed as a Priority Class II species (the rank assigned to species that invade undisturbed habitats) by Stapleton *et al.*, 1998 and as Category 3 (moderately invasive) by Havinga *et al.* (2000). *Sorbus aucuparia* was found in the innermost plots in this study and

Table 2.10: A comparison of mean tree diameters at breast height (DBH) reported by Burke and Nol (1998) with those recorded in the PEI study. Because of differences in sample sizes and the location of sample plots between the two studies, this comparison is for interest rather than direct analysis.

Distance from edge (m)	Mean DBH (cm) from Burke and Nol (1998, Figure 3, page 50)	Mean DBH (cm) from PEI study
20	11.0	6.4
35	11.0	N/A
40	N/A	6.8
50	10.7	N/A
80	N/A	7.2
100	10.0	N/A
120	N/A	6.4

is listed among species classed as invasive by the Canadian Botanical Conservation Network (undated). These species are not reported in comparable studies (Brothers and Spingarn, 1992; Fraver, 1994; Burke and Nol, 1998), although study locations are within their North American range (Kartesz, 1999). Eleven of the non-native species found in PEI forests were suggested as invasive by Havinga *et al.* (2000), the Canadian Botanical Conservation Network (undated) or Stapleton *et al.* (1998), while 12 of those cited by Burke and Nol (1998) were listed by these sources. It would thus appear that, based on a current understanding of which species are the most problematic invasives, Prince Edward Island's taxa are not more aggressive invaders than those recorded in Ontario.

It could be suggested that the greater cover of and distance penetrated by non-natives in this study may be a result of smaller forest fragments on PEI as compared to the other studies. However, as reported in Table 2.6, fragment size was not correlated with species richness, or the number or proportion of non-native species. Additionally, the PEI study sites were larger than those examined by Brothers and Spingarn (1992) and in the largest of four size classes studied by Burke and Nol (1998) (Table 1.2). Fraver (1997) did not report the sizes of his study areas, so a comparison with that work cannot be made.

In both the PEI and Ontario studies, species found in interior forests typically had characteristics such as seed adaptations (*e.g.* the pappus of members of the aster family; food such as the berries of *Sorbus aucuparia* that are eaten and spread by wildlife) or vegetative growth (*e.g. Veronica officinalis*) that contribute to invasion. A discussion of the morphological features that can give non-native species an advantage over their native counterparts is given in Section 3.

A comparison of the proportion of forest species that were non-native is conspicuously absent from this discussion because none of the other authors reported the total number of species found. As noted in Table 2.8, 15 of 133 forest species in the PEI study (11.3%) were non-native. While the Ontario study (Burke and Nol, 1998) uncovered 18 non-native species, it is not known whether this represents a higher, lower or comparable proportion to that of the PEI study. A higher proportion of non-native flora among PEI's forests could have given added support to the suggestion that our forests have had greater historical anthropogenic influences than those of other areas. A lower or comparable proportion would have suggested a higher degree of invasiveness among PEI species rather than greater forest disturbance. In the absence of this information and given the intense historical human use of the Island's forests, it seems probable that the greater coverage and further distance at which non-native species were found in the PEI study is indicative of a greater level of historical anthropogenic disturbance.

2.4.2 Depth of Edge - Non-native Taxa

Some non-native species were found to extend 300 m into PEI study sites, but this does not mean that this entire width is edge. As reported in Figures 2.6 and 2.7, at least 50% of the total cover of all but one of the ten invasive species persisting beyond 5.7 m was restricted to the first 40 m of the transect. Forty metres was also the critical threshold for efficacy of non-native capture. At this point, 13% of the transect captured more than half of the total non-native cover; beyond it, increases in distance from the edge did not result in proportional increases in non-native cover captured (Figure 2.8). For example, a

20% increase in the non-native cover captured would require a 30% increase in distance from the edge, while a 35% increase in non-native cover captured would require a 55% increase in distance from the edge. Based on these results, the buffer zone that provides the greatest return on investment (*i.e.* that has the most efficient non-native cover capture per unit of buffer) is 40 m.

While in terms of cost per unit effort (ratio of non-native cover captured to width of buffer), 40 m would be the optimal depth of edge to control plant invasions, there can be ecological reasons for setting the minimum capture rate above 50%. Chen, Franklin and Spies (1992) suggested that depth-of-edge influences extend to the point where the variable in question reaches a level two-thirds of that found in interior habitat. Chen, Franklin and Spies (1992) give the equation:

$$Y = Y_E \pm \tfrac{2}{3}\,[Y_E - Y_I]$$

where Y is the value of the focal variable at the depth of edge, Y_E is the value of the focal variable at the edge (5.7 m plots in this study) and Y_I is the value of the focal variable in the interior (300 m). For increasing trends $\tfrac{2}{3}\,[Y_E - Y_I]$ is added to the edge value; for decreasing trends it is subtracted (Chen, Franklin and Spies, 1992). When this equation is applied to the decreasing trend of frequency of occurrence of non-natives along edge-to-interior transects (Figure 2.5), depth of edge is 80 m: $Y=17 - \tfrac{2}{3}[17-2] = 7.0$. The frequency of occurrence of non-native species does not drop to seven species until 80 m from the edge (Figure 2.5). Although the equation does not apply to the increasing trends of cumulative cover or percent of non-native cover captured because the observations at each distance are dependant upon those at earlier distances, two-thirds of the non-native cover are captured within the first 27% (80 m) of the transect (Figure 2.8). Based on Chen, Franklin and Spies' (1992) "⅔ criterion", the depth-of-edge influence of non-native taxa in PEI Acadian forests is 80 m. This may therefore be a useful minimum for conservation planning.

2.4.3 Depth of Edge - Plant Community

Cluster analysis suggests different depth-of-edge influences between those sites with a hard edge and Townshend, the site with an embedded edge. As reported in Figure 2.11 and Figure 2.13, analyses of both types of sites separated sample plots greater than 160 m from an edge from those within 120 m. The near-edge cluster for Townshend, however, extends to only 20 m while that for the hard-edge sites persists to 40 m. This suggests a slightly greater depth-of-edge for sites with active and ongoing anthropogenic activity at their edges. Given the continual disturbance in the adjacent habitat at these sites, the frequent intentional and accidental re-introduction of both non-native and native ruderal species, and the different environmental conditions (*e.g.* warmer soil temperature, lower canopy) at the periphery of hard-edge sites, the wider depth-of-edge influence is to be expected. The cluster analysis of Townshend also shows external (−5.7 m) and first forest (5.7 m) plots to be very similar, which is consistent with the analysis of environmental and composite variables (Figure 2.3). External plots were omitted from cluster analysis of the hard edge sites because they represented communities clearly distinct from the forest (Figure 2.3).

While this first analysis of plant community data suggested a depth-of-edge less than that indicated by non-native taxa alone, ordination suggested more extensive depth-of-edge influences. Ordination of plots at Townshend using cover of all species placed all quadrats up to 40 m from an edge and one of those at 80 m below position 1 on axis 1 (Figure 2.9). Axis 1 eigenvalue was 0.4096, lower than the optimal but sufficient to indicate a meaningful ordination (Walker, 1998). Adding taxa to the ordination (Figure 2.10), suggested that axis 1 may represent a moisture gradient, with plots in closer proximity to the edge having more xerotolerant species. Given that xerotolerant species are typically shade intolerant, axis 1 could equally represent a light gradient. Either way, this is consistent with the notion that edges are drier and have fewer shade-tolerant species (Saunders, Hobbs and Margules, 1991; Matlack, 1993; Fraver, 1994; Murcia, 1995; Adkison and Jackson, 1996; Burke and Nol, 1998).

The Townshend DCA points to a depth-of-edge of at least 40 m and up to 80 m. When this information is applied to interpretation of the cluster analysis for Townshend, the relatively close linkage of 40 m and 80 m plots with those at 120 m suggests that the first separation of plots greater than 160 m from those less than 120 m may actually be a better indicator of the depth-of-edge suggested by the plant community (Figure 2.11).

Ordination of plant cover data from the five sites with a hard edge highlights the increasing similarity of interior plots among sample sites, although this must be interpreted with caution as eigenvalues are low (Figure 2.12). The edge plots are at the extremes of the ordination, which reflects the different ways in which the hard edges are maintained. For example, the Lewes site (coded L on the ordination) was immediately adjacent to a field of *Avena sativa* (Oats) while the Middleton site (M) abutted a field of *Solanum tuberosum* (Potato). Such differences in adjacent habitats result in a different suite of near-edge species. The Victoria West site (V) is separated from the others by the ordination. Although it did have the required tree species, height and age requirements to make it a Class I/II forest comparable with the other sites, Victoria West was the only site with *Fraxinus americana* (White Ash), which was present in all forest plots in this study area. That this tree was present only in the westernmost site in this study is attributable to the primary distribution of this species on PEI. For example, Sobey (1993) noted *Fraxinus* among those species located mostly or exclusively west of Summerside.

Fraver (1994) reported a similar trend of increasing similarity among sample plots along his edge-to-interior transects, and concluded that this represented plots being sufficiently interior to escape edge-related effects. This is a reasonable explanation for the arrangement of sample plots on the ordination (Figure 2.12). Although environmental variables such as soil temperature and canopy were very similar among edge plots in sites with a hard edge, the plant communities were disparate because of the differing anthropogenic activities in the adjacent habitats. As plots moved towards the interior, they became less influenced by edge and began to equilibrate to a state more representative of the Acadian forest community. While the fit is not perfect on the ordination - for example, this pattern is not as clear for the Victoria West study site and the eigenvalues are low - the trend is apparent. The 200 m sample plots for three of the five sites are within one unit of beta diversity (about 25% species turnover in the community, Walker [1997]); those for four of the five sites are within two units. This suggests 200 m and beyond as interior habitat. This is greater than Fraver's (1994) estimate of 50 to 60 m, but his interior plots were only 100 m from an edge. Had they persisted to 300 m, analysis may have shown that while the 50 m to 100 m plots were similar, differences existed between these plots and more interior stations. While this is conjecture, such a scenario is possible and would have resulted in a different conclusion about depth of edge in that study. Similarly, replicating the PEI study with a greater maximum distance from an edge (if such study sites could be found) would show if the presumed trend continues. Regardless, both Fraver (1994) and this PEI study suggest that there are two ways of looking at interior forest habitat: from the outside in (*i.e.* where effects from the surrounding habitat are minimized) or from the inside out (*i.e.* where there is the strongest similarity among sample sites within the community).

2.4.4 Relation of results to study objectives

Objective 1: Identify which invasive vascular plants are present in Prince Edward Island's Acadian forest. Although 15 non-native species were found in PEI's upland hardwood forests, *Veronica officinalis* and *Hieracium lachenalii* were found to be the most serious invaders, both in terms of penetration into the forests and on the ground coverage. These species were thus selected for additional study which is detailed in Section 3.

Objective 2: Identify the extent to which non-native species and typical edge environmental factors have penetrated these forests, and *Objective 3: Identify whether a minimum buffer through which invasive plants are unlikely to extend can be prescribed.* Typical edge environmental factors do not extend beyond 20 m from an edge, and may be restricted to within 5.7 m. Non-native species were found even in the interior plots, 300 m from an edge, and it is thus unlikely that a buffer of any width could ensure interior habitat totally free of non-native species. That said, buffers could be prescribed that would capture much of the non-native species cover and ensure interior habitat conditions do exist within forest protected areas. While the most cost efficient buffer would be 40 m, this would only capture a little more than half of the invasive species cover. This may not be adequate for natural areas protection and management, where important goals include conserving pre-colonial systems (where they exist) and discouraging anthropogenic degradation (Noss, 1987). Setting a buffer based on cost per unit effort criteria may make political sense, but only rarely ecological sense. Conservation of the upland hardwood component of the Acadian forest - areas that are among the best remaining examples of elements of PEI's pre-colonial landscape - demands a more precautionary approach. Chen, Franklin and Spies' (1992) suggestion of a two-thirds criterion comes closer to an ecological approach but is - as those authors acknowledge - an arbitrary cutoff. However, any criterion less than 100% capture is to a large extent arbitrary; presumably, having your focal variable return to a condition representing 90% of its state in the interior environment is better than 75% which is better than two-thirds. In this light, Chen, Franklin and Spies' (1992) suggestion is a useful minimum for conservation planning, and its application to the PEI situation would prescribe a buffer of 80 m. Such a minimum buffer would capture some invasive species totally and dramatically reduce the coverage of most others. For example, 98 m^2 of *Hieracium lachenalii* and 68 m^2 of *Veronica officinalis* were found beyond 80 m in this PEI study. For relatively small infestations such as this, mechanical control with subsequent monitoring can be a viable option for eradication (Mack *et al.*, 2000). The low level of infestation combined with the high value of this type of habitat (*i.e.* relatively uncommon in this province, harbouring provincially rare species), would make this a high priority for invasive control efforts under Ontario's invasive plant management strategy (Havinga *et al.*, 2000); no similar strategy exists for Prince Edward Island.

2.4.5 Conclusion

The original study objectives focussed on invasive species with the inherent assumption that these taxa would prescribe the definitive depth of edge. Analysis of the plant community as a whole shows that this is not the case, and that sample plots within 120 m of an edge are more similar to edge habitat than interior. The most precautionary approach to conserve interior habitat within Acadian forest protected areas on Prince Edward Island would be to ensure that such sites have as much area as possible that is greater than 120 m - and ideally at least 160 m from an edge. Study of additional sample plots between these distances could pinpoint the critical limit more precisely. Based on this, Acadian forest protected areas smaller than 240 m on a side (5.75 ha) are unlikely to include interior habitat (as defined by the plant communities), and sites should be at least 320 m on all sides (10.24 ha) to ensure interior habitat is present. [This critical limit is suggested with a strong note of caution that a minimum goal for conservation must never be interpreted as an ideal, as discussed in section 4.2.2]. This assumes that the 300 m plots of this study did indeed represent interior habitat, however this assumption is supported by the literature (Palik and Murphy, 1990; Brothers and Spingarn, 1992; Chen, Franklin and Spies, 1992; Fraver, 1994; Burke and Nol, 1998).

Finally, it must be acknowledged that forests are dynamic. Natural processes including tree death, windfall and decay, changing environmental conditions, fire, extreme weather events, disease and predation can bring about changes in distribution and abundance of both native and non-native species. In this dynamic environment, edge effects can creep inward over time (Fraver, 1994). Intuitively, the reverse should also be true and, as the forest matures, interior effects can creep outward. If PEI's forests have had a greater history of anthropogenic disturbance as has been suggested here, protecting remnant woodlands, controlling human use and allowing natural successional processes to take place may, in time, reduce depth of edge influences. Regardless, given the dramatic under-representation of upland hardwood forest in PEI's natural areas network (Arsenault, 1997), protecting these sites must remain high priority. While government and conservation groups may preferentially choose sites in which all sides are greater than 240 m, smaller sites should not be routinely discounted as potential protected areas. For example, a narrow band of riparian forest (less than 50 m wide as measured on the provincial Geographic Information System forest layer) in western PEI has this province's only known population of *Polystichum braunii* (Braun's Holly Fern), as well as a number of other provincially rare plants (MacQuarrie and Schaefer, 2001). Similarly, two sides of the 4 ha Royalty Oaks Natural Area are less than 200 m, but this is among the last remaining stands of merchantable oak on PEI (UPEI, 1982). Clearly, smaller sites can have conservation value and must not be ignored.

3.0 AND SOME RAN WILD

3.1 Introduction

Movement of species beyond their native ranges has been essential to the development of agriculture and industrialized society. Every day we rely on these benign introductions for food, clothing, medicine and a host of other uses. However, when an introduced species escapes the barriers of cultivation and develops the potential to cause environmental or economic harm, or harm to human health, it is considered invasive (Office of Technology Assessment, 1993).

Biological invasions are considered second only to habitat loss as the greatest threat to biodiversity on both a global and local scale (Cronk and Fuller, 1980; Center, Frank and Dray, 1995; Vitousek *et al.*, 1996; Baker, 2001). Globally, the human-caused change in species distribution seen over the past few centuries has been compared to that brought about by cycles of glaciation and deglaciation, even though it has occurred in a fraction of the time (Mack *et al.*, 2000). The intentional and accidental transportation of plants and animals around the globe is said to be resulting in homogenization of Earth's wildlife and habitats (Mooney and Hobbs, 2000). Some predict this will result in largescale loss of natural resource industries such as farming, fishing and forestry in some regions (Mack *et al.*, 2000).

On a more local scale, invasive organisms can endanger native plants, animals and habitats through displacement of or hybridization with native species, spread of pathogens and alteration of ecosystems (Cronk and Fuller, 1980; von Broembsen 1989; Woods, 1993; Campbell, 1997; Reichard and White, 2001). For example, non-native plants have displaced native plant communities in more than 437,000 km^2 of grasslands and wetlands in the United States (Campbell, 1997); are considered threats to nearly one-fifth of plants considered endangered or threatened in Canada and the United States (Haber, 1998); and are cited as serious problems in more than half of Canada's national parks, including remote wilderness areas such as Kluane and Pacific Rim (Parks Canada, 1998). Furthermore, some are also vectors of devastating pathogens such as chestnut blight (von Broembsen, 1989).

Biological invasions also incur enormous economic expense. It has been estimated that the costs directly attributable to invasive species in the United States alone exceed $125 billion annually (Baker, 2001). For example, control of individual species such as *Hydrilla verticillata* (Hydrilla) in the United States can cost as much as $25 million each year (Mullin *et al.*, 2000).

The enormity of the biological and economic impacts of invasive species is made more impressive by the fact that this is the legacy of only a small proportion of the species that are introduced. Given that many species do not survive the trip to a new location, and those that do often face a host of biological, physical and climatic obstacles upon their arrival (Mack *et al.*, 2000), the extent of the invasive species problem is remarkable. While it is impossible to know how many species begin the journey from their native ranges but perish en route, the "tens rule" has been shown to apply to many groups of organisms, including species introduced to North America (Williamson and Fitter, 1996). In its simplest form, the tens rule predicts that 10% of introduced species will escape, 10% of these escapes will become naturalized, and 10% of naturalized species will become problems. As with most rules, this should be treated as a relative guide rather than a firm number, and some authors prefer to think of the tens rule as meaning “a small proportion”, between 5% and 20% (Williamson and Fitter, 1996). This broader interpretation takes into account sampling error, variances in how the various terms of introduced, naturalized and invasive are defined, and resulting differences in classification among authors (*e.g.* one author’s naturalized taxon may be considered invasive by another).

For example, Canada’s flora includes at least 884 introduced species that have become naturalized (Scoggan, 1979). The tens rule would lead one to expect approximately 88 problematic invasive species; White *et al.* (1993) identify 57 introduced taxa known to have a negative impact in natural habitats in Canada, which is consistent with the broader interpretation of the tens rule. It is important to note that the tens rule may not be applicable to all groups of organisms. For example, plants introduced for agriculture are selected because they are able to tolerate the climate of the new area, and it would be reasonable to expect a larger proportion of introduced perennial crop plants to become naturalized. Similarly, vigorous testing of organisms introduced for biological control is designed to ensure they do not become problematic in natural habitats, and a smaller proportion (ideally none) of these introductions should adhere to the tens rule (Williamson and Fitter, 1996).

Understanding why some species are successful invaders while most are not is important to predicting which taxa will be problematic. Among other things, such predictive ability would be useful in preventing future invasions through such means as helping the horticultural industry in assessing which new plants could be safely introduced for landscaping, or allowing land managers seeking biological control for pests to select species which are least likely to escape (Mack *et al.*, 2000). As research and use of genetically modified organisms increases, so does the need for a predictive model (Williamson, 1989).

While anthropogenically affected habitats often have a higher proportion of non-native species than natural areas (Hobbs and Huenneke, 1992; Williamson, 1996), it is difficult to separate cause and effect. There is debate between those who view disturbed habitats as being more easily invaded (*e.g.* Hobbs and Huenneke, 1992) and those who suggest that, because of human use, such habitats have simply had contact with greater numbers of non-native species (*e.g.* Mooney and Drake, 1989; Lonsdale, 1999). Linked to this is the prediction that complex and diverse communities will be resistant to invasion (Elton, 1958). While this has been supported by some studies (*e.g.* Tilman, 1997) there are many examples of species-rich habitats being more susceptible to invasion than their comparatively depauperate counterparts (Center, Frank and Dray, 1995; Stohlgren *et al.*, 1999; Lonsdale, 1999). Further complicating efforts to predict habitat vulnerability are studies that have shown comparable habitats such as temperate grasslands on different continents are not equally vulnerable to invasion (Mack, 1989). The lack of clear consensus among studies has lead some to conclude that, in general, habitat complexity is not a good predictor of whether an introduction will be successful (Williamson, 1996).

While habitat is not a good predictor, morphology can suggest warning signs for invasion. As outlined in Table 3.1, traits such as high seed production, small seed mass,

Table 3.1: A summary of traits that contribute to the success of invasive plants and the presumed advantage conferred by each.

Trait	Advantage
Broad habitat requirements	Increased probability of finding suitable habitat in the new community.
Broad germination requirements	Increased probability of finding suitable environmental conditions in the new community.
Short life cycle (early germination, fast growth, early flowering and seed production)	Ability to use available resources (light, nutrients, moisture) before competition from other vegetation in the community. Increased ability to out-compete other vegetation either vertically (*e.g.* growing taller, reaching more light, shading lower vegetation) or horizontally (*e.g.* spreading throughout the community consuming limited space).
High seed production	Rapid expansion of the population, even if seed viability is low.
Small seed mass	Increased number of seeds produced, greater dispersal capacity (Guo *et al.*, 2000, found small seeded species produce more seeds).
Seed adaptations (*e.g.* hooks, wings, palatable fruit)	Increased ability to disperse seed, sometimes via native animals (ants, birds, mammals), contributing to rapid dispersal of the population over large areas.
Vegetative reproduction including rhizomatous and stoloniferous growth	Rapid expansion of the population, establishment of dense populations that can exclude native species, ability to spread via fragmentation. Mechanical control of such species can contribute to their spread.
Suckering growth	Rapid return of the population after mechanical control such as cutting or natural grazing/browsing.
Vine-like growth	Increased ability to out-compete other vegetation either vertically (*e.g.* climbing up and/or covering other species, depriving them of light or moisture) or horizontally (*e.g.* sprouting at nodes and spreading rapidly and densely throughout a community).
Positive feedback	The establishment of some non-native species can alter soil moisture, nutrients or little buildup in a way that facilitates its own spread (*e.g. Bromus japonicus* [Japanese Brome], Whisenant, 1999).

fast growth, early flowering, vegetative reproduction and broad germination and habitat requirements can each give a non-native species an advantage in its new habitat (Baker, 1965; Rejmánek and Richardson, 1996; Parendes and Jones, 2000). It is important to note that no one plant is likely to exhibit all these traits, and a species with few or none of these attributes may still be invasive. While Noble (1989) suggests such factors are more useful as potential warning signs of invasion rather than as true predictors, Reichard and Hamilton (1997) showed that it is possible to predict successful invasions based on morphological traits and global distribution.

In addition to the morphological advantages it may have, a non-native species may be freed from homeland pressures such as predation or disease through its arrival in a new habitat. A prime Canadian example is *Lythrum salicaria* (Purple Loosestrife), which in its native European range is controlled by insects which did not occur in North America until they were introduced in 1992 for biological control (Blossey and Nötzold, 1995). In the absence of such predators, *L. salicaria* spread rapidly.

Once they reach their new habitats, some non-native species may grow faster, produce more seed, have greater fitness and live longer (Blossey and Nötzold, 1995). Escape from predation, competition and disease may give non-native species a competitive advantage even if they have no particularly advantageous morphology (Mack *et al.*, 2000).

While morphology and lack of biological constraints contribute to the success of an invasive species, even an ideal invader may be unable to become established because of the unpredictable variables of chance and timing (Crawley, 1989). The occurrence of a chance meteorological or geological event to which native species have adapted but the invader has not can prevent what would otherwise have been a successful invasion. Similarly, an invader's arrival too early in the season may mean the required resources are not yet present; too late, and native competitors or predators may be too abundant to allow establishment (Crawley, 1989).

Although the issue of invasive species is gaining increasing attention among the scientific community (Mooney and Hobbs, 2000) and the number of articles written on the topic has been growing exponentially (Reichard and White, 2000), the general public remains largely unaware of the biological and economic impacts of invasions (Vitousek *et al.*, 1996; Colton and Alpert, 1998). Of ten studies that considered the forests of Prince Edward Island (Taschereau, 1974; UPEI, 1982; Parks Canada, 1984; PEI Forest Biomass Inventory, 1991; Sobey, 1993, 1995a, 1995b; Hovingh, 1995; MacQuarrie, Schaefer and Schoenrank, 1999 and 2000), only the latter two commented specifically on the presence and potential impacts of non-native species.

Recently, a gap analysis of Prince Edward Island's protected areas showed that upland hardwood, remnant pockets of Acadian Forest, are under-represented in the provincial natural areas network (Arsenault, 1997). Priority has thus been placed on identification, mapping and conservation of these areas, defined as those having *Fagus grandifolia* (American beech), *Acer saccharum* (sugar maple), and *Betula alleghaniensis* (yellow birch) comprising at least 30% of the stand, and the stand being at least 14 m tall and 80 years old in 1990 (Island Nature Trust, 2000). Although these areas are thought to be the best remaining areas of PEI's pre-colonial forest cover, there is no information about the presence of invasive vascular plant species in these areas or what morphological adaptations such species may have. The main objectives of this study are to identify: (1) whether non-native species that invade PEI Acadian Forests have morphological features that give them an advantage over native species; and (2) whether seed weight and viability of selected species differs between edge and interior plots.

3.2 Materials and Methods

As described in section 2.2, six Acadian forest study sites, each with a straight, well-defined edge and interior habitat at least 300 m from an edge in any direction, were selected for study. Three equidistant transects on an azimuth perpendicular to the edge were established in each study site, and ten 100 m^2 circular sample plots were established along each transect at distances of −5.7 m (in adjacent habitat) 5.7 m, 20 m, 40 m, 80 m, 120 m, 160 m, 200 m, 250 m, and 300 m from the edge. In each plot, all vascular plants were identified to the species level and a visual estimate of percent cover to the nearest percent was made. When positive identification was not possible in the field, specimens were collected and labelled for later examination using standard regional floral keys, primarily Zinck (1999), Hinds (2000) and Scoggan (1979).

As reported in section 2.3.3, two species - *Veronica officinalis* (Common Speedwell) and *Hieracium lachenalii* (Hawkweed) - were the most abundant non-native species present in sample plots, with *V. officinalis* present 250 m from an edge and *H. lachenalii* persisting to 300 m (Table 2.5). Together, *V. officinalis* and *H. lachenalii* covered 559 m^2 of the area sampled, and represented 75% of the total non-native cover found (Figures 2.6 and 2.7). These two species were selected for additional study.

In September 2000, the Borden study site was re-visited and seed heads were collected from the focal species in both edge and interior habitats. *H. lachenalii* was not found in the specific edge plots established for this study (Table 2.5), but was present along a road adjacent to this study site; that roadside population was sampled as edge habitat.

Edge habitats were immediately adjacent to anthropogenic lands (*i.e.* road, shale pit, agricultural field) and had tree canopy closure of less than 30% as measured with a Model C spherical densiometer (Forest Densiometers, Bartlesville, OK). Interior habitats were 300 m and 250 m from an edge for *H. lachenalii* and *V. officinalis* respectively and had tree canopy closures of more than 90%. In both edge and interior habitats, the entire mature seed head was collected from 20 plants; because *Veronica* spreads vegetatively, care was taken to select disparate individuals. Seed heads from each species were placed in separate Ziploc® bags and air-dried at room temperature for 14 days. The bags were then sealed and frozen at -7°C for six months to simulate vernalization or overwintering conditions (Baskin and Baskin, 1998).

Overwintered seeds were thawed at room temperature and 100 seeds were randomly selected from each species and each habitat (a total of 400 seeds: *Veronica* at edge and interior; *Hieracium* at edge and interior). These were weighed using a Mettler model AE 100 scale (Mettler Instruments, Greifensee, Switzerland). Following testing of the assumptions of parametric statistics, differences between edge and interior habitats were evaluated with t-tests and differences among the six combinations of species and habitats were tested with ANOVA and Tukey's post-hoc. Parametric testing was done with Systat ver. 8.0.

From the remaining seed collections, seeds were selected from each species at edge and interior habitats for viability testing with 1% 2,3,5-triphenyl tetrazolium chloride (TTC) solution. TTC staining is a common method for assessing seed viability (Delpech, 2000). If tissues are respiring, the solution turns pink, staining the tissues red; the deeper the red, the greater the metabolic activity (Delpech, 2000).

Firm *H. lachenalii* seeds were selected (soft seeds were hollow, indicating no embryo present) and soaked on filter paper overnight. The achene covering (ovary wall) was manually removed and the thin, transparent seed coat was removed from the embryo. Embryos were then placed in the tetrazolium solution at 35°C for two hours before being evaluated as viable or not. *V. officinalis* seeds were dissected from the ovary wall and soaked on filter paper overnight. The endosperm covering was removed from the embryo, which was placed in the tetrazolium solution for three hours at 35°C before being evaluated for viability.

Because not all embryo excisions were successful, final sample sizes were not equal between species or habitats. Thirty five seeds of *H. lachenalii* from interior plots and 40 seeds from edge plots were tested; 50 *V. officinalis* seeds from interior plots and 33 seeds from edge plots were tested. For analysis, edge habitat was coded 0 and interior habitat coded 1; non-viable seeds were coded 0 and viable seeds coded 1. These categorical data required the use of non-parametric statistics. Mann-Whitney U-tests using Prism ver. 3.0 were used to compare results from edge and interior habitats for each species and Kruskall-Wallis was used to test for differences in viability between species in each habitat.

3.3 Results

Veronica officinalis seeds weighed significantly less in interior habitats (1.07 mg ± 0.08 mg) as compared to edge habitats (1.34 mg ± 0.09 mg; t-test, $p<0.0001$; Figure 3.1). *Hieracium lachenalii* seeds weighed slightly more in interior (3.58 mg ± 0.5 mg) as compared to edge habitats (2.56 mg ± 0.7 mg), but this was not statistically significant (t-test, $p=0.1035$; Figure 3.1).

Although seed viability was slightly higher in interior habitats for both species (Figure 3.2), this was not statistically significant for either *H. lachenalii* (Mann-Whitney U-test, $p=0.0804$) or *V. officinalis* (Mann-Whitney U-test, $p=0.2550$). There were no significant differences in viability between species (Kruskall-Wallis $p=0.1069$).

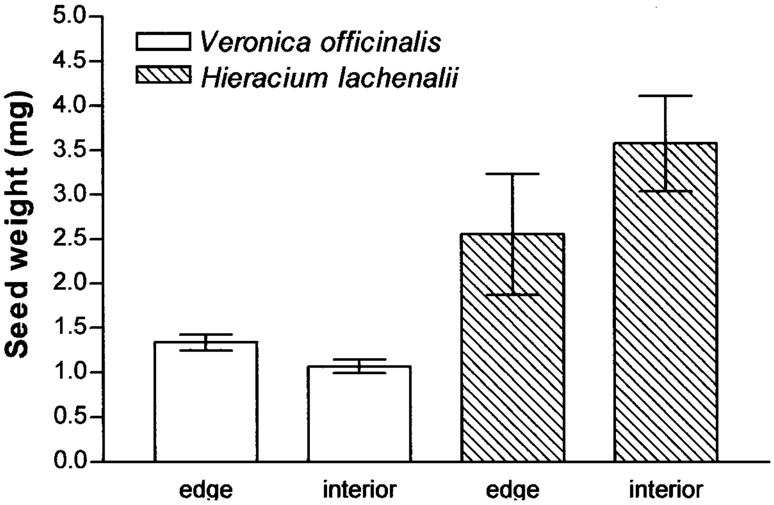

Figure 3.1: Seed weights (mg ± standard deviation) from edge and interior habitats for two species found to be invasive in Prince Edward Island Acadian forests. *Veronica officinalis* seeds weighed significantly less in interior habitats ($p<0.001$), while no significant difference was found between habitats for seeds of *Hieracium lachenalii* ($p=0.1035$).

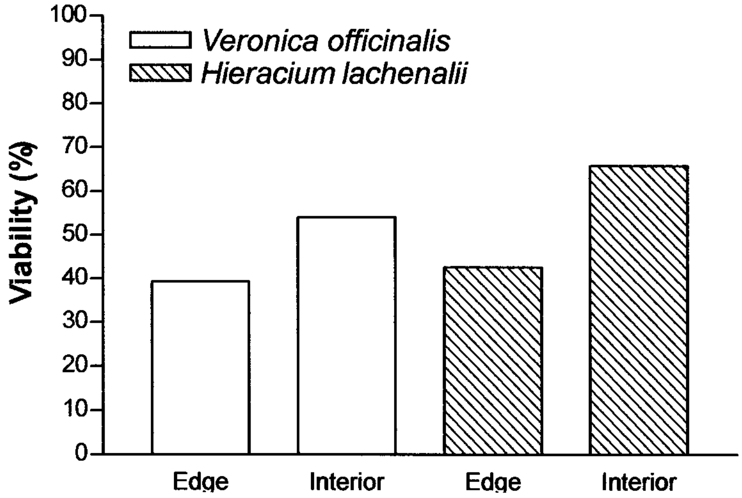

Figure 3.2: Results of seed viability testing using a 1% 2,3,5-triphenyl tetrazolium chloride solution. Viability was not significantly different between edge and interior habitats for either *Veronica officinalis* (p=0.2550) or *Hieracium lachenalii* (p=0.0804). There were no differences in viability between species in either habitat (p=1069).

3.4 Discussion

Both *Veronica officinalis* and *Hieracium lachenalii* exhibited traits characteristic of invasive species.

3.4.1. Veronica officinalis

As a small-seeded perennial, *V. officinalis* exhibits one of the traits that contributes to the success of invasive plants. Small seeds are reported to be more readily dispersed, more persistent in soil seed banks and less susceptible to predation by birds and small mammals (Parendes and Jones, 1999; Guo *et al.*, 2000). The lower weight of *V. officinalis* seeds from interior habitat (Figure 3.1) could support the notion that smaller seeds are dispersed more widely (Guo *et al.*, 2000), however this would assume that interior *V. officinalis* plants were descendants of those at the edge and that smaller seeded parents give rise to smaller seeded progeny. There is no empirical evidence to support either assumption, and the smaller seeds of interior *V. officinalis* plants are more likely attributable to environmental factors such as nutrient or light availability.

Shading has been shown to influence the proportion of biomass devoted to sexual reproduction (Dale and Causton, 1992c and 1992d). Additionally, mean seed mass in *Veronica* species (including *officinalis*) has been shown to be negatively correlated with ash content, which is higher in both vegetative and reproductive tissues when members of this genus are grown under shade (Dale and Causton, 1992d). Based on this evidence and observations from the PEI study, it is probable that the difference in seed weights between *V. officinalis* in edge and interior habitats is due to environmental factors rather than dispersal ability of the seeds. Seed size has also been shown to be negatively correlated with seed number; in general, small-seeded species produce larger numbers of seeds (Guo *et al.*, 2000). Production of large numbers of seeds may also offset low seed viability in *V. officinalis*, which ranged from 40% to 54% in this study (Figure 3.2).

Veronica is among the many genera of myrmecochores (ant-dispersed taxa) in temperate deciduous forests (Baskin and Baskin, 1998). Seed dispersal by ants is important in eastern North America, and it is estimated that these insects contribute to the distribution of as many as 30% of the spring flowering forest plants of eastern North America (Baskin and Baskin, 1998; Morales and Heithaus, 1998). As a myrmecochore, *Veronica* exhibits a second trait that contributes to the success of invasive plants (Table 3.1): the ability to use local animals to disperse seed.

Vegetative reproduction is important in *Veronica* species (Dale and Causton, 1992a), giving *V. officinalis* a third advantageous trait of successful invaders. Although Dale and Causton (1992c) suggest apical growth in *V. officinalis* is more vertical than that of related species, PEI specimens observed in this study were strongly horizontal and formed dense mats of vegetation on the forest floor (Figure 3.3). Efficient vegetative reproduction in *V. officinalis* enables plants to establish easily from cuttings (Dale and Causton, 1992a). This trait may also allow populations to expand or new populations to establish from plant fragments broken from the colony and transported by animals, wind or water. As illustrated in Figure 3.3, *V. officinalis* also exhibits a related, fourth advantageous trait: trailing, vine-like growth (Table 3.1).

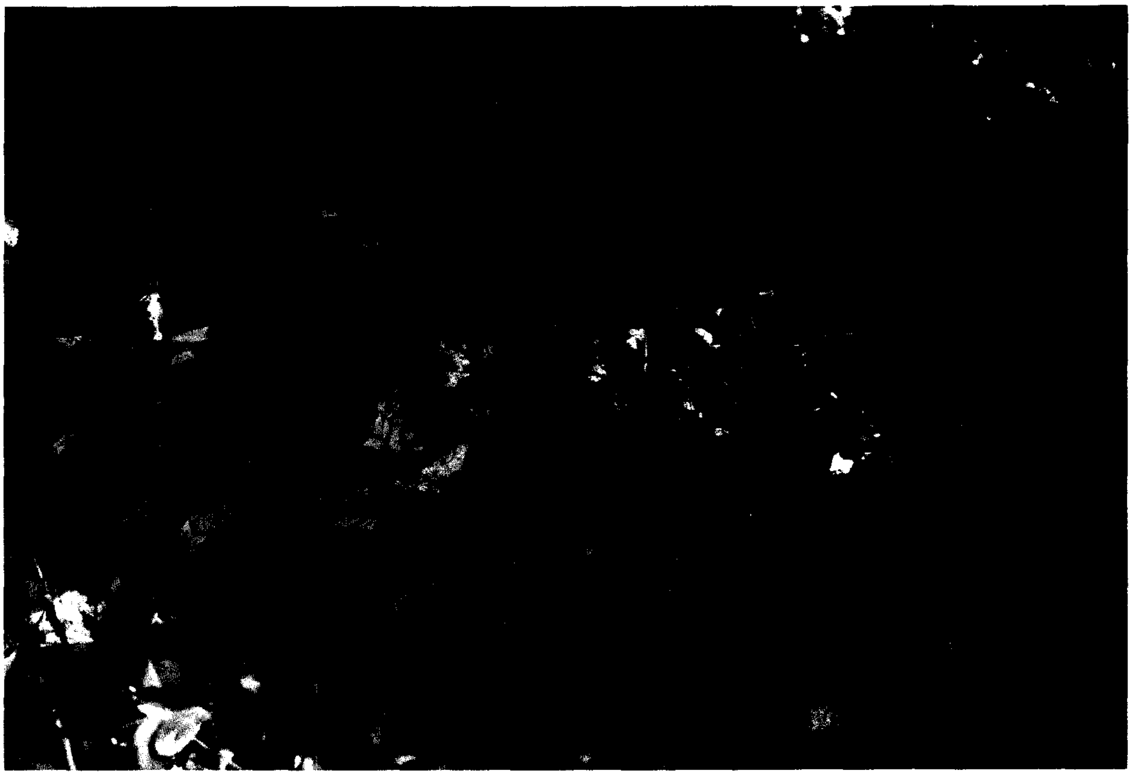

Figure 3.3: *Veronica officinalis* in a PEI Acadian forest study site. Note the horizontal and dense, mat-like growth.

Finally, the habitat requirements of *V. officinalis* may be broader than reported in studies from its native range. Dale and Causton (1992a through 1992d) examined a suite of physiological and morphological responses to shading in *V. officinalis* and two related species in Wales, within the native Eurasian range of these taxa. In their studies, Dale and Causton (1992a through 1992d) found *V. officinalis* restricted to open and often sparsely vegetated areas and rarely persisting in deeply shaded communities. Their analysis of a range of factors (including growth rate, leaf area ratio, leaf weight ratio, root weight ratio and allocation indices for biomass and nutrients) in *Veronica* species under full light and shaded conditions repeatedly led to the conclusion that *V. officinalis* is not able to tolerate long-term shading. In one study (reported in Dale and Causton, 1992c and 1992d), *V. officinalis* failed to grow in shade because of predation by slugs, which preferentially selected this species over the other two (*V. chamaedrys* and *V. montana*).

The shade intolerance of *V. officinalis* reported by Dale and Causton is not consistent with the results of the PEI study or other North American reports. On PEI, this species was found in Acadian forest study sites under dense canopy closure (>90%) 250 m from an edge. Burke and Nol (1998) similarly report *V. officinalis* in their innermost forest plots, 100 m from an edge, where light intensity was reduced to just over 10% of that recorded in adjacent, non-forested habitat. Stapleton *et al.* (1998) cite this species as having invaded undisturbed habitats in Cape Breton and as being more shade tolerant than other non-native species.

This difference between the reported shade tolerance of *V. officinalis* in its Old World (native) and New World (non-native) habitats could be a result of it being freed from predators, such as the slugs reported by Dale and Causton (1992c and 1992d). While slugs were present in PEI Acadian forest study areas, there was little or no predation by these or other invertebrates on *V. officinalis* (personal observation). However, Dale and Causton (1992a through 1992d) found a host of other factors that led to the conclusion that *V. officinalis* was not shade tolerant. For example, the failure of *V. officinalis* to develop morphological adaptions to shade such as increased leafiness or changes in internode lengths and branching patterns were cited as support of shade intolerance in this species. Dale and Causton (1992d) concluded that even if slug predation did not occur, *V officinalis* would persist only where shade was minimal.

Genetics may better explain this species' shade tolerance in North America. Dale and Causton (1992a) sought to minimize genetic variability and the *V. officinalis* propagated in their study was collected from a relatively sunny habitat (the south facing slope of a rocky outcrop). Interspecific variation in tolerance of and response to varying environmental conditions is common, and frequently results in different ecotypes (Salisbury and Ross, 1992). Although *V. officinalis* did not adapt to shaded conditions during the 18 months of Dale and Causton's study (1992a through 1992d), it is clearly shade tolerant in North America. Lack of predators may have given North American *V. officinalis* the opportunity to become established in shaded conditions, from which it was able to develop a shade tolerant ecotype. The notion that evolutionary adaptation and the development of genetically different ecotypes can assist invasion has been termed "evolution of increased competitive ability" and observed in both woody and herbaceous species (Siemann and Rogers, 2001; Blossey and Nötzold, 1995).

Finally, *V. officinalis* is a garden plant. If its provenance on Prince Edward Island is a result of horticulture, hardier individuals may have been selectively brought to this province giving this species an added genetic advantage. Regardless of the reason for *Veronica*'s increased shade tolerance in North America, it does thrive in a range of habitats, giving it a fifth trait of successful invaders (Table 3.1).

3.4.2 ***Hieracium lachenalii***

Hieracium lachenalii[1] is a perennial member of the Asteraceae, one of a handful of families responsible for many of the most invasive species (Mack *et al.*, 2000). The notoriety of Asteraceae is likely due in part to the family's large size (more than 19,000 species worldwide [Zomlefer, 1994]), popularity as garden plants (Mack and Lonsdale, 2001), and seed adaptations that aid in dispersal by animals or wind (Zomlefer, 1994).

Seeds of *H. lachenalii* were significantly heavier than those of *V. officinalis* (Figure 3.1, page 91), and in the high end of the range of seeds examined by Guo *et al.* (2000). However, seed weights have been estimated to range from 0.016 mg in members of the *Orchidaceae* to nearly nine kilograms (9,000,000 mg) in *Arecaceae* (Mauseth, 1988). With an average weight of 3.58±0.5 mg (interior sample, Figure 3.1), *H. lachenalii* is not an especially large or heavy seed. It weighs approximately one-tenth that of grain seeds (Alberta Agricultural Food and Rural Development, 2001) and one-third that of related *Liguliflorae* such as *Tragopogon pratensis* (Goat's Beard; 100 seeds collected and weighed

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[1] *Hieracium lachenalii* is synonymous with *H. acuminatum* (Catling, Erskine and MacLaren, 1985) and includes *H. vulgatum* (Zinck, 1998).

for comparison).

Each *H. lachenalii* seed has a pappus of fine hairs to facilitate wind dispersal and rows of tiny barbs to assist in dispersal by animals. The wind-dispersal mechanism is highly effective: light agitation of *H. lachenalii* with mature seed causes large numbers of them to fall from the plant. Even a slight breeze can carry these seeds hundreds of metres (personal observation). Although dispersal by animals was not observed, the barbs did allow the seeds to cling lightly to skin, and are likely even more effective in attaching to fur or feathers. Animal transport is common among *Hieracium* species (Rice and Wilhelm, undated), and the barbed seeds have been reported to stick to clothing and vehicles, in addition to hair, fur or feathers (Callihan *et al.*, 1997). *H. lachenalii* has two seed adaptations that assist dispersal and contribute to successful invasion (Table 3.1).

H. lachenalii is among the largest of this region's hawkweeds, generally more than 0.2 m and often up to 1 m tall (Hinds, 2000; Zinck, 1998). This may give it a competitive advantage over smaller members of the genus. On taller plants, seed heads may be exposed to more wind and released seeds may travel further on air currents. However, PEI's native species (*H. canadense*, *H. scabrum* and *H. umbellatum*) are similar in height to *H. lachenalii* (Zinck, 1998; Hinds, 2000); any advantage conferred by plant size would thus only apply to competition with other non-natives.

Vegetative growth plays a minimal role in North America's native *Hieracium* species but is very important to non-native members of this genus (Callihan *et al.*, 1997); *H. lachenalii* produces extensive networks of stolons (personal observation). It has been estimated that once a population of *Hieracium* becomes established, less than 2% of the reproduction within the colony is from seed (Callihan *et al.*, 1997). Unlike *V. officinalis*, in which vegetative growth results in dense mats of connected plants, *Hieracium* stolons do not persist once a new plant becomes established (Callihan *et al.*, 1997). However, fragments of *Hieracium* stolons, rhizomes or roots can develop into new plants (Callihan *et al.*, 1997). This genus thus has a second of the traits that contribute to successful invasion (Table 3.1).

In addition to vegetative growth, apomixis is common among *Hieracium* (Hinds, 2000; Callihan *et al.*, 1997). Asexual seed production has the advantage of allowing a plant to reproduce in the absence of pollinators, and this trait is common in many flowering plants particularly members of *Poaceae*, *Rosaceae* and *Asteraceae* (Sengbusch, 2001). The cosmopolitan occurrence of apomixis in both native and non-native species, coupled with the fact that many species are able to reproduce sexually without pollinators, would suggest that this does not confer a competitive advantage to *H. lachenalii.*

Finally, like *V. officinalis*, *H. lachenalii* seems to have broad habitat requirements. In its native Eurasian range, it is a plant of meadows and this species is considered invasive in meadows in southern Ontario (Urban Forest Associates, 2002). In the PEI study, it was found in Acadian forest study sites 300 m from an edge in canopy cover greater than 90%. This represents distinct habitats, with great differences in light, soil temperature and plant communities.

3.4.3 Summary of traits of species found to be invasive in PEI Acadian forest study sites

As listed in Table 2.5, 15 non-native species were found within Acadian forest study sites in Prince Edward Island. *V. officinalis* and *H. lachenalii* were the most invasive in terms of both distance penetrated and area covered and so were selected for additional study, however each of the remaining 13 species exhibited traits that contribute to successful invasions. A summary of these traits as observed during this study or reported in the literature is given in Table 3.2.

3.4.4 Relation of results to study objective

Objective 1: Identify whether non-native species that invade PEI Acadian Forests have morphological features similar to those outlined in Table 3.1. Each of the two major non-native species found to invade PEI's Acadian forests has morphological features that may facilitate invasion. *Veronica officinalis* had small seed mass (which is correlated with high seed production [Guo *et al.*, 2000]), seed dispersal aided by ants, vegetative reproduction, vine-like growth and the ability to tolerate a broad range of habitats. *Hieracium lachenalii* had a pappus of fine hairs to aid seed dispersal by wind, barbed seeds to aid in dispersal by animals, small seed mass, vegetative reproduction and broad habitat requirements.

Objective 2: Identify whether seed weight and viability differs between edge and interior plots. Seeds of *Veronica officinalis* from interior plots were significantly lighter than those collected from edge habitats, and this is likely due to environmental factors, particularly light. There was no significant difference in seed weight in *Hieracium lachenalii* between edge and interior habitats, and no significant differences were found in seed viability in either species between edge and interior habitats.

Table 3.2. Traits that contribute to successful invasion that were exhibited by 15 non-native species found within PEI Acadian forest study sites. Information is from personal observation in the field, USDA Natural Resources Conservation Service (2001) and Royer and Dickinson (1999). The key to species codes is given in Appendix 1. X indicates the species exhibits that trait.

TRAIT *(see Table 3.1 for details)*	**GALETETR**	**HIERAURA**	**HIERCAES**	**HIERLACH**	**LEUCVULG**	**MALUPUMI**	**PLANMAJO**	**POAPRATE**	**RANUA CRI**	**RANUREPE**	**RIBESATI**	**SORBAUCU**	**TARAOFFI**	**VEROOFFI**	**VICICRAC**
Broad habitat requirements	X	X	X	X	X		X		X	X		X		X	
Broad germination requirements	X	X	X	X	X		X		X	X		X		X	
Short life cycle							X	X					X		
High seed production								X					X	X	
Small seed mass		X	X	X				X					X	X	
Seed adaptations		X	X	X		X					X	X	X	X	
Vegetative reproduction		X	X	X				X	X	X	X			X	
Suckering growth						X						X			
Vine-like growth											X			X	X
Positive feedback															X
Number of study sites in which species was found	2	3	6	2	4	1	3	1	4	1	2	4	3	5	4

4.0 CONCLUSION

4.1 The future of invasive species

The issue of invasive species is receiving growing attention in North America. For example, in 2001, the United States launched its first National Management Plan to control the introduction and spread of non-native species (Baker, 2001). That same year, Canada's federal, provincial and territorial ministers of natural resources ordered a plan to address the issue of invasive species in this country by autumn, 2002 (National Workshop on Invasive Alien Species, 2001 [draft report]). Individual provinces have prepared lists ranking the relative invasiveness of non-native species (*e.g.* Urban Forest Associates, 2002) and some have developed plans to prevent further introductions and control the spread of invasives already present (*e.g.* Havinga *et al.*, 2000). In 2002, the issue of invasive species was the special topic for "Envirothon" (an international educational competition among high schools) and it will be the theme of Canada's National Wildlife Week in 2003 (S. Baumgartner, personal communication). In a special issue of Bioscience devoted to the topic of invasive species, Reichard and White (2001) reported that the number of non-scientific articles on this topic has increased from fewer than 50 in 1986/87 to more than 250 in 1995/96. Clearly, there is a growing interest in this issue among both the scientific community and the general public.

Despite this interest, accidental and intentional introduction of non-native species continues. The horticultural trade is a major source of intentional introductions (Reichard and White, 2001); it is estimated that in 1993, 456 million non-native plant individuals were imported to the United States for horticulture (Center, Frank and Dray, 1995). New accidental introductions continue to arrive, and those already established in North America continue to expand their ranges. For example, in the past few years three invasive aquatic species have expanded their range north along the eastern seaboard and appeared in waters around Prince Edward Island: *Codium fragile tomentosoides* (Oyster thief), *Styela clava* (clubbed tunicate) and *Carcinus maenas* (green crab) (Fisheries and Oceans Canada, 2002).

Increasing globalization of trade and pleasure travel is expected to increase the spread of non-native species (Kolar and Lodge, 2000). Increased trade with jurisdictions that have temperate climates similar to Canada's (for example, Russia and China) suggests that more of these non-native species may become invasive (Allen, 2001). Additionally, it has been suggested that increasing levels of carbon dioxide in the atmosphere may change the abundance and distribution of some invasives (Dukes, 2000). Reichard and White (2001) estimate that as many as 22,000 plant species have yet to be introduced to new ranges, and suggest that as many as 1,000 of these have the potential to become invasive.

Prevention of new introductions is a top priority for invasive species management plans (Havinga *et al.*, 2000; Mack *et al.*, 2000; National Workshop on Invasive Alien Species, 2001 [draft report]). Both Canada and the United States have phytosanitary guidelines aimed at preventing problematic species and pathogens from entering North America. In Canada, this is governed by the Canadian Food Inspection Agency (CFIA), which calls itself the national plant protection organization of Canada (CFIA, 2001). CFIA's list of regulated pests focusses strongly on pathogens of commercial crops such as apple, potato and grape and on forest pathogens (CFIA, 2002a). While it does control import and movement within Canada of invasive taxa such as *Berberis* (Barberry), it is because these species are alternate hosts of diseases of forests or agricultural crops (CFIA, 2002b), not because they are considered invasive (Havinga *et al.*, 2000; Urban Forest Associates, 2002). For example, *Berberis thunbergii* (Japanese barberry) is resistant to black stem rust disease which infects wheat and oats, and thus is exempt from CFIA regulations that restrict other members of this genus (CFIA, 2002b), even though this species is considered invasive in Ontario (Havinga *et al.*, 2000; Urban Forest Associates, 2002).

Canada's phytosanitary regulations do not appear to adequately guard against species that may invade natural habitats. Campbell (2001) reports that United States Department of Agriculture phytosanitary safeguards are similarly ill-equipped to prevent invasion, and Mullin *et al.* (2000) note that many invasive species are not restricted by federal legislation in the USA. There appears to be a large gap between recognizing that prevention is an important component of invasive species management and implementing effective screening, quarantine and controls. The draft report from the National Workshop on Invasive Alien Species (2001) places emphasis on risk analysis and application of the precautionary principle ("guilty until proven innocent") in dealing with proposed introductions, which may reduce the number of intentional introductions that become invasive. The proposed national plan to address invasive species can only improve the current state of prevention in Canada.

While prevention is the best long-term and most cost-efficient strategy to deal with invasive species (Mack *et al.*, 2000), no preventative measures will be 100% effective.

Even with increased regulation of international trade and restrictions on import and movement of problematic species, some new species will still arrive. For example accidental and intentional introductions by individuals (such as global travellers) or range expansions by invasive species already in North America is virtually impossible to control. If a new invader is detected early, before it has become extensively established, eradication is sometimes possible (Mack *et al.*, 2000). The draft report of the National Workshop on Invasive Alien Species (2001) recommends that Canada's national plan include provisions for monitoring and rapidly responding to eradicate newly-detected invasions. Unfortunately, the huge economic expense required to control existing infestations (Baker, 2001) combined with the difficulty in convincing regulatory bodies to act <u>before</u> a non-native species becomes invasive (Mack *et al.*, 2000) and the overwhelming volume of material being transported (Mullin *et al.*, 2000) means that early detection and response will be largely ineffective, as it has been in the United States (Mullin *et al.*, 2000). As demonstrated by funding for endangered species conservation in Canada, government and non-government agencies are more inclined to finance emergency recovery efforts than preventative measures.

When prevention and eradication fail, management is the final option. To help focus limited financial resources where they will be most effective, Havinga *et al.* (2000) have identified the highest-priority (most problematic) invasives in Ontario, and suggested criteria for determining priority areas for control. For example, protected natural areas, sites with rare species, and areas where infestations are not widespread and control or eradication is possible are highest priority. Habitats that are isolated and far from remnant natural areas are low priority. Control of invasive species in these areas is still important, but does not have the same degree of urgency (Havinga *et al.*, 2000). Under this scheme, control of highly invasive species such as many of the non-native *Lonicera* species (honeysuckles) in a natural area would be a high priority project, while control of a potentially invasive species such as *Linaria vulgaris* (Toadflax) in a forest fragment would be lower priority. Other provinces and states have prepared similar lists of priority species to help guide management efforts (*e.g.* Stapleton *et al.*, 1998 in Nova Scotia; Virginia Department of Conservation and Recreation and Virginia Native Plant Society, 2001).

The triad of prevention, eradication and management must be complimented with public support to succeed. If the public does not adequately understand the threat invasive species pose to natural habitats and native taxa, there will be little support to expend public dollars on this issue, restrict access to certain horticultural species, implement new restrictions on international trade, or create buffers around protected areas (as recommended in section 2.4.5). In general, the public does not adequately understand the concept of invasion or its potential consequences (Colton and Alpert, 1998), and increased educational efforts are needed to deter people from buying and planting invasive species (Reichard and White, 2001). Education is a priority in the plan for managing invasive species in Ontario (Havinga *et al.*, 2000), but takes a much lower priority in the draft report of the National Workshop on Invasive Alien Species (2001). In this latter report, education is thirteenth on a list of 15 elements that are to be incorporated in a national framework. Additionally, there is no obvious recognition that education has a role to play in the other elements, such as stewardship and regulation.

The final component of invasive species management is research, which can facilitate prevention, eradication, management and education. Although Australia has implemented a risk assessment system to predict which introductions may become invasive and direct these taxa to quarantine, more information about invasive species is needed to improve the reliability of such an approach (Mack *et al.*, 2000). Devising an early-warning risk assessment system that could predict invasions is key to preventing infestations (Havinga *et al.*, 2000; Mack *et al.*, 2000) and has been identified as an important component of a national invasive species strategy (National Workshop on Invasive Alien Species, 2001 [draft report]). Research into the efficacy of existing eradication and management options has been identified as a priority in the Ontario invasive species strategic plan (Havinga *et al.*, 2000). Integrated pest management and biological control mechanisms have been suggested as appropriate for eradication or management of invasions (Center, Frank and Dray, 1995; Mullin *et al.*, 2000), although some researchers feel that additional research and regulatory controls are needed before largescale adoption of such measures (Simberloff and Stiling, 1996). Increased information about invasions and control will help dispel misconceptions held by both the public and industry. Examples include the myths that non-native species are only invasive in disturbed areas, that gardeners can grow invasive species but prevent them from escaping, or that there are no native alternatives for horticultural uses (Reichard and White, 2001). Additionally, better information about invasions can contribute to development of management strategies that protect natural habitats and taxa without undue or excessive restrictions on horticulture, agriculture or wildlife industries (Mack *et al.*, 2000). It will also provide policy makers with a sound basis on which to make management decisions and allocate public funds. Finally, the success of educational campaigns should be assessed through regular surveys similar to Colton and Alpert (1998) or Reichard and White (2001) to ensure they are having the desired impact.

Preventing new invasions and eradicating infestations will never be possible for all non-native species. Given increasing international trade and travel, it is probable that the problem of invasive species will increase rather than decrease in coming years. In this light, management strategies such as that for Ontario (Havinga *et al.*, 2000) coupled with habitat conservation (section 4.2, below) and the proposed national plan to coordinate and encourage regulations, research and education (National Workshop on Invasive Alien Species, 2001 [draft report]) are among the best options for control of the invasive species problem.

4.2 Recommendations for conservation of Acadian forests on Prince Edward Island

4.2.1 Eradication benefits must outweigh risks

Application of Ontario's invasive species management strategy (Havinga *et al.*, 2000) to the results of the PEI study would suggest that invasive species in Acadian forests are high priorities for control. As Class I and II forests, these areas have high natural value and provide habitat for rare species, and the Townshend study site is a protected natural area. Infestation in these sites was found to be more extensive than has been reported from other hardwood forest areas, and the total coverage of non-native species was 750 m^2 or 4.6% of the 16,200 m^2 area sampled. Extrapolated to the 19,800 ha of Class I and II forest on PEI, this would suggest a provincial infestation of approximately 910 ha. Eradication of non-natives from all Class I and II forests is not feasible, but such control could be possible in high-priority areas such as the Townshend study site.

Attempts at eradication should only be considered if the potential of these non-native taxa to cause environmental harm as suggested below is (or is likely to be) realized. Unintended consequences of removing species in a sensitive natural area could include damage to native flora (including rare species), damage to nests of ground-nesting birds, or fragmenting a species with aggressive vegetative growth and exacerbating rather than alleviating the problem. The benefits of eradication must outweigh the risks.

Determining the impacts of the non-native taxa found in the PEI study was beyond the scope of this work, but it was noted that the common, native *Linnaea borealis* (twinflower) was not present in sample plots with *Veronica officinalis*. *L. borealis* has a growth form similar to that of *V. officinalis* and occupies similar habitat in upland hardwood forests. It is possible that *V. officinalis* is out-competing or otherwise negatively affecting *L. borealis*, but additional study is required to confirm or correct this suggestion. Similarly, *Hieracium* species readily hybridize (Hinds, 2000) and the invasive *H. lachenalii* may hybridize with native species, including the rare *Hieracium umbellatum*. If additional study were to find this is the case, control of the non-native species could be warranted.

4.2.2 Minimum size must not become the ideal

The suggestion of a critical limit for depth of edge influences outlined in section 2.4.5 should not be interpreted as a sharp cut-off point. Clearly, such influences represent a gradient, with changes in the plant community along an edge-to-interior continuum. For the purposes of conservation, larger areas are generally better than small areas (Noss, 1987). This principle of conservation biology can be difficult to apply in a highly fragmented landscape such as Prince Edward Island where large forest blocks are rare and large land mammals ["umbrella species" whose home ranges are often used to suggest minimum or optimal sizes for conservation areas (Noss, 1993)] are absent. However, it is possible to suggest a specific critical limit or size for a potential protected area, where edge influences are minimized and interior habitat exists. This approach was taken in Section 2.

Whenever a conservation guideline is suggested, caution must be applied to ensure the minimum does not become the standard. While the logical leap from "*forest protected areas smaller than 240 m on a side (5.75 ha) are unlikely to include interior habitat*" to "*forest protected areas should be 240 m on a side*" is great, the practical or political distance between these two thoughts can be minuscule. An example of this is World Wildlife Fund (Canada)'s Endangered Spaces Campaign which in 1989 challenged Canada to adequately protect a representative sample of each of this country's 486 terrestrial natural regions by 2000; WWF set an area of 12% as its target for adequate representation of each natural region (World Wildlife Fund, 2000). In many cases, this 12% ***minimum*** target was interpreted by political leaders as a ***maximum*** goal for a jurisdiction, beyond which no further land protection would be needed. This approach was never endorsed by WWF and was clearly not the goal of the Endangered Spaces Campaign (World Wildlife Fund, 2000). Similarly, the suggestion of a ***minimum*** target of 5.75 ha for Acadian forest protected areas must not become an ideal, with little or no effort focussed on securing forests with areas greater than this. Rather, all else being equal, this could be used as a guideline to set protection priorities, or for ecological restoration around smaller sites.

4.2.3 Manage with caution

The results of this study suggest that invasion of forests by non-native species can be more extensive than previously reported and that depth of edge can extend to 120 m. Not only does this have implications for the design of forest protected areas as discussed in section 2.4.2, above, it suggests that traditional management such as trail creation may have a greater footprint than land managers expect. Government and non-governmental groups are taking more care to ensure that rare taxa are not harmed by trail creation. In recent years, it has become more common for such groups to complete a botanical inventory of the trail corridor before construction, but such work is typically limited to the proposed trail bed and a narrow strip on either side that may be disturbed during construction (personal observation). While the large, open adjacent habitats of the five hard-edged sites in this study are not immediately comparable to narrow trail corridors, the embedded edge of Townshend is reasonably similar. Even the most skeptical interpretation of results from this site would identify a footprint of 20 m, much more extensive than the two to three metres suggested by Adkison and Jackson (1996). While additional trail-specific research could better assess their impact on natural areas, land managers should be aware that trails or other openings in the forest may have effects beyond the construction corridor. Creation of trails (edge) in interior forest habitat (greater than 120 m from an edge) would be contrary to conservation in this context.

4.2.4 Class I and II forests are priorities for conservation

Much of Prince Edward Island's pre-colonial forest has been lost, and remnants have been heavily influenced by centuries of anthropogenic use (Sobey, 1999, supported by results of this study). Even so, these areas are descendants of PEI's original forest (Sobey, 1999) and are dramatically under-represented in PEI's natural areas network (Arsenault, 1997). Loss of forest cover to agriculture and blueberry production increased by more than 560% during the 1990s (Island Nature Trust, 1999); two of eight Class I and II forests identified as potential sites for this study were harvested before field research could take place. Finally, these sites are habitat for provincially rare species such as *Listera cordata* (twayblade), *Mitchella repens* (partridgeberry), *Solidago flexicaulis* (zigzag goldenrod) and *Botrychium lanceolatum* (lance-leaved grape fern), all S1 species (extremely rare) identified in this study (Appendix 1). As noted in section 2.4.4, while sites with interior habitat may be preferentially chosen for protection, smaller sites are also important. Permanent protection of remnant Class I and II forests on Prince Edward Island should be a high priority for government and non-governmental conservation groups.

4.2.5 Future research

Areas for additional research suggested by this study include:

(i) Impacts of invasive species on PEI Acadian (upland hardwood) forests and other plant communities;

(ii) Impacts of trail creation and maintenance on PEI Acadian forests;

(iii) Changes in environmental, composite and plant community variables beyond 300 m from an edge (if study sites can be found);

(iv) Comparison of PEI Acadian forests with those at similar latitude and elevation on the mainland to assess species composition and anthropogenic disturbance;

(v) Future replication of this study to assess whether depth of edge creeps inward (or outward) over time.

5.0 APPENDIX 1

A list of codes used to identify taxa and the provincial status (S-rank) and number for each. Numbers apply to Figure 2.10. S-ranks follow Blaney, MacQuarrie and Curley (2000) and are defined by standard Conservation Data Centre terminology as follows:

S1 - extremely rare throughout its range (typically 5 or fewer occurrences or very few remaining individuals). May be especially vulnerable to extirpation.

S2 - rare throughout its range in the province (6 to 20 occurrences or few remaining individuals). May be vulnerable to extirpation due to rarity or other factors.

S3 - uncommon throughout its range in the province, or found only in a restricted range, even if abundant at some locations (21 to 100 occurrences).

S4 - usually widespread, fairly common throughout its range in the province, and apparently secure with many occurrences, but the Element is of long-term concern (*e.g.* watch list) (100+ occurrences).

S5 - demonstrably widespread, abundant and secure throughout its range in the province, and essentially ineradicable under present conditions.

SE - a non-native established in the province; may be native in nearby regions.

S#S# - a range between two consecutive numeric ranks. Denotes range of uncertainty about the exact rarity of the Element (*e.g.* S1S2).

CODE	NAME	S-RANK	NUMBER
ABIEBALS	*Abies balsamea* Balsam Fir	S5	1
ACERPENS	*Acer pensylcanicum* Striped Maple	S5	2
ACERRUBR	*Acer rubrum* Red Maple	S5	3
ACERSACC	*Acer saccharum* Sugar Maple	S5	4
ACERSPIC	*Acer spicatum* Mountain Maple	S5	5
ACHIMILL	*Achillea millefolium* Yarrow	S5	6
ACTAPACH	*Actaea pachypoda* White Baneberry	S4	7
ACTARUBR	*Actaea rubra* Red Baneberry	S5	8

CODE	NAME	S-RANK	NUMBER
AGROSTOL	*Agrostis stolonifera* Spreading Bentgrass	SE	9
ALNUINCA	*Alnus incana* Speckled Alder	S5	10
ANAPMARG	*Anaphalis margaritacea* Pearly Everlasting	S5	11
ARALNUDI	*Aralia nudicaulis* Sarsaparilla	S5	12
ARCEPUSI	*Arceuthobium pusillum* Dwarf Mistletoe	S3	13
ARISTRIP	*Arisaema triphyllum* Jack-in-the-pulpit	S4	14
ASTEACUM	*Aster acuminatus* Whorled Wood Aster	S5	15
ASTELATE	*Aster lateriflorus* Starved Aster	S5	16
ASTEMACR	*Aster macrophyllus* Large-leaved Aster	S3	17
ATHYFILI	*Athyrium filix-femina* Lady Fern	S5	18
AVENSATI	*Avena sativa* Oat	SE	19
BETUALLE	*Betula alleghaniensis* Yellow Birch	S5	20
BETUPAPY	*Betula papyrifera* Paper Birch	S5	21
BETUPOPU	*Betula populifolia* Grey Birch	S5	22
BOTRLANC	*Botrychium lanceolatum* Lance-leaved Grape Fern	S1	23
BOTRVIRG	*Botrychium virginianum* Rattlensnake Fern	S3S4	24

CODE	NAME	S-RANK	NUMBER
CALTPALU	*Caltha palustris* Marsh Marigold	S5	25
CAREARCT	*Carex arctata* Sedge	S5	26
CAREBRUN	*Carex brunnescens* Sedge	S5	27
CAREDISP	*Carex disperma* Sedge	S5	28
CARENOVA	*Carex novae-angliae* *Sedge*	S4	29
CHRYAMER	*Chrysosplenium americanum* Golden Saxifrage	S4	30
CINNLATI	*Cinna latifolia* Wood Reedgrass	S4	31
CIRCALPI	*Circaea alpina* Small Enchanters Nightshade	S5	32
CIRSARVE	*Cirsium arvense* Canada Thistle	SE	33
CLINBORE	*Clintonia borealis* Blue-bead Lily	S5	34
COPTTRIF	*Coptis trifolia* Goldthread	S5	35
CORATRIF	*Corallorhiza trifida* Early Coral-root	S4S5	36
CORNALTE	*Cornus alternifolia* Alternate-leaf Dogwood	S5	37
CORNCANA	*Cornus canadensis* Bunchberry	S5	38
CORYCORN	*Corylus cornuta* Beaked Hazelnut	S5	39

CODE	NAME	S-RANK	NUMBER
CYPRACAU	*Cypripedium acaule* Pink Lady's Slipper	S5	40
DANTSPIC	*Danthonia spicata* Poverty Grass	S5	41
DENNPUNC	*Dennstaedtia punctilobula* Hay-scented Fern	S5	42
DEPAACRO	*Deparia acrostichoides* Silvery Spleenwort	S2S3	43
DRYOCRIS	*Dryopteris cristata* Crested Wood Fern	S5	44
DRYOSPIN	*Dryopteris spinulosa* Spinulose Wood Fern	S3S5?	45
ELYMREPE	*Elymus repens* Quack Grass	SE	46
EPIFVIRG	*Epifagus virginiana* Beech Drops	S4	47
EPILANGU	*Epilobium angustifolium* Fireweed	S5	48
EPILCILI	*Epilobium ciliatum* Hairy Willow-herb	S5	49
EQUIARVE	*Equisetum arvense* Field Horsetail	S5	50
ERIGSTRI	*Erigeron strigosus* Daisy Fleabane	S5	51
EUTHGRAM	*Euthamia graminifolia* Narrow-leaf Goldenrod	S5	52
FAGUGRAN	*Fagus grandifolia* America Beech	S5	53
FESTRUBR	*Festuca rubra* Red Fescue	S5	54
FRAGVIRG	*Fragaria virginiana* Wild Strawberry	S5	55

CODE	NAME	S-RANK	NUMBER
FRAXAMER	*Fraxinus americana* White Ash	S4	56
GALETETR	*Galeopsis tetrahit* Hemp Nettle	SE	57
GALIMOLL	*Galium mollugo* Wild Madder	SE	58
GALITRIF	*Galium triflorum* Sweet-scented Bedstraw	S5	59
GERAROBE	*Geranium robertianum* Herb Robert	S2	60
GOODREPE	*Goodyera repens* Rattlesnake Plantain	S2	61
GYMNDRYO	*Gymnocarpium dryopteris* Oak Fern	S5	62
HIERAURA	*Hieracium aurantiacum* Orange Hawkweed	SE	63
HIERCAES	*Hieracium caespitosum* Field Hawkweed	SE	64
HIERFLOR	*Hieracium floribundum* King Devil	SE	65
HIERLACH	*Hieracium lachenalii* Hawkweed	SE	66
HIERPILO	*Hieracium piloselloides* Mouse-ear Hawkweed	SE	67
HYPEPERF	*Hypericum perforatum* St. John's Wort	SE	68
IMPACAPE	*Impatiens capensis* Spotted Touch-me-not	S5	69
JUNCTENU	*Juncus tenuis* Slender Rush	S5	70
LACTCANA	*Lactuca canadensis* Canada Lettuce	S5	71

CODE	NAME	S-RANK	NUMBER
LEONAUTU	*Leontodon autumnalis* Fall Dandelion	SE	72
LEUCVULG	*leucanthemum vulgare* Ox-eye Daisy	SE	73
LINAVULG	*Linaria vulgaris* Toadflax	SE	74
LINNBORE	*Linnaea borealis* Twinflower	S5	75
LISTCONV	*Listera convallarioides* Twayblade	S1?	76
LONICANA	*Lonicera canadensis* Fly Honeysuckle	S5	77
LOTUCORN	*Lotus corniculatus* Bird's Foot Trefoil	SE	78
LYCOANNO	*Lycopodium annotinum* Stiff Clubmoss	S5	79
LYCOCLAV	*Lycopodium clavatum* Running Pine	S5	80
LYCOCOMP	*Lycopodium complanatum* Trailing Clubmoss	S3?	81
LYCODEND	*Lycopodium dendroideum* Treelike Clubmoss	S3S5?	82
LYCOHICK	*Lycopodium hickeyi* Hickey's Clubmoss	S1S3?	83
LYCOLUCI	*Lycopodium lucidulum* Shining Clubmoss	S5	84
LYCOOBSC	*Lycopodium obscurum* Tree Clubmoss	S5	85
LYCOAMER	*Lycopus americanus* American Bugleweed	S5	86
LUZUACUM	*Luzula acuminata* Hairy Wood Rush	S5	87

CODE	NAME	S-RANK	NUMBER
MAIACANA	*Maianthemum canadense* Wild Lily-of-the-Valley	S5	88
MALUPUMI	*Malus pumila* Apple	SE	89
MATRMATR	*Matricaria marticarioides* Pineapple Weed	SE	90
MATTSTRU	*Matteuccia struthiopterus* Ostrich Fern	S5	91
MEDEVIRG	*Medeola virginiana* Indian Cucumber-root	S5	92
MITCREPE	*Mitchella repens* Partridge-berry	S1	93
MITENUDA	*Mitella nuda* Naked Bishop's Cap	S5	94
MONEUNIF	*Monesis uniflora* One-flowered Shinleaf	S5	95
MONOUNIF	*Monotropa uniflora* Indian Pipe	S5	96
MYRIPENS	*Myrica pensylvanica* Bayberry	S5	97
ONOCSENS	*Onoclea sensibilis* Sensitive Fern	S5	98
OENOBIEN	*Oenothera biennis* Evening Primrose	S5	99
OSMOCLAY	*Osmorhiza claytonii* Hairy Sweet Cicely	S2	100
OSMUCINN	*Osmunda cinnamomea* Cinnamon Fern	S5	101
OSMUCLAY	*Osmunda claytoniana* Interrupted Fern	S5	102
OXALSTRI	*Oxalis stricta* Yellow Wood Sorrel	S4	103

CODE	NAME	S-RANK	NUMBER
PHEGCONN	*Phegopteris connectilis* Beech Fern	S5	104
PHLEPRAT	*Phleum pratense* Timothy	SE	105
PICEGLAU	*Picea glauca* White Spruce	S5	106
PLANMAJO	*Plantago major* Common Plantain	SE	107
PLATLACE	*Platanthera lacera* Green Fringed Orchis	S5	108
POAPRATE	*Poa pratensis* Kentucky Blue Grass	SE	109
POLYPERS	*Polygonum persicaria* Lady's Thumb	SE	110
POLYACRO	*Polystichum acrostichoides* Christmas Fern	S2S3	111
POPUGRAN	*Populus grandidentata* Large-tooth Aspen	S5	112
POPUTREM	*Populus tremuloides* Trembling Aspen	S5	113
POTERECT	*Potentilla recta* Sulphur Cinquefoil	SE	114
PTERAQUI	*Pteridium aquilinum* Bracken Fern	S5	115
PRENALTI	*Prenanthes altissima* Tall Rattlesnake Root	S4	116
PRENTRIF	*Prenanthes trifoliolata* Three-leaf Rattlesnake Root	S5	117
PRUNVULG	*Prunella vulgaris* Heal All	S5	118

CODE	**NAME**	**S-RANK**	**NUMBER**
PRUNVIRG	*Prunus virginiana* Choke Cherry	S5	119
PYROELLI	*Pyrola elliptica* Shinleaf	S5	120
PYROROTU	*Pyrola rotundifolia* American Wintergreen	S5	121
PYROSECU	*Pyrola secunda* One-sided Wintergreen	S5	122
QUERRUBR	*Quercus rubra* Red Oak	S4S5	123
RANUACRI	*Ranunculus acris* Tall Buttercup	SE	124
RANUREPE	*Ranunculus repens* Creeping Buttercup	SE	125
RIBEGLAN	*Ribes glandulosum* Skunk Currant	S5	126
RIBELACU	*Ribes lacustre* Bristly Black Currant	S5	127
RIBESATI	*Ribes sativum* Red Currant	SE	128
RUBUALLE	*Rubus allegheniensis* Blackberry	S5	129
RUBUIDAE	*Rubus idaeus* Raspberry	S5	130
RUBUPUBE	*Rubus pubescens* Dwarf Raspberry	S5	131
RUMEACET	*Rumex acetosella* Sheep Sorrel	SE	132
RUMECRIS	*Rumex crispus* Curled Dock	SE	133
SALIBEBB	*Salix bebbiana* Bebb's Willow	S5	134

CODE	NAME	S-RANK	NUMBER
SAMBCANA	*Sambucus canadense* Common Elderberry	S5	135
SAMBPUBE	*Sambucus pubens* Red Elderberry	S5	136
SMILRACE	*Smilacina racemosa* False Soloman's Seal	S5	137
SOLICANA	*Solidago canadensis* Canada Goldenrod	S5	138
SOLIFLEX	*Solidago flexicaulis* Zigzag Goldenrod	S1	139
SOLIRUGO	*Solidago rugosa* Rough Goldenrod	S5	140
SOLITUBE	*Solanum tuberosum* Potato	SE	141
SONCARVE	*Sonchus arvensis* Sowthistle	SE	142
SORBAUCU	*Sorbus aucuparia* European Mountain Ash	SE	143
SORBAMER	*Sorbus americana* American Mountain Ash	S5	144
SPARPECT	*Spartina pecinata* Rough Cord Grass	S5	145
SPERRUBR	*Spergularia rubra* Purple Sandspurrey	SE	146
STELGRAM	*Stellaria graminea* Grass-leaved Stitchwort	SE	147
STELMEDE	*Stellaria media* Common Stitchwort	SE	148
STREAMPL	*Streptopus amplexifolius* Green Twisted Stalk	S5	149
STREROSE	*Streptopus roseus* Rosy Twisted Stalk	S5	150

CODE	NAME	S-RANK	NUMBER
TAXAOFFI	*Taraxacum officinale* Dandelion	SE	151
TAXUCANA	*Taxus canadensis* Ground Hemlock	S5	152
THELNOVE	*Thelypteris noveboracensis* New York Fern	S5	153
TRIFAURE	*Trifolium aureum* Yellow Clover	SE	154
TRIFCAMP	*Trifolium campestre* Low Hop Clover	SE	155
TRIFPRAT	*Trifolium pratense* Red Clover	SE	156
TRIFREPE	*Trifolium repens* White Clover	SE	157
TRILCERN	*Trillium cernuum* Nodding Trillium	S4	158
TRILUNDU	*Trillium undulatum* Painted Trillium	S5	159
TRIEBORE	*Trientalis borealis* Starflower	S5	160
TSUGCANA	*Tsuga canadensis* Eastern Hemlock	S4	161
TUSSFARA	*Tussilago farfara* Coltsfoot	SE	162
ULMUAMER	*Ulmus americana* American Elm	S5	163
VACCANGU	*Vaccinium angusitfolium* Blueberry	S5	164
VERBTHAP	*Verbascum thapsis* Common Mullein	SE	165
VEROOFFI	*Veronica officinalis* Common Speedwell	SE	166

CODE	NAME	S-RANK	NUMBER
VIRBNUDU	*Virburnum nudum* Wild Raisin	S5	167
VIRBOPUL	*Viburnum opulus* Highbush Cranberry	S3	168
VICICRAC	*Vicia cracca* Tufted Vetch	SE	169
VIOLCUCC	*Viola cucullata* Blue Violet	S5	170

6.0 APPENDIX 2

Table 6.1 Constrained seriation for taxa found in six Prince Edward Island Acadian Forest study sites, with columns representing distance from the edge in metres. An "X" indicates a species' presence at that distance from the edge and non-native species are shaded in grey. Of 15 non-native species occurring within the forest, seven (47%) were restricted to within 40 metres of the edge. Excluding those species that were restricted to external (-5.7 m) sample plots, the probability of the arrangement being random (no edge-to-interior gradient) is $p<0.001$. The key to species codes is given in Appendix 1.

Species	-5.7	5.7	20	40	80	120	160	200	250	300
PHLEPRAT	X									
AGROSTOL	X									
LOTUCORN	X									
OENOBIEN	X									
DANTSPIC	X									
LINAVULG	X									
TRIFREPE	X									
LEONAUTU	X									
GALIMOLL	X									
STELMEDI	X									
SPARPECT	X									
TRIFAURE	X									
TRIFPRAT	X									
POPYPERS	X									
FESTRUBR	X									
HIERFLOR	X									
TRIFCAMP	X									
RUMEACET	X									
MATRMATR	X									
HIERPILO	X									
PLATLACE	X									
STELGRAM	X									
ELYMREPE	X									
SOLATUBE	X									

Species	−5.7	5.7	20	40	80	120	160	200	250	300
RUBUALLE	X									
RUMECRIS	X									
CIRSARVE	X									
LUZUACUM	X									
TUSSFARA	X									
VERBTHAP	X									
POTERECT	X									
HYPEPERF	X									
SPERRUBR	X									
SONCARVE	X									
EUTHGRAM		X								
MYRIPENS		X								
JUNCTENU		X								
PYRUMALU		X								
PRUNVULG		X								
PLANMAJO		X								
ERIGSTRI		X								
CHRYLEUC		X								
FRAGVIRG		X								
SOLICANA		X								
LYCOAMER		X								
VICICRAC		X								
POAPRATE		X								
VIRBOPUL		X								
SOLIRUGO		X	X							
LYCOHICK		X	X							
TARAOFFI		X	X					X		
RIBESATI		X		X						
CARENOVE		X		X						
RUBUIDAE		X		X						
EPIFVIRG		X	X	X						
CORATRIF			X							

Species	-5.7	5.7	20	40	80	120	160	200	250	300
LYCODEND			X	X						
HIERCAES			X	X						
EPILANGU		X	X	X	X	X				
BETUALLE		X	X	X	X	X				
LYCOCLAV		X				X				
GALETETR		X	X	X		X		X		
RANUACRI		X			X			X		
POLYACRO				X						
MONEUNIF				X						
PYROROTU				X						
LISTCONV				X						
DEPAACRO				X	X					
BOTRLANC				X		X				
LYCOANNO				X	X	X				
HIERLACH		X	X	X	X	X	X			
FRAXAMER		X	X	X	X	X	X			
GALITRIF		X		X	X	X	X			
PTERAQUI		X		X	X	X	X	X		
ASTEMACR			X				X			
ALNUINCA			X				X			
ARISTRIP			X					X		
QUERRUBR		X		X				X	X	
ACTARUBR		X	X	X	X	X		X	X	
PRENALTI		X	X	X	X	X		X	X	
ATHYFILI		X	X	X			X	X	X	
ASTELATE		X	X	X	X		X	X	X	
VEROOFFI		X	X	X	X	X	X	X	X	
PRENTRIF		X	X	X	X	X	X	X	X	
CAREARCT		X	X	X	X	X	X	X	X	
GYMNDRYO		X	X	X	X	X	X	X	X	
CORNCANA		X	X				X			X
SORBAUCU		X	X	X			X	X		X

Species	-5.7	5.7	20	40	80	120	160	200	250	300
PYROELLI		X	X	X	X	X	X		X	X
PHEGCONN		X	X	X	X		X	X	X	X
HIERAURA		X	X	X	X	X	X	X	X	X
ACERSACC		X	X	X	X	X	X	X	X	X
TRIEBORE		X	X	X	X	X	X	X	X	X
CORYCORN		X	X	X	X	X	X	X		X
VIOLCUCU		X	X	X	X	X	X	X	X	X
MEDEVIRG		X	X	X	X	X	X	X	X	X
BETUPAPY		X	X	X	X	X	X	X	X	X
ABIEBALS		X	X	X	X	X	X	X	X	X
ACERPENS		X	X	X	X	X	X	X	X	X
DRYOSPIN		X	X	X	X	X	X	X	X	X
ACERSPIC		X	X	X	X	X	X	X	X	X
ARALNUDI		X	X	X	X	X	X	X	X	X
PICEGLAU		X	X	X	X	X	X	X	X	X
DENNPUNC		X	X	X	X	X	X	X	X	X
FAGUGRAN		X	X	X	X	X	X	X	X	X
ACERRUBR		X	X	X	X	X	X	X	X	X
MAIACANA		X	X	X	X	X	X	X	X	X
ASTEACUM		X	X	X	X	X	X	X	X	X
SMILRACE		X	X	X	X	X	X	X	X	X
CLINBORE		X	X	X	X	X	X	X	X	X
TRILUNDU		X	X	X	X	X	X	X	X	X
LYCOOBSC		X	X	X	X	X	X	X	X	X
TAXUCANA		X	X	X	X	X	X	X	X	X
STREROSE		X	X	X	X	X	X	X	X	X
SAMBCANA		X	X	X	X	X	X	X	X	X
LYCOLUCI		X	X	X	X		X	X	X	X
CORNALTI		X	X	X	X	X		X	X	X
THELNOVE		X	X		X	X	X	X	X	X
SAMBPUBE		X	X	X		X	X	X	X	X
CAREBRUN		X	X	X		X	X	X	X	X

Species	-5.7	5.7	20	40	80	120	160	200	250	300
RUBUPUBE		X		X	X	X	X	X	X	X
POPUTREM		X	X		X	X	X	X		X
LONICANA		X	X			X	X	X	X	X
PYROSECU		X			X			X	X	X
VIRBNUDU		X							X	X
VACCANGU		X			X	X				X
TRILCERN			X	X	X	X			X	
LACTCANA			X	X	X		X	X	X	
CYPRACAU			X	X	X	X	X	X	X	X
MONOUNIF			X	X	X	X	X	X	X	X
OSMUCINN			X		X	X	X	X	X	X
RIBELACU			X	X	X	X	X	X	X	
IMPACAPE				X	X	X	X	X		
CIRCALPI				X	X	X	X	X		
CINNLATE				X	X				X	
BOTRVIRG				X		X			X	
POPUGRAN				X	X	X			X	
MITENUDA				X	X	X	X	X	X	
MITCREPE					X					
ARCEPUSI					X					
CAREDISP					X	X				
ULMUAMER					X	X				
MATTSTRU					X	X				
ONOCSENS					X	X	X		X	
CHRYAMER					X		X			
SOLIFLEX					X	X		X		
PRUNVIRG					X	X	X	X		X
OSMOCLAY						X				
EPILCILI						X				
GEREROBE						X	X			
EQUIARVE						X		X		
OXALSTRI						X				X

Species	-5.7	5.7	20	40	80	120	160	200	250	300
OSMUCLAY							X			
DRYOCRIS							X			
CALTPALU							X			
RANUREPE							X			
SALIBEBB							X	X	X	
COPTTRIF							X	X	X	X
STREAMPLE							X	X	X	X
BETUPOPU							X	X	X	X
SORBAMER							X	X	X	X
LINNBORE								X		
RIBEGLAN								X		
ACTAPACH									X	
TUSGCANA										X
GOODREPE										X

Table 6.2 Constrained seriation for taxa found in the Borden study area, with columns representing distance from the edge in metres. An "X" indicates a species' presence at that distance from the edge and non-native species are shaded in grey. Excluding those species that were restricted to external (−5.7 m) sample plots, the probability of the arrangement being random (no edge-to-interior gradient) is $p<0.001$. The key to species codes is given in Appendix 1.

Species	−5.7	5.7	20	40	80	120	160	200	250	300
POTERECT	X									
TRIFPRAT	X									
JUNCTENU	X									
PLATLACE	X									
SPERRUBR	X									
PLANMAJO	X									
FRAGVIRG	X									
TRIFCAMP	X									
PHLEPRAT	X									
HIERPILO	X									
MYRIPENS	X									
ELYMREPE	X									
TUSSFARA	X									
PRUNVULG	X									
TRIFREPE	X									
SALIBEBB	X									
OXALSTRI	X									
HYPEPERF	X									
SPARPECT	X									
MATRMATR	X									
OENOBIEN	X									
VICICRAC	X	X								
SOLICANA	X	X								
ERIGSTRI	X	X								
PYRUMALU	X	X								
EUTHGRAM	X	X								

Species	−5.7	5.7	20	40	80	120	160	200	250	300
SOLIRUGO	X	X								
CHRYLEUC	X	X								
GALITRIF		X								
TARAOFFI	X	X	X							
POPUTREM		X								
VACCANGU		X								
POAPRATE	X	X		X						
RUBUIDAE	X	X		X						
CAREBRUN	X	X	X	X						
HIERAURA	X		X	X						
TRILUNDU		X	X	X	X					
EPILANGU	X	X	X	X	X	X				
RANUACRI	X	X							X	
BETUALLE	X		X	X	X	X				
CORYCORN	X	X	X	X	X	X	X			
PRUNVIRG	X				X	X				
VEROOFFI	X	X	X	X	X		X		X	
BETUPAPY	X	X	X		X		X		X	
ACERPENS	X	X	X	X	X	X	X	X	X	
HIERLACH		X	X	X	X	X	X	X		
CORNALTI		X	X	X	X				X	
GALETETR		X	X	X		X		X		
FAGUGRAN	X	X	X	X	X	X	X		X	
ACERRUBR	X	X	X	X	X	X	X		X	
PYROELLI	X			X					X	X
DENNPUNC	X	X	X	X	X	X	X	X	X	X
CLINBORE	X	X	X	X	X	X	X	X	X	X
ARALNUDI	X	X	X	X	X	X	X	X	X	X
ACTAPACH						X				
ACERSACC	X	X	X	X	X	X	X	X	X	X
SAMBCANA		X				X	X			
HIERCAES	X	X	X	X	X	X	X	X	X	X

Species	-5.7	5.7	20	40	80	120	160	200	250	300
SMILRACE	X	X	X	X	X	X	X	X	X	X
PICEGLAU	X	X	X	X	X	X	X	X	X	X
LYCOOBSC					X					
ABIEBALS	X	X	X	X	X	X	X	X	X	X
ACERSPIC		X	X		X	X	X	X	X	
PRENALTI			X	X	X	X				
DRYOSPIN		X	X	X	X	X	X	X	X	X
TRIEBORE		X	X	X	X	X	X	X	X	X
ULMUAMER					X	X				
MAIACANA		X	X	X	X	X	X	X	X	X
MEDEVIRG				X			X			
PRENTRIF		X	X	X	X	X	X	X	X	X
CAREARCT			X	X	X	X	X	X		
ASTEACUM				X	X	X	X			
SAMBPUBE			X	X		X	X	X		
IMPACAPE				X	X	X		X		X
GYMNDRYO			X	X	X	X		X	X	X
EPILCILI						X				X
PHEGCONN			X				X		X	X
TRILCERN				X		X			X	
TAXUCANA					X			X		
ONOCSENS						X	X			
MONOUNIF						X	X			
LONICANA							X			
OSMUCINN						X				
BETUPOPU							X		X	X
THELNOVE						X		X		X
OSMUCLAY							X			
EQUIARVE						X		X		
ASTELATE						X		X	X	X
ATHYFILI								X		X
CIRCALPI									X	

Species	-5.7	5.7	20	40	80	120	160	200	250	300
ARISTRIP									X	
ACTARUBR									X	X
CINNLATE										X

Table 6.3 Constrained seriation for taxa found in the Lady Fane study area, with columns representing distance from the edge in metres. An "X" indicates a species' presence at that distance from the edge and non-native species are shaded in grey. Excluding those species that were restricted to external (−5.7 m) sample plots, the probability of the arrangement being random (no edge-to-interior gradient) is $p<0.001$. The key to species codes is given in Appendix 1.

Species	−5.7	5.7	20	40	80	120	160	200	250	300
HYPEPERF	X									
SALIBEBB	X									
STELMEDI	X									
RUMEACET	X									
RUBUALLE	X									
PHLEPRAT	X									
LUZUACUM	X									
TRIFAURE	X									
CHRYLEUC	X									
OENOBIEN	X									
LEONAUTU	X									
RUBUIDAE	X									
HIERPILO	X									
STELGRAM	X									
AGROSTOL	X									
HIERAURA	X									
LOTUCORN	X									
FESTRUBR	X									
DANTSPIC	X									
ACTARUBR	X									
POAPRATE	X	X								
FRAGVIRG	X	X								
EUTHGRAM	X	X								
SOLICANA	X	X								
MYRIPENS		X								
RANUACRI		X								

Species	-5.7	5.7	20	40	80	120	160	200	250	300
VICICRAC		X								
TAXUCANA		X								
CORNALTI			X							
LYCOLUCI			X							
ASTEMACR			X							
PTERAQUI	X	X			X	X				
BETUALLE		X	X	X	X					
SOLIRUGO	X	X	X						X	
LYCOCLAV		X				X				
ASTELATE				X	X					
CAREARCT	X	X	X	X		X	X		X	
POPUTREM		X	X							X
PYROSECU					X					
ACERSPIC	X	X	X	X	X			X	X	X
PYROELLI		X	X	X	X	X	X			X
ATHYFILI			X	X					X	
ASTEACUM	X	X	X	X	X		X	X	X	X
ACERPENS	X	X	X	X	X		X	X	X	X
ABIEBALS	X	X	X	X	X		X	X	X	X
ARALNUDI	X	X	X	X	X		X	X	X	X
FAGUGRAN	X	X	X	X	X	X	X	X	X	X
ACERSACC	X	X	X	X	X	X	X	X	X	X
CAREDISP					X	X				
SAMBPUBE			X	X			X	X		
HIERCAES	X	X							X	X
PICEGLAU	X	X	X	X	X	X	X	X	X	X
VIOLCUCU	X	X	X	X			X	X	X	X
ACERRUBR	X		X	X	X	X	X	X	X	X
MAIACANA		X	X	X	X	X	X	X	X	X
POPUGRAN				X	X	X			X	
LYCOOBSC		X	X	X	X	X	X	X	X	X
SORBAUCU	X		X	X			X	X	X	X

Species	-5.7	5.7	20	40	80	120	160	200	250	300
DENNPUNC		X	X	X	X	X	X	X	X	X
LYCOCOMP						X				
TRILUNDU			X	X	X	X	X	X	X	
LYCOANNO				X		X		X		
PRENTRIF						X				
TRIEBORE		X	X	X	X	X	X	X	X	X
PRUNVIRG	X							X		X
STREROSE			X		X		X	X	X	
CYPRACAU						X	X			
MEDEVIRG			X	X	X	X	X	X	X	X
DRYOSPIN			X	X	X	X	X	X	X	X
PRENALTI			X					X	X	
CAREBRUN		X		X			X	X	X	X
CORYCORN					X	X	X		X	
MONOUNIF					X	X	X	X	X	X
GYMNDRYO							X			
CLINBORE							X			
BETUPAPY	X						X	X	X	X
SMILRACE			X			X	X	X	X	X
OSMUCINN						X			X	
EPIFVIRG									X	
BETUPOPU									X	
SORBAMER								X	X	X

Table 6.4 Constrained seriation for taxa found in the Lewes study area, with columns representing distance from the edge in metres. An "X" indicates a species' presence at that distance from the edge and non-native species are shaded in grey. Excluding those species that were restricted to external (−5.7 m) sample plots, the probability of the arrangement being random (no edge-to-interior gradient) is $p<0.001$. The key to species codes is given in Appendix 1.

Species	−5.7	5.7	20	40	80	120	160	200	250	300
POLYPERS	X									
SOLICANA	X									
EUTHGRAM	X									
PLATLACE	X									
LINAVULG	X									
CIRSARVE	X									
AVENSATI	X									
VICICRAC	X									
PLANMAJO	X									
OENOBIEN	X									
PRUNVULG	X									
OXALSTRI	X									
CHRYLEUC	X									
ERIGSTRI	X									
RUBUIDAE	X									
TARAOFFI	X									
RANUACRI	X									
PHLEPRAT	X									
VERBTHAP	X									
RUMEACET	X									
GALETETR	X									
SONCARVE	X									
CORNCANA	X	X								
FRAGVIRG	X	X								
DRYOCRIS		X								
LYCOAMER	X		X							

Species	-5.7	5.7	20	40	80	120	160	200	250	300
PICEGLAU	X	X	X							
ACTARUBR		X								
CAREARCT		X	X							
LYCOHICK			X							
TRIFCAMP			X							
ALNUINCA			X							
CORATRIF			X							
CAREBRUN			X							
ASTEACUM	X		X	X	X					
BETUALLE	X	X	X	X	X	X				
HIERCAES	X		X	X			X			
ACERSPIC	X	X	X	X	X			X		
PTERAQUI	X	X		X			X	X		
VEROOFFI	X	X	X	X	X	X	X	X		
PYROELLI		X					X			
ARALNUDI	X	X	X	X	X		X	X	X	
MITCREPE					X					
VIOLCUCU					X					
PRYOSECU					X					
POPUTREM		X	X		X	X	X	X		
ACERPENS	X	X	X	X	X	X	X	X	X	X
TRIEBORE	X	X	X	X	X	X	X	X	X	X
VACCANGU					X	X				
RUBUPUBE					X	X				
ACERRUBR	X		X	X	X	X	X	X		X
PRENALTI			X					X		
MAIACANA	X	X	X	X	X	X	X	X	X	X
PRENTRIF			X					X		
ACERSACC	X	X	X	X	X	X	X	X	X	X
ABIEBALS	X	X	X	X	X	X	X	X	X	X
CORYCORN		X	X	X	X	X	X	X		X
CYPRACAU				X	X			X		

Species	-5.7	5.7	20	40	80	120	160	200	250	300
DENNPUNC		X	X		X		X	X	X	
SORBAUCU		X					X	X		
EPILCILI						X				
FAGUGRAN		X	X	X	X	X	X	X	X	X
SAMBPUBE			X					X	X	
DRYOSPIN		X	X	X	X	X	X	X	X	X
SMILRACE		X	X	X		X	X	X	X	X
MONOUNIF			X	X		X	X	X	X	
LYCOOBSC				X	X	X	X	X		
PRUNVIRG					X	X	X	X		
TAXUCANA							X			
BETUPOPU							X			
TRILUNDU			X			X	X			
BETUPAPY					X	X	X	X	X	X
LYCOLUCI				X			X	X	X	X
THELNOVE									X	
STREROSE									X	X
CLINBORE										X
MEDEVIRG										X
TSUGCANA										X

Table 6.5 Constrained seriation for taxa found in the Middleton study area, with columns representing distance from the edge in metres. An "X" indicates a species' presence at that distance from the edge and non-native species are shaded in grey. Excluding those species that were restricted to external (−5.7 m) sample plots, the probability of the arrangement being random (no edge-to-interior gradient) is p=0.001. The key to species codes is given in Appendix 1.

Species	−5.7	5.7	20	40	80	120	160	200	250	300
GALIMOLL	X									
PHLEPRAT	X									
HIERAURA	X									
SOLIRUGO	X									
FRAGVIRG	X	X								
PTERAQUI	X	X								
COPTTRIF		X								
PHEGCONN		X								
POAPRATE		X								
VIRBOPUL		X								
JUNCTENU		X								
RUBUPUBE		X								
PYROSECU		X								
GALITRIF		X								
SORBAUCU	X	X	X	X						
ASTELATE	X	X	X	X						
BETUALLE	X	X		X	X					
OSMUCINN			X							
RIBESATI		X		X						
CAREDISP		X	X	X						
CORNCANA	X	X	X							X
ACTARUBR				X						
TRILCERN			X		X					
ATHYFILI				X						
LYCOHICK		X	X					X		
CORYCORN	X	X	X	X				X		
CAREARCT		X			X		X			

Species	-5.7	5.7	20	40	80	120	160	200	250	300
MAIACANA	X	X	X	X	X	X	X	X	X	
TAXUCANA		X	X							X
ACERRUBR	X	X	X	X	X			X	X	X
HIERCAES	X	X		X		X	X	X	X	
HIERLACH			X	X	X	X	X	X	X	X
PICEGLAU	X	X		X		X	X	X	X	
CORNALTI		X	X	X	X			X		
ABIEBALS	X	X	X	X	X	X	X	X	X	X
ARALNUDI	X	X	X	X	X	X	X	X	X	X
ACERSACC	X	X	X	X	X	X	X	X	X	X
VEROOFFI		X	X	X			X	X	X	
ACERPENS	X	X	X	X	X	X	X	X	X	X
TRIEBORE	X	X	X	X	X	X	X	X	X	X
CAREBRUN		X	X	X			X	X		X
LYCOLUCI		X	X	X			X	X		X
QUERRUBR		X		X				X	X	
LACTCANA			X	X	X			X	X	
STREROSE		X	X	X	X	X	X	X	X	X
DRYOSPIN		X	X	X	X	X	X	X	X	X
LYCOOBSC		X	X	X		X		X	X	X
SMILRACE		X	X	X	X	X	X	X	X	X
CLINBORE		X	X	X	X	X	X	X	X	X
ASTEACUM			X	X	X	X	X	X	X	
TRILUNDU		X	X	X	X	X	X	X	X	X
SAMBCANA		X	X	X	X	X	X	X	X	X
SAMBPUBE		X	X	X		X		X	X	X
RUBUIDAE	X							X		X
CINNLATE					X			X		
DENNPUNC			X		X	X	X	X		X
ACERSPIC		X		X		X	X	X	X	X
PYROELLI			X				X			X
FAGUGRAN		X			X	X		X	X	X

Species	-5.7	5.7	20	40	80	120	160	200	250	300
POPUTREM							X			
ASTEMACR							X			
PRENTRIF				X				X	X	
MONOUNIF							X	X		
BETUPAPY				X			X	X	X	X
MEDEVIRG					X		X	X	X	X
TARAOFFI								X		
SALIBEBB							X	X	X	
BETUPOPU						X				
DRYOCRIS									X	

Table 6.6 Constrained seriation for taxa found in the Townshend study area, with columns representing distance from the edge in metres. An "X" indicates a species' presence at that distance from the edge and non-native species are shaded in grey. Excluding those species that were restricted to external (−5.7 m) sample plots, the probability of the arrangement being random (no edge-to-interior gradient) is $p<0.001$. The key to species codes is given in Appendix 1.

Species	−5.7	5.7	20	40	80	120	160	200	250	300
POAPRATE	X									
OSMUCLAY	X									
FRAGVIRG	X									
RUBUIDAE	X									
EUTHGRAM	X									
RUBUALLE	X									
RUMECRIS	X									
PTERAQUI	X									
RIBESATI	X									
CAREBRUN	X									
SORBAUCU	X									
VEROOFFI	X	X								
DENNPUNC	X	X								
LYCOAMER	X	X								
PRUNVULG	X	X								
PLANMAJO	X	X								
HIERCAES		X								
TRILCERN	X			X						
CORNALTI		X	X							
ARISTRIP			X							
BETUALLE	X	X	X	X	X					
ACTARUBR	X		X			X				
SAMBPUBE	X	X		X				X		
LISTCONV				X						
BOTRLANC				X						
POLYACRO				X						

Species	-5.7	5.7	20	40	80	120	160	200	250	300
MONEUNIF				X						
PYROROTU				X						
PRENALTI	X	X		X	X	X		X		
DEPAACRO				X	X					
SMILRACE	X	X	X	X	X	X	X	X		
CINNLATE				X	X					
ATHYFILI	X	X					X	X		
MEDEVIRG	X	X	X	X				X		X
PICEGLAU		X		X				X		
RANUACRI					X					
CORYCORN	X	X	X	X	X	X	X	X		X
PHEGCONN	X	X	X	X	X			X	X	X
LYCOLUCI		X		X	X					X
ACERRUBR	X	X	X	X	X		X	X	X	X
MAIACANA	X	X	X	X	X		X	X	X	X
MATTSTRU					X	X				
VIOLCUCU	X	X	X	X	X	X	X	X	X	X
DRYOSPIN	X	X	X	X	X	X	X	X	X	X
ONOCSENS	X				X				X	
ACERPENS	X	X	X	X	X	X	X	X	X	X
ABIEBALS	X	X	X	X	X	X	X	X	X	X
ARALNUDI	X	X	X	X	X	X	X	X	X	X
CLINBORE	X	X	X	X	X	X	X	X	X	X
ACERSACC	X	X	X	X	X	X	X	X	X	X
FAGUGRAN	X	X	X	X	X	X	X	X	X	X
GALITRIF				X	X	X	X			
ASTELATE		X	X					X	X	
TRIEBORE	X	X	X		X		X	X	X	X
THELNOVE	X	X	X		X	X	X	X	X	X
ACERSPIC	X	X	X		X	X	X	X	X	X
IMPACAPE					X					
CIRCALPI				X	X	X	X	X		

Species	-5.7	5.7	20	40	80	120	160	200	250	300
CHRYAMER					X		X			
CAREDISP						X				
TAXUCANA		X	X	X	X	X	X	X	X	X
OSMOCLAY						X				
ASTEACUM		X	X	X			X	X	X	X
STREROSE		X	X	X			X	X	X	X
PRENTRIF	X					X	X	X	X	
RUBUPUBE	X			X	X	X	X	X	X	X
SOLIFLEX					X	X		X		
BOTRVIRG				X		X			X	
LONICANA		X	X			X	X	X	X	X
BETUPAPY		X	X			X	X	X	X	X
CYPRACAU			X							X
MITENUDA				X	X	X	X	X	X	
GYMNDRYO						X	X			
GERAROBE						X	X			
RIBELACU				X	X	X	X	X	X	
TRILUNDU		X						X		X
ALNUINCA							X			
LACTCANA							X			
DRYOCRIS							X			
CALTPALU							X			
RANUREPE							X			
PYROELLI				X			X		X	X
OSMUCINN					X		X	X	X	X
RIBEGLAN								X		
LINNBORE								X		
COPTTRIF							X	X	X	X
STREAMPL							X	X	X	X
CORNCANA							X			X
SORBAMER							X	X	X	X
MONOUNIF							X		X	X

Species	-5.7	5.7	20	40	80	120	160	200	250	300
PYROSECU								X	X	X
ACTAPACH									X	
VIRBNUDU									X	X
VACCANGU										X
BETUPOPU										X
GOODREPE										X

Table 6.7 Constrained seriation for taxa found in the Victoria West study area, with columns representing distance from the edge in metres. An "X" indicates a species' presence at that distance from the edge and non-native species are shaded in grey. Excluding those species that were restricted to external (−5.7 m) sample plots, the probability of the arrangement being random (no edge-to-interior gradient) is $p<0.001$. The key to species codes is given in Appendix 1.

Species	−5.7	5.7	20	40	80	120	160	200	250	300
VICICRAC	X									
SOLATUBE	X									
EUTHGRAM	X									
CHRYLEUC	X									
STELMEDI	X									
CORNCANA	X									
POAPRATE	X									
LUZUACUM	X									
HIERCAES	X									
VEROOFFI	X									
OXALSTRI	X									
SOLIRUGO	X	X								
BETUALLE	X	X	X	X	X					
EPIFVIRG		X	X	X						
PYROELLI	X	X		X		X				
LYCODEND			X	X						
ASTEACUM	X	X	X		X		X			
TAXUCANA		X	X			X				
GYMNDRYO		X	X				X			
CLINBORE			X	X	X					
VIRBNUDU		X				X				
LONICANA			X	X		X				
FRAXAMER		X	X	X	X	X	X	X	X	X
ACERRUBR	X	X	X	X	X		X			X
ARALNUDI		X	X	X	X				X	
ACERSPIC			X		X	X				

Species	-5.7	5.7	20	40	80	120	160	200	250	300
PICEGLAU		X		X		X	X			
ACERPENS	X	X	X	X	X	X		X	X	
DENNPUNC		X		X	X			X		
ARCEPUSI					X					
LYCOANNO					X					
PHEGCONN					X					
ABIEBALS	X	X	X	X	X	X	X	X	X	
VIOLCUCU		X	X	X	X	X	X	X		
CAREBRUN		X				X	X			
TRILUNDU		X	X	X	X	X	X		X	
SMILRACE	X	X	X	X	X	X	X		X	X
MEDEVIRG		X	X	X	X	X	X			X
FAGUGRAN	X	X	X	X	X	X	X	X	X	X
PRENTRIF				X			X			
TRIEBORE	X	X	X		X	X		X	X	X
SAMBPUBE		X					X	X		
STREROSE		X	X	X		X			X	X
CORNALTI						X				
CAREARCT						X				
CORYCORN		X		X	X		X	X		X
ACERSACC			X	X	X	X	X	X		X
BETUPAPY			X		X	X		X	X	
DRYOSPIN		X	X			X		X	X	X
MAIACANA		X		X		X		X	X	X
LYCOOBSC					X	X		X	X	
THELNOVE						X			X	
PRUNVIRG								X		
MONOUNIF									X	
LYCOLUCI								X		X

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