

extinction spasm: Habitat loss, Introduced species, Population, Pollution, and Over-harvesting.

Invasive species rank second after habitat loss for their importance in reducing native biodiversity, according to Wilson (but see Marris 2005), and this ranking may also apply in the AME. Few vascular plants are known or suspected to have been extirpated from the region, but habitat loss is clearly implicated in the apparent extirpation of *Oligoneuron album* syn. *Solidago ptarmicoides* and *Celastrus scandens* from the flora of the Maritime Provinces. These species were lost in New Brunswick due to the flooding of Saint John River valley by hydroelectricity dams. Despite the number of exotic species in the regional flora and their dominance in certain communities, we cannot yet ascribe any extirpations in the AME to the influence of invasive species.

The database of the Atlantic Canada Conservation Data Centre (ACCDC) reveals that roughly a third of the total plant diversity is exotic in Nova Scotia, New Brunswick, and Prince Edward Island; their floras contain 36, 32, and 34% exotic species, respectively) that lie within the AME (similar data are not available for the southeastern portion of Quebec in the AME). These figures are similar to the proportion of exotics in New England's flora (35 and 45% exotic in Connecticut and Massachusetts; Lundgren et al. 2004). A strong majority (59% — 484 species) of the 759 exotic species presently recorded by ACCDC for the Maritime Provinces are rare within the region (Blaney, unpublished data) and so may little influence ecosystem function or community diversity patterns at present. Many of the others, however, are common enough to have become naturalised in many plant communities, and the unanswered question is to what extent is this influx of predominantly European species a symptom of environmental damage, and to what extent is it a driver modifying plant interactions and changing the structure of biological communities (cf. MacDougall and Turkington 2005).

Given the numbers of exotic species cited above, it is undeniable that our flora has been altered and that exotic plants are now influencing evolution in populations of some of our native species. Our goal in this chapter is to take stock and to try to understand the processes involved in the invasion, naturalisation, and dominance of exotic plants in the AME. We begin this chapter with a historical overview of the periods of isolation and invasion in the AME to demonstrate how our flora in the AME has always been invaded by plant populations that evolved in other areas. Subsequently, we describe the patterns of exotic species in the most anthropogenically disturbed habitats and in less disturbed, more natural areas to indicate that habitats that are frequently disturbed by humans contain many exotic species and to differentiate the natural areas that have potential pest problems from those that are relatively uninvaded by exotics. We examine the processes that can lead to the naturalisation of exotic species and to the usurpation of the niches of native species by exotics. We discuss attempts made to predict what species are most likely to be able to invade other regions. Finally, we compile two lists: the first identifies

plants that may be having significant impacts on the structure or composition of native habitats in the AME, and the second alerts land managers and conservationists to plants we feel could well become such pests in the future.

For clarity, we define some key words used to describe the status of exotic plants. We use the most neutral word, “exotic”, when referring to introduced plants in the AME unless we mean to convey that a particular species is well established and may be influencing community dynamics; in such cases, species are said to be “invasive”.

Definitions

- (a) exotic species — a species that evolved in another geographic region and has arrived through any agency into a new area in recent times.
- (b) to establish — to complete the life cycle (usually but not necessarily via sexual reproduction) successfully in the wild in the new area.
- (c) to naturalise — to establish stable populations in the new area.
- (d) invasive species — an exotic species that is regenerating in the wild in sufficient numbers to influence the dynamics of native plant communities.
- (e) pest — an invasive species that is likely reducing native species biodiversity or is markedly affecting ecosystem function. Note that there has been no incontrovertible demonstration that any exotic species in the AME fits this definition.

History of invasion and migration

This period of accelerated extinction rates, at least 1000 times greater than the pre-human, “edenic” rates (Wilson 2002), has been likened to those associated with the five major asteroid events (Leakey and Levin 1995). After such natural catastrophes, levels of biodiversity observable in the fossil record rebounded (Raup 1991), and the surviving lineages gave rise to new species to fill vacant niches (Wilson 2002). As asteroid events undoubtedly produced profound changes in habitat quality worldwide, it is undeniable that worldwide, undisturbed habitat is being fragmented or replaced with disturbed habitat. The species best equipped to survive and enlarge populations in such a time are ruderals, inherently opportunistic and able to colonise, rapidly exploit and complete reproduction in short-lived, disturbed habitats (Grime 1979). Before we discuss the success of these uninvited “weeds” that may threaten our native plant communities, it is important to root our flora in time and space and understand that though we are living through an extinction spasm that threatens the biodiversity fabric of our ecosystems, our flora has always been dynamic and has been subject to periods of invasion and isolation throughout geological time.

In the early Cretaceous, angiosperms dispersed from Gondwanaland to Laurasia, although the Tethys Sea presented an obstacle to dispersal. Throughout the Cretaceous until the

Miocene (mid-Cenozoic), North America was intermittently connected to Europe via Greenland (Brouillet and Whetstone 1993), and land connections between North America and Asia appear also to have been intermittently available throughout the first half of the Tertiary, although migration of plants through this corridor into North America was probably limited by the adverse climate at the paleolatitudes of Beringia during this period (Graham 1993). During the warm early Eocene (beginning 54 000 ka (ka equals thousands of years ago; ages expressed as noncalibrated radiocarbon years)), migration of species from Europe to North America may have been most rapid and have occurred via Scotland and via northern Scandinavia. By the time of the early Oligocene (34 000 ka), plant migrations may have involved mostly deciduous forest elements coming from Scandinavia into what are now the islands of the Canadian Arctic (Graham 1993).

Intermittent periods of invasion and isolation are, theoretically, the ideal conditions to effect allopatric speciation through a vicariance model. Such conditions not only pertained to the ampho-Atlantic populations but also to populations that were distributed across the North American continent throughout the Tertiary until the late Miocene through the Pliocene when, coincident with a general cooling and uplift of the Sierra-Cascades, drying out of interior regions of North America caused a secondary vicariance event and another possible period of speciation (Xiang et al. 1998). Invasion, subsequent isolation, and reinvasion are processes that have brought biological diversity to its present levels.

In contrast, the Pleistocene glaciations screened plants for their ability to migrate out of the AME, to survive in small areas throughout a glacial maximum, and to migrate back to suitable climate stations with each glacial retreat. Plants thus were tested multiple times for their dispersal abilities and ability to maintain sufficient genetic variability in small populations. There are records of only a few plant species extinctions over this period of extreme disturbance and reorganisation. Palynological records showed that species returned to the AME after glacial melting much quicker than could be predicted from their average dispersal distances, a finding that has highlighted the importance of rare cases of long-distance dispersal in understanding migration capability (Reid 1899; Cain et al. 1998).

Humans appear to have arrived in the AME a few millennia after the retreat of the continental glaciers some 10 ka (Davis 1991). Although there may not have been any formal system of agriculture documented for aboriginal groups living in the AME, there is a suspicion that they transported some economically important species that were part of their livelihood. MacDougall's review (2003) of references to Native American use of plants suggests that aboriginal people made use of and hence could well have dispersed at least the following in the AME region: *Juglans cinerea* (butternut), *Prunus nigra* (Canada plum), *Cornus amomum* (silky dogwood or "red willow"), *Viburnum lentago* (nannyberry), *Acorus americanus* (sweet flag), *Allium tricoccum* (wild leek or ramps), *Apios americana* (groundnut), *Apocynum cannabi-*

num (Indian hemp), and *Chenopodium berlandieri* (Berlandier's goosefoot). The limited or patchy distribution of some of the above (e.g., *Apios americana* and *Allium tricoccum*) suggests that there are populations that may be remnants of distribution and cultivation by Native American peoples. *Apios americana* rarely sets seed in the Maritimes, though it can disperse downstream in river systems via floodwater transport of tubers. Movement of tubers, a valuable food item, by Native Americans seems a likely explanation for its wide distribution along coastal marshes, lakes, and rivers within the Maritimes. *Cornus amomum* and *Viburnum lentago* are largely restricted within the Maritimes to New Brunswick's Eel River (a major aboriginal route between two important river systems, the St. Croix and St. John), and to the St. Croix River.

In later times, the Acadians intentionally brought a selection of useful plants to L'Acadie. Among these, *Inula helenium*, *Lysimachia nummularia*, *Fragaria vesca* Forma *landonii* Boivin, *Daphne mezereum*, and *Tanacetum vulgare* have been identified as characteristic of Acadian settlements (Erskine 1975). All of these species still persist in areas of the AME settled by the Acadians, and the distribution of *Inula helenium* mirrors Acadian settlements particularly closely (Map 526, Roland and Smith, 1969).

Several conclusions can be drawn from the survival and development of the flora over time:

- (1) All our species were once exotics.
- (2) Human introductions of plants may have started shortly after the end of the Wisconsin glaciation.
- (3) Small areas can conserve much diversity (consider the survival of deciduous forest species in favourable pockets bordering the Gulf of Mexico; Delcourt and Delcourt 1977).
- (4) Migration rates are driven by the rare, exceptional events (Cain et al. 1998); any invasive plant now in North America can be dispersed to the AME.
- (5) Different floral elements use different migration routes. Atlantic Coastal Plain species and deciduous forest elements invaded by different migration pathways after glaciation (Roland and Smith 1969). Today, gravel roadsides can suit grassland plants from western North America, wet ditches will work for many wetland species, and beach wrack can support and transport agricultural weeds.

If we want to slow the process of invasion of exotic species, we must consider the areas where exotics establish and build their numbers, the corridors they use to infiltrate the AME, and the species we choose to grow in our gardens.

Habitats available to exotic species

The main focus of this chapter is the exotic plants that have, or will, become invasive of our native plant communities. Here, we assess some common habitat types in the AME that should be available for colonisation by populations of exotic plants. Our aim is to draw attention to the obvious difference among habitats in their susceptibility to being colonised

by exotic plants. We begin by considering “anthropogenically disturbed” habitats where disturbance by humans is relatively frequent; ditches, highway verges, and agriculturally modified ecosystems are typical examples. We then consider habitats that we class to be “native” because they are less frequently disturbed by humans and less obviously shaped by human design. We have included forests in the native category, although the composition of many wooded landscapes is now largely determined by forest harvesting practices. We separate these native habitats into those that support large numbers of established exotic species and those that appear to be relatively immune to invasion. Table 1 is provided to outline general features of the disturbance and fertility regimes of these habitats.

Anthropogenically disturbed habitats

Urban waste areas

These areas are often the point of first entry for new exotic species because of their higher frequency of inadvertent long distance seed transport associated with human commerce. Dozens of exotic species have only been recorded within New Brunswick or Nova Scotia from the vicinity of ports where species may arrive as contaminants in grains headed to grain elevators or, in earlier times, as ship-ballast contaminants.

The open, disturbed conditions of urban wastelands are suitable for a large variety of exotic species. Dwarf annuals fill in cracks in pavement (e.g., *Sagina procumbens*, *Polygonum aviculare*, *Poa annua*), rank annuals fill in disturbed soils (e.g., *Galinsoga ciliata*, *Raphanus raphanistrum*, *Sisymbrium*

altissimum), and mixed herbaceous communities dominated by exotics emerge with time (e.g., *Linaria vulgaris*, *Tanacetum vulgare*, *Dactylis glomerata*, *Sonchus arvensis*, *Cirsium arvense*, *Medicago sativa*, *Melilotus albus*, and *M. officinalis*). In abandoned gardens, some garden plants persist through an aggressive rhizomatous guerilla strategy (e.g., bellflower, *Campanula rapunculoides*; lily of the valley, *Convallaria majalis*; periwinkle, *Vinca minor*) or a phalanx strategy of densely packed stout shoots (e.g., day lily, *Heemerocallis fulva*; and Japanese Knotweed, *Polygonum cuspidatum*).

The high rate of introduction of new exotic plants in urban areas is due in part to the large populations of ornamentals in urban gardens and in well-stocked nurseries. Woody plants may escape from such plantings and spread throughout the region (e.g., *Sorbus aucuparia*, *Quercus robur*, *Acer platanoides*). A local cautionary tale begins at Mount Saint Vincent University, Nova Scotia, with the planting of about a dozen *S. aucuparia* (rowan) trees in the 1960s. These are now starting to die, but their progeny are reproductive at woodland edges, and birds disperse the fruit throughout the fragmented urban deciduous woodland where *S. aucuparia* seedlings outnumber those of all other trees in the understory of these forests. Nurseries are arguably the Trojan horses bringing potential pests to a mostly unsophisticated public who will always be interested in novelty. In the United Kingdom, the horticulture market offers 75 000 exotic species and cultivars, overwhelming a native diversity consisting only of 1500 plant species (Perrings et al. 2005). Almost all woody invasive plants and many invasive herbaceous species were introduced to North American primar-

Table 1. Classification of common habitats in the Atlantic Maritime Ecozone in terms of disturbance, productivity (i.e., soil fertility), and numbers of exotics (mod., moderate; range, varying conditions).

Habitat class (case number)	Specific habitat	Disturbance frequency	Predictability of disturbance	Productivity	Open	Exotic numbers
Anthropogenic (1-a)	Urban wasteland	Mod.–high	No	Range	Yes	High
Anthropogenic (1-b)	Railway	Mod.	No	Low	Yes	High
Anthropogenic (1-c)	Roadside	Mod.	No	Low	Yes	High
Anthropogenic (1-d)	Ditch	Mod.	No	Range	Yes	High
Anthropogenic (1-e)	Pasture	Low	No	Usually high	Yes	High
Anthropogenic (1-f)	Old field	Low	No	Low-mod.	Yes	High
Anthropogenic (1-g)	Arable	High	No	High	Yes	High
Anthropogenic (1-h)	Blueberry barren	Mod.	Yes	Low	Yes	Mod.
			(alt. years)			
Anthropogenic (1-i)	Reservoir shore	High	No	Low–mod.	Yes	Mod.
Native (2-a)	Riverside	High	Yes	Range	Yes	Mod.
	Floodplain	Mod.	Yes	Usually high	Range	Mod.
Native (2-a/3-d)	Woodland edge	Low	No	Range	Range	Mod.
Native (2-b)	Seashore & dunes	High	Yes	Low	Yes	Mod.
Native (2-c)	Maritime headland	Low	No	Low–mod.	Yes	Mod.
Native (3-a)	Salt marsh	Mod.–high	Yes	High	Yes	Low
Native (3-b)	Bog	Low	No	Low	Yes	Low
	Fen	Low	No	Low–mod.	Yes	Low
Native (3-c)	Lakeshore	High	Yes	Low–mod.	Yes	Low
Native (3-d)	Deciduous forest	Low	No	Mod.–high	No	Low
Native (3-d)	Coniferous forest	Low	No	Mod.	No	Low

ily as ornamentals, and this is true of the AME as well (Blaney, unpublished data; see Current and Potential Pests).

Highways

Cars and trucks may directly transport seeds in attached soils. Some surprising long-distance dispersal events in the AME have probably started in this way. In the mid-1990s, a discrete population of the tower mustard (*Arabis glabra*) appeared on granite outcrops beside a secondary road travelled by truckers near New Ross, Nova Scotia, some 320 km by road from the closest population in New Brunswick (Zinck 1998). In 2004, the first eastern North American population of *Rorippa curvisiliqua* was discovered in Kouchibouguac National Park in a former gravel pit along the edge of Highway 117. The roadside location and anthropogenic origin of the site suggest that this population was founded by vehicular dispersal. No other populations are known from any closer than British Columbia, Montana, and Wyoming.

Highways are effective corridors for the linear migration of populations of exotic plants. The first noticeable Scotch Broom (*Cytisus scoparius*) population in Nova Scotia began near Shelburne (Zinck 1998), but in recent decades, this plant has spread throughout southwestern Nova Scotia and into other counties, using the highway as migration route. This is an evergreen-stemmed, nitrogen-fixing shrub, which has become a noxious weed throughout western North America. It now has large populations on highway verges in southwest Nova Scotia where it appears to outcompete the native nitrogen-fixing shrub *Comptonia peregrina*.

Other nitrogen-fixing exotics in the highway setting may have started as deliberate introductions (*Melilotus albus* and *M. officinalis*, *Trifolium hybridum*, *Lotus corniculatus*, *Coronilla varia*) to stabilise or even to decorate the verges (*Lupinus polyphyllus*). While none of the herbaceous legumes appear to pose a threat in native ecosystems, we should monitor populations of *Cytisus scoparius* and determine whether its germination is greater under field conditions in hot summers, as might be predicted from studies of its germination ecology that show that the physical dormancy of its seeds is overcome by incubation at diurnal temperatures of 22 and 17°C or by short exposure to 130°C (Baskin and Baskin 1998). If there is an increase in summer temperatures in the AME, this could lead to greater seedling recruitment of *Cytisus scoparius* through earlier germination in summer or through the exposure of more seed populations to fires.

The gravelly margins at the immediate edges of paved roads are dominated more thoroughly than any other communities in the AME by small exotic annual species. In these habitats, snow ploughing, vehicle traffic, and occasional mowing prevents the establishment of perennials and promotes the dispersal of annuals. Extensive construction of four-lane highways with broad gravel margins in the past 20–30 years has resulted in the rapid spread of a number of annual exotics. All of the following species have become very abundant, at least locally, in the last 30 years on highway margins and

sometimes also on gravel roads in the AME (Blaney, pers. obs.; Roland and Smith 1969; Hinds 1986): *Sporobolus vaginatus* (throughout), *Hypericum gentianoides* (eastern shore Nova Scotia, Halifax to Yarmouth), *Panicum dichotomiflorum* (throughout mainland Nova Scotia, scattered in southern New Brunswick), *Bulbostylis capillaris* (throughout most mainland Nova Scotia, abundant in several regions of New Brunswick), *Nuttallanthus* (*Linaria*) *canadensis* (most of mainland Nova Scotia, scattered in southern New Brunswick), *Polygonella articulata* (Saint John area and westward in New Brunswick), *Lactuca serriola* (most of north-central Nova Scotia and New Brunswick), *Crepis tectorum* (most of New Brunswick; scattered in Nova Scotia, primarily westward), *Puccinellia distans* (throughout), *Chenopodium botrys* (TransCanada Highway from Halifax area, Nova Scotia, to Saint John and Fredericton area, New Brunswick), and *Dittrichia graveolens* (TransCanada Highway from Halifax to Amherst, Nova Scotia). The latter two species are the most recent arrivals among the above, with most of their range extension having occurred in the past 5 years. The first 6 of the 11 species above are North American natives from further south and west. We cannot tell how much of their recent range extension is due to a change in climate and how much is simply a delayed response to the availability of larger highways and increased traffic.

Other characteristic plants of the highway assemblage include *Trifolium arvense*, *T. campestre*, *T. aureum*, *Digitaria ischaemum*, *Panicum capillare*, *Senecio viscosus*, *Matricaria discoidea*, *Tripleurospermum* (*Matricaria*) *maritima*, *Setaria glauca*, *S. viridis*, *Spergularia rubra* (occasionally with the native, otherwise coastal *S. salina*), *Radiola linoides* (along the eastern shore of Nova Scotia), and *Chamaesyce vermiculata* (western New Brunswick and locally in northern mainland Nova Scotia). Two halophytic annuals, *Centaurium pulchellum* and *Symphyotrichum ciliatum*, are also recent arrivals spreading rapidly on highway margins. Both are now widely known in New Brunswick and are present in the Amherst–Halifax corridor.

Railway lines

Railway lines provide linear corridors for plant migration similar to highways. Propagules may be transported in western grains moved by rail car to eastern Canada and also through ballast materials moved to build and repair the track base (*Bromus tectorum*; *Chaenorrhinum minus*, Arnold 1981). The railway line habitat is exceptionally poor, with generally coarser gravels that are even drier than those on highway margins, and this selects for short-lived, low-stature, stress-tolerant ruderals. The exotic community along railroads is very similar to but generally less diverse than that along highways. Among the most characteristically railroad-associated exotics in the AME are *Bulbostylis capillaris*, *Collomia linearis*, *Chamaesyce maculata*, *C. glyptosperma* (all North American natives from further south and west), and the Eurasian *Chaenorrhinum minus* and *Lappula squarrosa*, with only *Chaenorrhinum minus* being common and nearly ubiquitous on railways.

Species Diversity in the Atlantic Maritime Ecozone

It must be noted that many of the railway lines no longer serve trains and that such abandoned habitats will support a plant community that is slowly undergoing secondary succession. A group of secondary successional plants become established along such lines that include the non-natives *Hypericum perforatum*, *Tanacetum vulgare*, *Linaria vulgaris*, and *Matricaria discoidea*.

Ditches

Ditches are most often features of roads and highways and are thus an intermittent linear corridor for species' migrations. Many exotics occupy this zone, but those of greatest concern as invasives are *Phalaris arundinacea* (common in the AME), *Lythrum salicaria* (locally common in the AME, primarily in more fertile regions), and the European form of *Phragmites australis* (Catling et al. 2004), which is still fairly local in the AME. All of these are tall herbs that are competitive dominants, which can greatly reduce the diversity of the communities they invade (Keddy 2001). The highway ditch serves as a corridor for plant dispersal, as is evident in the case of *L. salicaria* on the stretch of the TransCanada Highway between Moncton and Fredericton, New Brunswick. This highway was completed in 2001, and since that time *L. salicaria* has become fairly common in roadside ditches over an 80 km stretch through a sparsely populated area where the species is otherwise absent or uncommon.

Pastures

Pastures are predominantly composed of European species. The most ubiquitous pasture grasses throughout the AME include the exotics *Poa pratensis*, *Agrostis capillaris*, *A. gigantea*, *Alopecurus pratensis*, and *Phleum pratense*. In similar fashion, exotic legumes would almost always include *Trifolium repens* and *Trifolium pratense*. All of these grasses and legumes have been intentionally introduced, and all of these have become widely established in old fields, waste areas, and headland meadows. *Poa pratensis* and *Phleum pratense* can also be abundant in some arable cropping systems where they can establish large soil seed reserves (maximum values = 6380 and 4120 seeds m⁻², in Hill et al. 1989). Many of the most common forbs in pasture systems are naturalised introductions. These usually include *Ranunculus repens*, *R. acris*, *Cirsium arvense*, *Vicia cracca*, *Galium mollugo* (extensive spread in past 20–30 years and highly invasive in some pastures), *Achillea millefolium* (native and European forms), *Rumex acetosella*, *Hieracium* spp., *Leucanthemum vulgare*, and *Stellaria graminea*.

Old fields

Across North America, the extent of forested land was lowest in the early twentieth century (Fredericksen 1998; McLachlan and Bazely 2001). Thereafter, much land that had been agricultural was left to undergo secondary old-field succession. In the AME, many old fields are now forest or dense shrublands where the cover of exotic species is typically in decline as native woody species shade out open-ground exotics.

Invasive woody exotic species are not nearly as common in the AME as they are in more heavily settled areas to the south and west, but glossy buckthorn (*Rhamnus frangula*) is locally problematic and is rapidly spreading in at least six separate regions of New Brunswick and Nova Scotia. Where present in the AME, it is often more frequent within relatively natural riparian forest systems than in old fields, but at least in the border region of New Brunswick and Nova Scotia, there are old fields where it reaches heavy dominance and is clearly filling the role typically occupied by native shrubs such as *Alnus incana* subsp. *rugosa*, *Amelanchier* spp., and *Viburnum nudum* var. *cassinoides*. Additional woody exotics noted as problematic invasives in other regions of North America but still rare or only locally common within the AME include *Lonicera tatarica* and related species and hybrids, *Berberis vulgaris* and *B. thunbergii*, *Rosa multiflora*, *Crataegus monogyna*, and *Rhamnus cathartica* (the latter three species reach high densities in a few locations in the AME).

In the herbaceous phase of old-field succession, there are many exotic species, generally including the same common species noted above under pastures and hay fields but also including many introduced species of *Hieracium* (e.g., *H. caespitosum*; *H. pilosella*; *H. × flagellare*, a hybrid between the first two species; *H. aurantiacum*; *H. floribundum*; and *H. piloselloides*). Most of these exotics are of limited consequence for native habitats because they require nearly full sun and are displaced by native species over time through succession. *Valeriana officinalis* is one rather invasive species of moist old fields that has spread a great deal in the AME over the past 20–30 years and may be worth further scrutiny. It is locally escaped from cultivation throughout the AME, but its distribution as a fully naturalised and spreading plant is centred in the New Brunswick–Nova Scotia border region where it has spread locally into native fens and graminoid wetland.

Arable land

The weed flora of arable land is principally made up of introduced plants. In a survey of cropped lands in Nova Scotia, 22 of the 25 dominant weeds among oats, beans, and winter wheat were introduced summer annuals, winter annuals, and perennial forbs and grasses (Hill et al. 1989). Weeds are introduced as impurities in livestock feed and in seed. Notable contaminants include *Raphanus raphanistrum*, *Vicia* spp., *Avena fatua*, *Abutilon theophrasti*, and *Barbarea vulgaris*. The noxious weed lists of Quebec and Nova Scotia are principally aimed at reducing the risk of weeds reaching arable or pasture lands. Nova Scotian concerns on arable land include *Abutilon theophrasti*, *Cyperus esculentus*, *Euphorbia esula*, and *Silene latifolia* (*Lychnis alba*). In the AME zone of Quebec, only three species of *Ambrosia* are listed as noxious weeds of which *Ambrosia trifida* and *A. artemisiifolia* are troublesome nonexotic weeds of arable land (Invaders Database System 2005). Of the four Nova Scotian noxious arable weeds, only *Silene latifolia* has become widely naturalised; the others have a scattered distribution. Of the scattered weeds, the Noxious Weed Act may

have helped curb the spread of *Cyperus esculentus*, although this species has generally low dispersal powers and largely relies on the distribution of its vegetatively produced nutlets in soils attached to farm machinery.

Burned barrens

The area of periodically burned and herbicide-treated barrens for the cultivation or enrichment of the lowbush blueberry has greatly increased in the AME. While naturally occurring barrens on sand have generally low cover of exotic species only, exotic species can dominate managed barrens. In an agricultural area, Wesley et al. (1986) observed high cover of introduced grasses, *Agrostis capillaris* and *Festuca filiformis*, whereas in a less fertile, upland region (Cobequids), there was substantial cover of *Hieracium pilosella*. Despite the cover of these weeds, there was no indication that interspecific competition involving these species had reduced the fruit yields of *Vaccinium angustifolium*.

Reservoir shores

Water bodies that are dammed for hydroelectricity generation normally include a head pond immediately above the turbines, which is maintained with little variation in water level, and a storage reservoir that is subject to greater intra- and inter-annual variation in water level fluctuations than naturally fluctuating lakes (Hill et al. 1998). Reservoirs may be viewed as the freshwater analogs of agriculturally or industrially disturbed terrestrial areas (Havel et al. 2005). Taken together, head ponds and storage reservoir shorelines had significantly more exotic plants than the shorelines of natural lakes. In addition, the number of exotic plants was greater on the shorelines of previously dammed or “recovering” lakes than on currently dammed systems (Hill et al. 1998). The differences between naturally regulated lakes, currently dammed lakes, and lakes recovering from damming suggested to Hill et al. (1998) that introduced species were excluded from these natural systems with predictable disturbance and stress but were able to invade systems where either intra-annual or inter-annual variations were excessive and surpassed the tolerance abilities of the natural community. At these hyper-variable levels, exotic species with short life cycles established in the modified systems. Interestingly, there were no exotics found on the wide shores of the largest inland water body of Nova Scotia, the Lake Rossignol reservoir. Exotics may fail to establish while many native upland species do, because the species pool of exotics in the forested land that surrounds the reservoir is very low (Hill et al. 1998).

Native habitats subject to invasion

Riversides and floodplains

The disturbance regime of rivers and streams sets up the open conditions required by many light-demanding, herbaceous species. There is a wide range in the intensity, period, and variability in disturbance that is dictated by the position of

a plant community in the catchment area of the river as well as its vertical position on the river bank and its relationship to the river’s meanders. In addition, the herb plant community is greatly influenced by the geography within the AME and by the native soil type, as MacDougall (2001) has noted with reference to the deciduous forest flora of the Saint John River Valley.

The seasonally dry, open sand, gravel, or cobble bars and shoreline rock outcrops of most rivers (even those in relatively unsettled areas such as the Restigouche River in northern New Brunswick) support a range of exotic species, few of which are specialised to these habitats within the AME. Some of the most characteristic plants of these habitat types include *Tussilago farfara*, *Silene vulgaris*, *Hypericum perforatum*, *Melilotus albus*, *Barbarea vulgaris*, *Galium mollugo*, and *Centaurea nigra*. Closer to the shoreline, or in moist, seepy areas, *Phalaris arundinacea* (which probably includes both native and exotic types in the AME) can form extensive monocultures. Along the Saint John River in the vicinity of Hartland, New Brunswick, an increase in *P. arundinacea*, perhaps associated with nutrient enrichment from agricultural runoff, has been implicated in the decline of diverse shoreline seepage meadows over limestone outcrops, which support a large number of rare species, including the regional endemic *Symphyotrichum anticostense*. Wetter river-shore habitats support a different range of exotics, with *Polygonum hydropiper*, *P. persicaria* (including *P. minus* on the Saint John River), *Gnaphalium uliginosum*, and *Panicum capillare* (perhaps partially native) being common annuals of exposed wet mud or sand. *Myosotis scorpioides*, *Rorippa microphylla* (*Nasturtium aquaticum* var. *microphyllum*), *Rorippa sylvestris* (locally on the Saint John River), and *Lythrum salicaria* are often present along river shores or in shallow water.

Relatively low numbers of exotic species (*Galeopsis tetrahit*, *Taraxacum officinale*, *Ranunculus repens*, *Veronica officinalis*, *Senecio jacobea*, and *Solanum dulcamara*) were recorded in surveys of hardwood communities in the flood zone of several rivers in Nova Scotia (Hill, unpublished). In general, however, floodplain deciduous forests having calcareous soils are the most heavily invaded forest habitats within the AME, presumably as a result of the combined effects of the following:

- (1) Natural flood disturbance regularly creating open niches and promoting propagule dispersal;
- (2) Higher human populations in the surrounding areas, associated with the fact that agriculture is better within rich river valleys than within surrounding, often acidic, uplands. The surrounding human populations provide introduction opportunities for more agricultural weeds and ornamentals, and create more disturbance within forest communities than in areas of lower population density;
- (3) Fertile soils providing potential habitat for a greater range of exotics.

There is a substantial suite of invasive exotics restricted to, or strongly associated with, calcareous floodplain forests in the AME. This complex of invasives is most diverse and dominant

along the Saint John River north of Woodstock, New Brunswick, but is also evident on many smaller rivers within generally agricultural regions (i.e., Blaney 2004). *Salix* × *rubens* and *Acer negundo* can both become important canopy trees in disturbed floodplains. Norway maple (*Acer platanoides*) has dispersed from plantings in the fertile floodplain of Smiley's Provincial Park on the Meander River in Nova Scotia, but although saplings have become established in thickets at the edge of Sugar Maple (*Acer saccharum*) woodlands, which contain populations of the provincially rare herb *Caulophyllum thalictroides*, only saplings of the native maple were present in the woodland interior (more than 10 m from the edge; Hill and Mount Saint Vincent University class obs., 2002). *Rhamnus frangula*, and less commonly *R. cathartica*, can form dense subcanopy layers. The *R. frangula* subcanopy layer under mature, undisturbed silver maple near the Saint John River, east of Fredericton, New Brunswick, is so dense that it clearly reduces the total cover and individual plant size in the herbaceous dominant *Onoclea sensibilis* (Blaney, pers. obs.).

Herbaceous exotic plants achieving high percentage cover in floodplain forests include *Alliaria petiolata*, *Poa nemoralis*, *Lapsana communis*, *Geum urbanum*, *Hylotelephium* (*Sedum*) *telephium*, *Hesperis matronalis*, and more locally *Scrophularia nodosa*, *Cardamine impatiens*, *Anthriscus sylvestris*, *Aegopodium podagraria*, and *Impatiens glandulifera*. At forest edges, thickets and meadows, *Polygonum cuspidatum*, *Arctium lappa*, *Angelica sylvestris*, and *Helianthus tuberosus* (which may have been introduced before European settlement by Native Americans) can all form dense stands.

Seashores and dunes

Seashore communities are disturbed by erosion driven by the waves and by salt spray, which kills vegetation. Few native or introduced species are open-beach specialists, but among them are two exotics, *Atriplex laciniata* and *Salsola kali*, which probably never occur at densities high enough to be considered invasive. Upper-beach communities receive large nutrient inputs from rotting seaweed in the wrack zone. Common introduced plants in this zone include *Atriplex littoralis*, *Chenopodium album*, *Raphanus raphanistrum*, *Brassica rapa*, *Sonchus arvensis*, *Tripleurospermum* (*Matricaria*) *maritima*, *Artemisia stelleriana*, and *Senecio sylvaticus*. Among these, *Sonchus arvensis* and *Artemisia stelleriana* can both achieve high densities at times, usually in areas subject to intense natural or human disturbance.

On coastal sand dunes, the exotics *Elymus repens*, *Poa pratensis* and *P. compressa*, *Melilotus alba*, *Trifolium campestre*, *T. repens*, *Linaria vulgaris*, *Vicia cracca*, and *Hieracium* spp. often occur at fairly high densities. The large shrub *Rosa rugosa* is also widely present on dunes and coastal headlands, appearing locally invasive in extreme southern Nova Scotia. *Rosa rugosa* is rampant on seashores in Sweden and Latvia and could well increase its range in the AME. Despite its potential for becoming invasive in this natural habitat, it is widely planted in the AME, a good example being the miles-long

corridor of *Rosa rugosa* planted in the median of Dunbrack Avenue in Halifax, Nova Scotia. Since this is a route leading to sandy beach habitat, seeds from these plantings could easily found populations of *R. rugosa* on nearby beach habitats.

Maritime headland grasslands

There would have been a limited amount of native grassland in the AME before the widespread clearances for agricultural grazing by the Europeans. The grasslands on seaside headlands and islands are, in some cases, altered examples of native communities maintained by wind and sea spray or sometimes by fire. The extent of these communities has, in many cases, probably been greatly expanded from their original condition, as forest clearance and intensive grazing created new open habitats that regenerate to forest very slowly owing to harsh coastal conditions. In settled areas, these headland communities are now generally a mixture of native and non-native species typical of old field and pasture. No exotic species, with the possible exception of the uncommon *Carex panicea* in Nova Scotia, seem to be strongly restricted to coastal headlands, but several exotic, hemiparasitic Scrophulariaceae (*Rhinanthus minor*, *Euphrasia stricta*, *E. nemorosa*, and *Odontites vernus*) are especially common in these habitats. Efforts to rid native grassland of introduced species are widespread in central North America, California (Wolfe and Klironomos 2005), and in the Pacific Northwest (MacDougall and Turkington 2005), but no serious attention has been given to grassland restoration of maritime meadows in eastern Canada.

Relatively uninvaded native habitats

Identifying native habitat that does not support exotic species is as important as identifying the problem areas. By examining the qualities of these ecosystems, we may appreciate better why exotics establish in other habitats. How are the relatively exotic-free habitats below able to resist invasion? How is this resistance related to disturbance, light availability, or fertility characteristics? If light availability and fertility are required to support the fast growth of exotic ruderals, it may be no coincidence that in all the habitats where exotics are rare, soil fertility is low (bogs, fens, swamps, lakeshores, alpine zones) when light is available at ground level and light availability is low where nutrient availability may be in moderate supply (deciduous forests). In low fertility, low biomass ecosystems, disturbance resulting in a temporary increase in soil nutrient availability (Gross et al. 2005), or fertilisation (Leishman and Thompson 2005), increased the prevalence of exotic species in native communities.

Salt-marsh grasslands

Salt-marsh grasslands have not been invaded by any dominating species in eastern Canada, although the east-coast *Spartina alterniflora* and European *Spartina anglica* have invaded the intertidal in the Pacific Northwest as has *Spartina* × *townsendii* invaded European and New Zealand mudflats. *Atriplex littoralis* and *Suaeda maritima* are common in the

Spartina patens intertidal zone in many areas, and *Sonchus arvensis* and various old-field exotics can occur along the inland edge of salt marshes. Scarcer salt-marsh specialist exotics in the AME include the South African *Cotula coronopifolia* and the recently arrived European *Centaureum pulchellum* and *Symphyotrichum ciliatum*, which is native to saline wetlands of west-central North America. All in all, however, the salt-marsh communities of the normal intertidal zone in the AME seem minimally influenced by exotics at present.

Bogs and fens

When hydrological regimes in these wetlands are unmodified, few exotic species colonise them. *Pinus sylvestris* and *Rhamnus frangula* are both capable of becoming invasive in open peat, but these are not known to be invasive in this habitat in the AME. Species lists from peatland systems in the AME are generally exclusively native. When such wetlands are modified by road construction, robust native clonal graminoids such as the cosmopolitan *Typha latifolia* or *Calla palustris* can spread through the wetland. There are, however, generally no exotic species present nearby that are capable of taking advantage of altered hydrological regimes in such cases. Wilcox (1995) cites both *T. latifolia* and *Lythrum salicaria* as disturbance species that invaded wetlands with altered hydrological regimes. It is probable that a lowering of the water table in hydrologically disturbed sites led to increased mineralisation rates in the sediment, which would thereby increase the supply of nutrients to the exotic plants. In cases where the fertility remains poor despite hydrological modification (e.g., mined peat bogs), there may be no such invasion by exotics.

Aquatic habitats and lakeshores

In hydrologically unmodified lakes in a region of very acidic soils in southwest Nova Scotia, Hill et al. (1998) found no exotic species on the shores of nine large catchment area (>50 000 ha) lakes and only one exotic species at 12 low catchment area (<2000 ha) lakes. Since intense flood and ice scour disturbance occurs in large catchment area systems, these results indicate that either lakeshore plant communities exclude would-be invasive plants or the exotics are not capable of tolerating the stresses and disturbances of the natural system. The relatively high species richness (average 2.6 species per lake) of exotics on shores of lakes that were dammed but are now subject to natural fluctuations, in comparison with that on lakes that were never dammed (average 0.08 species per lake), suggests that the plant community of the intact systems resists invasion by exotic herbs (Hill et al. 1998). In later unpublished field work (2002) in the same region, Blaney also observed very few exotics on the shores of hydrologically unmodified lakes; a summary report indicated that while exotics were abundant in the surrounding agroecosystems, they were curiously rare on the lakeshores themselves (Eaton and Boates 2003).

We are fortunate in the AME to be largely free of invasive aquatic plants, which are problematic in the Great Lakes region and many areas of the eastern United States. The Eurasian

Myriophyllum spicatum has only recently been discovered in the Maritimes from single, small lakes in New Brunswick and Prince Edward Island. The western *M. quitense* (considered potentially native in the east, i.e., Day and Catling 1991) has long been known from Prince Edward Island and no other eastern North American sites, and has recently been found to be common in a large area of the lower Saint John River estuary (McAlpine et al. 2007). *Myriophyllum heterophyllum*, an eastern North American native, grows very densely locally on the lower Saint John River. The native origin of *M. heterophyllum* has never been questioned, and there are many other southern species with disjunct populations in the same region, but the species is considered an invasive exotic in Maine. *Butomus umbellatus* has been found in a handful of Maritimes locations, but is only abundant at one site on the estuary of the Eel River in northwest New Brunswick. Further time and search effort will likely document the spread of other invasive aquatics of limited current distribution in the AME, such as *Nymphoides peltata*, *Hydrocharis morsus-ranae*, and *Potamogeton crispus*, as there appear to be no environmental barriers to their occurrence over large portions of the region.

Upland forest

Exotic woody species are commonly present within forests at edges or in open woodlands and are common in small, fragmented forests within agricultural or urban landscapes. Several bird-dispersed woody exotics (e.g., *Sorbus aucuparia*, *Rhamnus frangula*, *R. cathartica*, *Ribes rubrum*, *Daphne mezereum*) may be capable of establishing populations in undisturbed forest in the AME. The *Rhamnus* species and *Sorbus aucuparia* are capable of reaching high densities in deciduous forest and could limit the establishment of native shrubs. *Rhamnus cathartica*, although currently less frequent than *R. frangula*, may pose a greater risk for intact forest communities than its congener, since it occurs in more shaded habitats (White et al. 1993). The success and threat of *R. cathartica* may lie in its extended growth period, since Harrington et al. (1981) reported that its leaves persisted 58 days longer than the average for native shrubs. The European Rowan, *Sorbus aucuparia*, has naturalised across North America. In fragmented urban hardwoods in Nova Scotia, it was observed to be dispersed principally by crows and to establish on woodland edges and on moss patches within the woodland. In St. John's, Newfoundland, it occurs with *Sorbus americana* in dense natural thickets on Signal Hill, although outside the city limits, it was rarely observed (Hill and S.P. VanderKloet, pers. obs., 2003).

In a recent seed-bank study of an old-growth, hardwood forest on Mont St. Hilaire, Quebec, Leckie et al. (2000) recorded 8 “alien/weedy” species in a seed bank that included 51 species and reported that the density of the exotic seed bank was “usually one or two orders of magnitude less than that of native species” (Leckie et al. 2000, p. 190). With the exception of *Taraxacum officinale*, “alien species from the developed landscape around this fragment of old-growth forest do not seem able to colonize the forest seed bank” (Leckie et al.

2000, p. 190). Morash and Freedman (1983) also reported low numbers of exotic weeds in mature and clear-cut hardwoods in Nova Scotia. The exotic herbs most commonly present within the AME forests include *Ranunculus repens*, *Veronica serpyllifolia* subsp. *serpyllifolia*, and *Rumex obtusifolius* (all generally associated with seepage or forested streams), *Galeopsis tetrahit*, *Veronica officinalis*, and *Hieracium lachenalii*. Of these, *Ranunculus repens* and occasionally *H. lachenalii* occur in sufficient densities to potentially cause reductions in native plant diversity on a very local scale. All of the above species are most common in more disturbed forests but can be present in apparently undisturbed sites as well. *Poa nemoralis*, *Alriaria petiolata*, and perhaps *Impatiens parviflora* (relatively common on Prince Edward Island) are all uncommon at the level of the whole AME, but they can be locally abundant and may become widespread invaders in time.

Processes

Before outlining the various models that try to account for the outbreak of invasive species, it is worth mentioning that only infrequently do studies of invasives document whether their abundance is any higher in the foreign, invaded land than it is in the home range of the exotic (Hierro et al. 2005). There are, however, many undeniable cases where such a demonstration would be a formal exercise only, as in the cases of *Cytisus scoparius* and *Rubus discolor* in the Pacific Northwest, kudzu (*Pueraria lobata*) in the American south, and *Lythrum salicaria* in wetlands of southern Ontario and New England. Whether there are such cases in the AME needs to be documented, but the relative abundances of *Hieracium pilosella* and *H. × flagellare*, *Leucanthemum vulgare*, *Centaurea nigra*, *Solanum dulcamara*, *Polygonum cuspidatum*, and *Linaria vulgaris* in the AME could well be greater than in their native ranges.

Exotics as indicators of disturbance

It was evident in the last section that exotics were often associated with disturbed conditions. Disturbance, defined as the removal of biomass (Grime 1979), provides a high light environment where the competition for nutrients and moisture is reduced. Such conditions allow establishment and growth of fast-growing, ruderal species (sensu Grime 1979). In fact, Jenkins and Pimm (2003) map the putative size of the “global weed patch” by mapping three types of disturbed areas: croplands, drylands, and cleared forests. Farnsworth (2004) used a clustering technique to divide sites occupied by rare species that might be subject to invasion by exotics. The first split separated sites on the basis of threat types to deliver one lead without invasives and one lead with invasives that was subject to a variety of threats including seven that were related to disturbance (dumping, altered hydrology, trampling, herbicide use, drought, erosion, and natural disturbance). Whether such sites actually had invasive species was a split that depended upon the presence of roads nearby. In similar fashion, Gross et al. (2005) found that grassland community invasibility de-

pended upon disturbance, a finding similar to those described above for wetlands (Hill et al. 1998; Wilcox 1995). In these latter cases, disturbance may have led to invasion by exotics, but it may have done so by causing a temporary increase in the availability of soil nutrients (Gross et al. 2005). This mechanism has been termed the “fluctuating resources hypothesis”, and it can be brought about by disturbances that impair the uptake abilities of the resident native species or by increases in nutrient availability, which are in excess of the uptake abilities of the native flora (Davis et al. 2000).

It would be comforting to think that the distribution pattern of naturalised introduced plants simply mirrored anthropogenic disturbance patterns (e.g., Jenkins and Pimm 2003). In this case, we could look at introduced species as a quick response team of species that are simply better able to repair disturbance and set in motion secondary succession. This view is not without merit, and it was long ago suggested by Aldo Leopold (1949) that the effects of the Dust Bowl had been minimised by the efficient spreading of the exotic *Poa pratensis*. The question becomes, How do exotic species preempt native species, modify the structure of plant communities, and change the course of succession?

Invaders affect and are facilitated by soil processes

In some cases, invasive species themselves can modify soil processes to either facilitate invasion by individuals of their own species or by other invasive species. Humans have been taking advantage of this process since the dawn of agriculture whenever they planted legumes to enrich the soil to benefit non-nitrogen-fixing crops. When an exotic nitrogen-fixing invasive plant naturalises in natural areas that contain species that have lower rates of nitrogen fixation, the relative enrichment of the soil brought about by the invader can profoundly alter community dynamics. The most publicised of these cases is the invasion of Hawaiian natural areas by *Myrica faya*, which has led to the enrichment in nitrogen of wild areas and to the facilitated invasion of these areas by other weeds (Vitousek and Walker 1989). A less documented case is occurring in the Pacific Northwest where Scotch broom (*Cytisus scoparius*) has overrun grasslands and all low-elevation nonwooded habitats. All land-holding conservation organisations are involved in an effort to rid native habitat of this invader, which as was the case in Hawaii, is the only dominant nitrogen-fixing shrub. Although there is no documentation to support the link, it appears that the invasion of grasslands in the Pacific Northwest by *Arrhenatherum elatius*, *Hypochaeris radicata*, and a suite of other herbaceous species may be facilitated by the fixation of atmospheric nitrogen by Scotch broom. In the AME, *Trifolium repens*, introduced in the eighteenth century (Mack 2003), could well have altered community structure of native coastal grasslands, since they would receive large nitrogen inputs from this productive legume (Elgersma and Hassink 1997). The fact that *Cytisus scoparius* is displacing the native nitrogen-fixing shrub *Comptonia peregrina* on sandy, nutrient-poor highway verges and woodland edges in Nova Scotia suggests that

Scotch broom may rival the indigenous nitrogen-fixing shrub in its nitrogen-fixing capabilities in the AME. The abundance of this species in the climatically mildest corner of Nova Scotia (Shelburne Co.) suggests that its range expansion may be limited at present by prevailing climate. Should climate change and become warmer in future, this species could be a problem for the AME as it has been in the Pacific Northwest.

Exotic plants can bring about a variety of other changes to the soil community, and these affect decomposition and nutrient mineralisation rates, mycorrhizal relationships, pathogenic microorganisms, and soil structure (Wolfe and Klironomos 2005). At present, there are no documented examples of any of these phenomena associated with any invasive plant in the AME, however, several of the introduced species having such effects do occur in the AME. There is the potential for allelopathic interactions in grassland invaded by *Hieracium* spp. (e.g., *H. pilosella*, *H. × flagellare*, *H. aurantiacum*; c.f. *H. pilosella* in Makepeace et al. 1985) and for the alteration of decomposition characteristics in wetlands invaded by *Typha* or *Phragmites*. The non-mycorrhizal *Alliaria petiolata*, a problematic invasive locally within western New Brunswick, may undermine the mycorrhizal relationships of other woodland herbs, the majority of which are mycotrophic (Roberts and Anderson 2001). Roberts and Anderson (2001) observed a negative correlation between the presence of *A. petiolata* and mycorrhizal frequency in woodland communities of Illinois and found that water extracts of garlic mustard inhibited the germination of mycorrhizae spores. It is not clear whether populations of *Centaurea nigra* in the AME could exert similar impacts on the soil microbial community, as have been documented for *C. diffusa*, or whether the interactions between *C. nigra* and the soil microflora might be beneficial to growth in its foreign range (i.e., Nova Scotia), as has been found with congener *C. maculosa* (= *C. biebersteinii*) (Wolfe and Klironomos 2005).

Enemy escape and biotic control hypotheses

A long-standing and largely untested hypothesis that exotic species have greater population growth in their foreign, invaded lands than in their native ranges, because they escape their enemies (biotic interactions) in their native ranges, was upheld by two back-to-back papers in *Nature* (Mitchell and Power 2003; Torchin et al. 2003). In both papers, it was found that species had fewer parasites in their introduced ranges. For 26 animal taxa, the number of parasites in the native range was double that in the introduced range (Torchin et al. 2003), and this difference was more pronounced for plant species, which had six times the number (average 3.6 versus 0.6 species per plant) of fungal pathogens in the native range than in their introduced range (extrapolations from Fig. 2, in Mitchell and Power 2003). In the introduced range, fungi from the native range were a minority (ca. 40%), and clearly, fungi in the foreign land were not exploiting these new potential hosts. Blaney and Kotanen (2001) tested this escape hypothesis at the seed survival level using old-field representatives in Ontario. They

tested the relative abilities of seed of native and exotic taxa to survive seed predation in the soil but found no evidence that exotics survived in greater numbers than their confamilial native counterparts.

There are some indications that the escape from predators and pathogens may be temporary. The much proclaimed population explosion of *Linaria vulgaris* in eastern North America in the nineteenth century appears to have subsided. This may have resulted in part from competition from other aliens, although parasites and pathogens may have also played a role. As the escape hypothesis predicts that species will have more impact on ecosystems in foreign lands where they find fewer pathogens and predators, the biotic resistance hypothesis predicts that with time, pathogens and predators will recognise or adapt to the invading organism and will so reduce its impact. There is clear support for the biotic resistance hypothesis in Mitchell and Power (2003), and this process provides a potential long-term ecological solution as introduced species become first, naturalised; second, pests; and third, parts of the flora that have adapted to and coevolved with the surrounding biota. Understanding the potential for biotic resistance does not require a sit-and-wait approach. We can decrease the waiting time by actively exploring potential bio-control agents, as has been successfully accomplished with *Hypericum perforatum* and as has been attempted with *Lythrum salicaria* (Malacki et al. 1993). The potential dangers, however, inherent in introducing organisms to control introduced organisms needs no elaboration.

Predictions

Can we predict which species will reach our region, which will naturalise, and which will become pests? Many of our exotic species appear to fit in, having ranges and occurring at a frequency in keeping with a normal, uncommon native plant, while others expand rapidly and occur at densities sufficient to alter natural communities.

Goodwin et al. (1999) attempted to predict which European species were established in New Brunswick based on individual species characteristics. They compared naturalised and non-naturalised species using congeneric pairs from Europe. One hundred and sixty-five pairs were identified. Two thirds of the pairs were analysed to develop models to predict invasiveness from life history and geographical variables; one third of the pairs were reserved to test the models developed. Initially, it was found that naturalised species were significantly taller than noninvasive congeners, and the flowering period of naturalised species in Europe was significantly longer than that of the non-naturalised species (0.75 months on average). No confirmation could be obtained using the reserved species. A second model was developed that used the same life-history variables and European geographic range. These authors found that the influence of range was more important than life history, and when the range based model was tested, a significant logistic regression using the reserved species correctly predict-

ed 71% of the naturalised cases and 73% of the non-naturalised cases. Goodwin et al. (1999) reason that geographic range is correlated with flowering period. Furthermore, “The species that are likely to be inadvertently picked up and moved to new locations due to their wide distribution, are the same species that are likely to succeed in a new environment due to their wide environmental tolerance” (Goodwin et al. 1999, p. 424). So weedy plants are weedy because they have wide tolerances, which results in wide ranges, which results in greater sampling likelihood, and their inherent weediness (ruderal characteristics sensu Grime 1979) then starts the same process as the plants become invasive in the new land.

Despite the circularity of the above argument, the range-size observation has been linked to invasive potential in other studies. Scott and Panetta (1993) predicted weed status in Australia for plants of South African origin from geographic range size. Prinzing et al. (2002) analysed invasiveness in Argentina in a group of species of European origin, similarly using range size as a variable but also including the following: utilisation by humans, preadaptation environment (preference for warm, dry, nitrogen-rich conditions), versatility (representation among different floristic zones), and a ruderal life strategy. From these variables, they correctly predicted 81% of the alien species. It should be noted that 73% of the European species in two Argentine provinces listed in Prinzing, are also aliens in the AME.

Current and potential pests

Before we try to assemble a list of pests, it is important that we do not take frequency or cover alone as the measure of potential harm. In a recent review of *Plant Invasions: Ecological Threats and Management Solutions*, Rejmanek (2004, p. 401) notes that despite the progress in the field, “one chronic weakness . . . still remains: a lack of rigorous evidence for assumed harmful impacts of invasive taxa”. Given the immense challenge in controlling any weed that has reached pest status, this is an alarming conclusion by a worker who is well established in the invasion biology field. Anthropogenically disturbed areas are the havens for exotic species, and before we identify any prolific species as a pest, we should ask, or test through experiment, what would be in these disturbed areas if exotics were not present. This was done for arable land in Nova Scotia by Patriquin et al. (1986) who experimented with several field crops that were being grown with only mechanical control of weeds. In experiments where weeds were hand-pulled from field quadrats in a faba bean field, crop losses from weeds were 25% where total biomass was low (<6 tons/ha; $n = 8$) and less than 2% where total biomass was high (>6 tons/ha; $n = 7$). In two oat fields where weeds were eliminated by herbicide (MCPA), crop losses to weeds were 8% (not significant) and 20%. Whether such differences warrant weed control is not the domain of this paper, however, if a situation does call for weed control, one may not be able to identify the dominant weed as a particular pest if the weed complement is diverse; in these

cases, if one troublesome weed was removed, many other candidate species could fill the breach. Hill et al. (1989) documented large weed shifts in the absence of chemical control on two fields growing beans and winter wheat over one course of a four-course crop rotation (1979–1983). In beans, large decreases in cover of *Elymus repens* and *Euthamia graminifolia* were complemented with corresponding increases in *Polygonum hydropiper* and *Taraxacum officinale*; likewise, in winter wheat, *Galeopsis tetrahit* and *Vicia tetrasperma* gave way to *Cerastium fontanum* and *Poa pratensis* over the 4 years. Weed control in the narrow scope of a single farm must be seen as an equation where the costs of weeds include losses to the current crop and combining problems, but the gains include the conservation of nitrogen when crops are not actively growing, reduction in erosion and runoff, and the production of organic matter (Patriquin et al. 1986).

Similarly then, the exotics that naturalise in areas of anthropogenic disturbance must be seen as beneficial when they protect habitats from erosion and so protect freshwater ecosystems. We should separate the beneficial or neutral cases from the cases where introduced species are clearly pests. The designation of a species as a “pest” must be reached by a process through which it has been objectively demonstrated that a species (1) causes a significant reduction in crop yields, which is peculiar to that pest species, (2) clogs waterways, (3) has a deleterious impact on the outcome of succession, or (4) causes significant losses in populations of vulnerable species that are not related to the disturbances that facilitated population growth of the introduced species. We have to be clear in our objectives and science, otherwise costs of nontarget impacts of any programme aimed at reducing the populations of a third of our taxa may be unacceptably high.

In cases, the conservation goal of reducing the presence of introduced plants may be most easily achieved through herbicide application, as is claimed for many grassland communities where native plants have been outcompeted by exotic weeds (Wilson and Gerry 1995). For the most part, we still do not understand how much of the explosion in populations of exotic species in these areas is due to changed environmental conditions. In some ecosystems, the relationship between outbreaks of exotics and a changed environment is clearer. In the Pacific Northwest, the suppression of the fires that were part of a deliberate regime by aboriginal peoples to manage grasslands for their food production has allowed the invasion of such areas by *Cytisus scoparius*. In this case, both burning and herbicide use have reduced the populations of this pest in some ecologically valuable prairies (Fuchs 2002; Dunwiddie, pers. comm., 2005). The long-term goal in restoring such prairies is to find a management strategy that maintains a stable native prairie community without large populations of exotics. To get there will require intensive management where the ecological benefits (a fully functioning, diverse native prairie) may have significant environmental costs during the transition period (nontarget effects of herbicide, increased erosion rates, local smoke pollution).

In the case of the Pacific Northwest prairie, a return to an anthropogenic, traditional disturbance regime may enrich the native grassland community and keep exotics at bay. We are facing the opposite problem with some regional or global environmental changes when they present new disturbance regimes. In the AME, the deposition of acid rain continues to be a disturbance, which results in increased sulphur and nitrogen deposition on wild lands. This has caused a shift from native shrubland to grassland in Europe (Aerts and Berendse 1988). New disturbances (e.g., ozone thinning or climate warming) may unbalance native communities if the performance of key species is positively or negatively affected. If climatic disruptions are more rapid than the changes at the end of the Pleistocene, the members of plant communities may no longer be adapted to their present zones, and a large-scale migration of populations and a reorganisation of communities may occur, as it did often during Pleistocene time. Invasives may abound and provide a useful, fast-response, homeostatic ecosystem repair service. In such cases, campaigns to eliminate such stop gaps may be contraindicated if it deprives us of the ecological services that these species can provide. On the other hand, invasives may deprive less ruderal species of regeneration niches.

After this long preamble, what are the current and potential invasive species pests?

To designate current pest plants in the AME, we considered the scale of the current invasion and whether the problem was specific to the individual plant, that is, if that species were removed, could its niche be filled with other invasive species that are already in the habitat.

Using the list of plants above and our knowledge of the flora we suggest the following:

Current pests

- (1) *Rhamnus frangula* is rapidly expanding and may already be altering plant community structure in riparian silver maple forest in New Brunswick, as it has in floodplain forest in Quebec (White et al. 1993). Its seeds are dispersed by birds and by river flooding. Plants can invade forest and riparian areas (Catling and Porebski 1994) and become established over a wide range of moisture, light, nutrient, and disturbance conditions (Blaney, field obs.). Frappier et al. (2004) conducted shrub-removal experiments in woodland, and while there was no increase observed in species diversity or in the cover of herbs following the removal, *R. frangula* seedling densities increased five-fold, illustrating the potential of this shrub to inhibit tree seedling establishment.
- (2) *Alliaria petiolata* is one of the most problematic invasives in northeast North America (Cavers et al. 1979). It is a biennial from Europe that is thoroughly established and invasive in woodland in the middle Saint John River valley, which supports many rare species. Recently, the plant was discovered in both Nova Scotia and Prince Edward Island. Its biennial life history differs from all native species in its

habitat, it may be altering the mycorrhizal relationships of native herbs (Roberts and Anderson 2001), and it can displace native herbs (Cavers et al. 1979). Baskin and Baskin (1992) note that although the large seed banks are short-lived, “it seems possible that seeds could survive in the soil longer than three or four years” (p. 196), hence, it is imperative to eliminate new populations before it contaminates an area.

- (3) *Pinus sylvestris* is widely planted throughout North America. It has established populations in the Kingston sand barren in the Annapolis Valley of Nova Scotia, a rare example of this habitat in the AME and one that has been greatly reduced by urbanisation. Scot’s pine, *Pinus sylvestris*, is invasive in most of the northeastern United States. (Swearingen 2005), and it may displace the native pine species (*P. strobus* and *P. resinosa*) through its prolific seed production. Local nurseries in the Annapolis Valley should be approached and asked not to sell this popular, invasive, ornamental tree.
- (4) *Phalaris arundinacea* is robust and widespread in the AME in fertile, open habitats, and it may be reducing population sizes of rare plants in the St. John River Valley (Blaney, field obs.). Native and non-native forms of *Phalaris arundinacea* are ecologically similar and are difficult to distinguish (Dore and McNeil 1980 in White et al. 1993).

Potential pests

- (1) *Phragmites australis* subsp. *australis*. The European *P. australis* subsp. *australis* has been in the AME for almost 100 years, but now according to Catling et al. (2004) it is starting to be spread along roads by vehicles and may pose a threat to native wetland biodiversity, since it replaces a diverse community with a monoculture of monstrous grass. The exotic and native subspecies can be separated by the length of the first glumes and colour of lower stem internodes (Robichaud and Catling 2003).
- (2) *Celastrus orbiculatus*. This bird-dispersed vine has become one of the most problematic woody invasives in New England within the past 25 years. It is established in Annapolis Valley, Nova Scotia, and St. Andrews, New Brunswick, and is an occasionally used ornamental throughout the southern part of the AME, giving it many potential starting points for new escaped populations.
- (3) *Rhamnus cathartica*. Despite being less well established than *R. frangula*, *R. cathartica* may be as much of a threat, since it can shade out native species and may have a broader woodland habitat niche than its congener (White et al. 1993).
- (4) *Angelica sylvestris* has established dense stands along a 200-km stretch of the Saint John River in New Brunswick and is probably beginning to exclude native forest plants. It is also established around Sydney, Nova Scotia.
- (5) *Cytisus scoparius* is well established along highways in southwest Nova Scotia, and its population appears to have significantly increased in the past decade (Blaney 2001).

It is an aggressive invasive of prairie habitat in the Pacific Northwest where it has been controlled through herbicide and burning. It could be expected that our native open ecosystems (e.g., headlands, cliffs, sand barrens) will be invaded if global warming removes temperature limitations faced by *C. scoparius* in the AME (cf. Blaney 2001).

- (6) *Lythrum salicaria*. Despite the alarm called over this purple-flowered loosestrife, it fortunately has not lived up to its suppressive reputation within the AME. There is no doubt that this is a good competitor (Gaudet and Keddy 1988) and a good coloniser through copious seed production, however, in the AME it is primarily a ditch species and one that colonises hydrologically modified wetlands, or occurs at low densities in relatively natural habitats. It may become a problem in regions of richer soils, but it has not been recorded from intact systems in the acidic regions of southwestern Nova Scotia. In fact, a small clump of this plant has remained on the banks of the Mersey River for 10 years, at the very doorstep of the thousands of miles of lakeshores that support the endangered Atlantic Coastal Plain communities. The restriction of *L. salicaria* to disturbed areas of Nova Scotia is consistent with Wilcox's appraisal of this plant as an invasive that comes in when hydrological regimes themselves are disturbed (Wilcox 1995).
- (7) *Myriophyllum spicatum*. The Eurasian Milfoil, *M. spicatum* is known from single locations in New Brunswick and Prince Edward Island (both in National Parks). Its spread on both the east and west coast of North America over the past 50 years is a testament to its rapid growth and its dispersal via power boats. The dense growth of milfoil leads to a suppression of native aquatics. Quarantine measures where boats on contaminated lakes are prevented from transporting vegetative propagules to uncolonised lakes hold some promise, if only in slowing the rate of spread to new sites (White et al. 1993).
- (8) *Poa nemoralis*. This woodland bluegrass is broadly but sparsely distributed around the AME, and has been noted achieving substantial cover values in river floodplain forests in western Nova Scotia (Blaney 2001). It is robust (30–70 cm) in comparison with many understory herbs, and it has been noted as a locally invasive species in forests elsewhere in eastern North America (e.g., Massachusetts, Dibble et al. 2003; New York, Eckel 2002; and southern Ontario, Blaney, pers. obs.), but we need a clearer understanding of the impact that this plant has on native herb populations.
- (9) *Rosa rugosa* has established scattered populations on coasts throughout and dense populations near Yarmouth, Nova Scotia, and along the Saint Lawrence River near Rimouski, Quebec. It has demonstrated its invasive potential on the seashores in Sweden and Latvia. This attractive plant should be removed from wild areas, and cities should not consider it in landscaping. While it has

not spread as rapidly as might be expected, given the Scandinavian experience, it may go through a population explosion if climatic warming better fulfils the warm stratification that provides greatest germination (Baskin and Baskin 1998).

- (10) *Valeriana officinalis*. This garden escape has naturalised in many regions of North America. In the AME, it is invading moist areas within the Annapolis Valley (VanderKloet, pers. comm., 2005), and is especially well established and rapidly spreading in the Nova Scotia – New Brunswick border region. It occurs most densely in field habitats that are already substantially altered by humans but has potential to invade native wet meadow habitats.
- (11) *Rosa multiflora* has also established populations in fertile regions of the AME. This is a pernicious weed throughout the eastern United States where it dominates woodland edges and powerline right of ways. It was one of the three most frequent invasives in native habitat in rural, southern New England (Lundgren et al. 2004). Although it is not a problem in the AME at present, given its growth potential further south, it is a plant we should watch.

Conclusions

Although exotic plants are everywhere, their abundance is highly correlated with anthropogenic disturbance of habitats. The large reservoir of exotic species in these habitats means that there are many ruderal species (fast growth rates, high reproductive effort; Grime 1979) that are well equipped to colonise disturbed areas quickly. This has two main implications. First, disturbed soil will not be open to erosion long, and second, there is a long list of alternates: invasive weeds that can fill the same regeneration niche and are often registered in the same soil seed bank. There are two applied considerations that follow. Invasive plants now play a major role in protecting soils from the disturbance regimes we have put in place, and since there are many alternates (invasives that are functionally similar and available), one often cannot identify any particular species as the problem weed. Rather, invasive weeds are symptoms of anthropogenic environmental changes (Jenkins and Pimm 2003; Gross et al. 2005; Farnsworth 2004; MacDougall and Turkington 2005).

In the AME, approximately a third of the current species pool is exotic, but habitat loss may be the main cause of native species' endangerment. Most invasives appear to have colonised anthropogenically modified sites in the AME, but we should document whether there are threats from invasive species to populations of rare native plants. Farnsworth (2004) conducted such an assessment in New England and found that the decline in rare species' populations was higher in areas close to invasive species but that the decline was best explained "by the same habitat variables that were associated with invasive species presence" (p. 97). In the AME, there is conservation concern over many of the species we list as "current" or "potential" pests. These pests potentially threaten native diversity

in wetlands, riparian areas, seashore, hardwoods, and pine barren ecosystems, although as indicated, most of the undisturbed habitat (e.g., various wetland types, hardwood and softwood forest) appears to have a degree of resistance to invasion.

In Table 1, we presented a preliminary classification of habitats (anthropogenically modified and native) based on disturbance, productivity, and openness (tree cover or not). The majority of habitats that are routinely subject to anthropogenic disturbance have high or moderate amounts of established exotic species. There are anthropogenically disturbed habitats that support few exotics, and various factors may prevent the establishment of exotics such as poor soil fertility (coniferous forests that are clearcut, bogs mined for peat, reservoir shores, gravel quarries), isolation from source propagules of exotic species (clearcuts, bogs, reservoirs), and long intervals between disturbances (clearcuts). Native habitats that are susceptible to moderate numbers of invasive species are open to light, and have high frequency of disturbance or high productivity. In contrast, native habitats that are not invaded either have low disturbance and low productivity or they are closed woodland communities. This separation does break down when we look at an open lakeshore habitat that is thoroughly disturbed every spring or when we consider a frequently disturbed, high productivity, open salt marsh. These communities are united in having fairly predictable disturbance periods each year and a flooding regime that may select against many would-be invaders, however, the presence of bare areas in spring suggests that colonisation is ongoing within the community, and it may be that the native community members are more adept at precluding invasive species as long as there is a limited number of exotic propagules.

In addition to disturbance, fertility levels also contribute to the success of exotic invasive species (Leishman and Thompson 2005; Vitousek and Walker 1989). This increases the likelihood that we have the burden of responsibility for the current plague of exotic invasives. There is concern over the shift in the European flora that has resulted from the adoption of intensive agriculture and from nitrogen fertilising effects from acid precipitation (Aerts and Berendse 1988); the regional impact of such nitrogen deposition in the AME has not been assessed.

We purposely excluded weeds of arable land from consideration, since this chapter takes aim at plants that are capable of invading native plant communities. There are, however, many invasive agricultural pests that threaten the AME, and the threat is multiple but generalised, since introductions often stem from impurities in seed. The AME imports much western grain, and seed impurities in this seed should not be tolerated. The constant reimportation of *Abutilon theopasti* is a case in point. This species has been reported as a grain contaminant since the 1960s (Roland and Smith 1969), and although it scarcely makes seed to enable it to form a persistent seed bank under the present climatic conditions in the AME, it continues to reappear in grain crops. The qualitatively different nature of this species, combined with the probability of summer temperature increases in the AME due to climate change, should

be a signal to tighten restrictions on impurities in grains.

We have only a general ability to mathematically predict what species will be the next invader, and the more important consideration may be whether a species will become naturalised in wild areas and be a threat to native diversity. For this we must look to our neighbours and to countries with similar climatic conditions. Using this logic we identified *Rhamnus cathartica*, two roses, and *Cytisus scoparius* species as potential pests. The roses are both planted as ornamentals, and despite the danger signals from other regions, local authorities plant such species, despite the fact that both species are pests in areas with similar climatic conditions; cf. Sweden, southern New England, and Washington). There needs to be explicit communication between government departments of natural resources, transportation, agriculture, and customs about the issue of invasive species. Also, we need to update information provided to private nurseries so that they can “proactively” determine whether, for example, a particular bird-dispersed shrub from Tasmania represents a problem. The age of plant introductions to gardens is still with us as we import any novelty a country can supply (e.g., newly discovered Wollemi pines of Australia will reach North American gardens this year). We should stress that 10 (all seven woody plants and three herbs: *Valeriana officinalis*, *Angelica sylvestris*, and *Lythrum salicaria*) of the 15 plants listed got their start in North America as intentional introductions for gardens.

Finally, things could be a lot worse. As it has been understood that much of the hardwood community diversity in eastern North America survived in a small pocket on the shores of the Gulf of Mexico during the last glaciation, we have small areas with high diversities of native species that must be safeguarded and monitored during this period of great anthropogenic disturbance. Across eastern North America, there is more land in forest now than at any time during the last century (Fredericksen 1998; McGrory Klyza 1994), but much of this is secondary forest, which may not contain the most threatened elements of the flora. We need to identify ecologically important areas and provide wide buffers, since it is principally the well-lighted edges of forests that are affected by the rank growth of exotic species (Hunter 2002; Burke and Nol 1998; Brothers and Spingarn 1992). We will do more for conservation and agriculture if we treat exotics as a symptom of our land-use management than if we attempt to remove what has become a quick-response, homeostatic service provided by a suite of species that have evolved under disturbed conditions. Before we don protective clothing and set out with herbicide or hoe to meet these vegetative aliens (see Marris 2005), we need incontrovertible evidence that they are undermining native biodiversity at the habitat scale because the collateral damage of such measures may be unacceptable. If we concentrate on the weedy symptoms of anthropogenic disturbance instead of identifying and preserving the key habitats that sustain diverse biological communities and their rare elements, we will divert attention and conservation resources away from safeguarding of the biota of the AME.

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References

- Aerts, R., and Berendse, F. 1988. The effect of increasing nutrient availability on vegetation dynamics in wet heathland. *Vegetatio*, **76**: 63–69.
- Arnold, R.M. 1981. Population dynamics and seed dispersal of *Chaenorrhinum minus* on railroad cinder ballast. *American Midland Naturalist*, **106**: 80–91.
- Baskin, C.C., and Baskin, J.M. 1998. *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. Academic Press, New York.
- Baskin, J.M., and Baskin, C.C. 1992. Seed germination biology of the weedy biennial *Alliaria petiolata*. *Natural Area Journal*, **12**: 191–197.
- Blaney, C.S. 2001. Exotic and invasive plants in Maritime Canada. *Blomidon Field Naturalists Summer Newsletter*.
- Blaney, C.S. 2004. Vascular Plant Surveys of Northumberland Strait Rivers and Amherst Area Peatlands, 2003. A report to the Nova Scotia Museum of Natural History. 42 p.
- Blaney, C.S., and Kotanen, P.M. 2001. Post-dispersal losses to seed predators: an experimental comparison of native and exotic old field plants. *Canadian Journal of Botany*, **79**: 284–292.
- Brothers, R.S., and Spingarn, A. 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. *Conservation Biology*, **6**: 91–100.
- Brouillet, L., and Whetstone, R.D. 1993. Climate and physiography. *In Flora of North America. Edited by Flora of North America Editorial Committee*. Oxford University Press, New York. pp. 15–46.
- Burke, D.M., and Nol, E. 1998. Edge and fragment size effects on the vegetation of deciduous forests in Ontario, Canada. *Natural Areas Journal*, **18**: 45–53.
- Cain, M.L., Damman, H., and Muir, A. 1998. Seed dispersal and Holocene migration of woodland herbs. *Ecological Monographs*, **68**: 325–347.
- Catling, P.M., and Porebski, S.Z. 1994. The list of invasive plants and the current status of Glossy Buckthorn, *Rhamnus frangula*, in southern Ontario. *Canadian Field Naturalist*, **108**: 305–310.
- Catling, P.M., Mitrow, G., Black, L., and Carbyn, S. 2004. Status of the alien race of Common Reed (*Phragmites australis*) in the Canadian Maritime Provinces. *Botanical Electronic News* [online], **324**: 1–3. Available from <http://www.ou.edu/cas/botany-micro/ben/ben324.html> [accessed July 2006].
- Cavers, P.B., Heagry, M.I., and Kokron, R.F. 1979. The biology of Canadian weeds. 35. *Alliaria petiolata* (M.Bieb.) Cavara and Grande. *Canadian Journal of Plant Science*, **59**: 217–229.
- Davis, M.A., Grime, J.P., and Thompson, K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, **88**: 528–534.
- Davis, S.A. 1991. Two concentrations of palaeo-Indian occupation in the far northeast. *Journal of American Archaeology*, **3**: 31–56.
- Day, R., and Catling, P.M. 1991. The rare vascular flora of Prince Edward Island. *Syllogeus* No. 67. Canadian Museum of Nature, Ottawa, ON.
- Delcourt, H.R., and Delcourt, P.A. 1977. The Tunica Hills, Louisiana–Mississippi: Late glacial locality for spruce and deciduous forest species. *Quaternary Research*, **7**: 218–237.
- Dibble, A.C., Rees, C.A., Dacey, M.J., and Patterson III, W.A. 2003. Fuel bed characteristics of invaded stands. *In Using Fire to Control Invasive Plants: What's New, What Works in the Northeast, 2003 Workshop Proceedings*. University of New Hampshire Cooperative Extension, Durham, NH.
- Eaton, S.T., and Boates, J.S. 2003. Threats to ACPF: Water Quality and Alien Invasive Species Benchmarks, Assessment and Stewardship. Internal Report of Wildlife Division, Nova Scotia Department of Natural Resources, Kentville, NS.
- Eckel, P.M. 2002. Botanical Evaluation of the Goat Island Complex, Niagara Falls, New York [online]. Available from http://www.mobot.org/plantscience/ResBot/Flor/Bot_Goat/01_Cover.htm [accessed 17 November 2005].
- Elgersma, A., and Hassink, J. 1997. Effects of white clover (*Trifolium repens* L.) on plant and soil nitrogen and soil organic matter in mixtures with perennial ryegrass (*Lolium perenne* L.). *Plant and Soil*, **197**: 177–186.
- Erskine, J.S. 1975. The French Period in Nova Scotia, A.D. 1500–1758, and Present Remains: A Historical, Archaeological and Botanical Survey. Wolfville, NS. (Unpublished.)
- Farnsworth, E.J. 2004. Patterns of plant invasions at sites with rare plant species throughout New England. *Rhodora*, **106**: 97–117.
- Frappier, B., Eckert, R.T., and Lee, T.D. 2004. Experimental removal of the non-indigenous *Rhamnus frangula* (Glossy Buckthorn): effect on native herbs and tree seedlings. *Northeastern Naturalist*, **11**: 333–342.
- Fredericksen, T.S. 1998. Impacts of logging and development on central Appalachian forests. *Natural Areas Journal*, **18**: 175–178.
- Fuchs, M. 2002. Recovery strategy for Garry Oak (*Quercus garryana*) in Canada. *Botanical Electronic News* 298, November 18 [online]. Available from <http://www.ou.edu/cas/botany-micro/> [accessed 13 June 2006].
- Gaudet, C.L., and Keddy, P.A. 1988. Predicting competitive ability from plant traits: a comparative approach. *Nature*, **334**: 242–243.
- Goodwin, B.J., McAllister, A.J., and Fahrig, L. 1999. Predicting invasiveness of plant species based on biological information. *Conservation Biology*, **13**: 422–426.
- Graham, A. 1993. History of the vegetation: Cretaceous (Maastrichtian) – Tertiary. *In Flora of North America. Edited by Flora of North America Editorial Committee*. Oxford University Press, New York. pp. 57–94.
- Grime, J.P. 1979. *Plant Strategies and Vegetation Processes*. John Wiley, Chichester, U.K.
- Gross, K.L., Mittelbach, G.G., and Reynolds, H.L. 2005. Grassland invasibility and diversity: responses to nutrients, seed input and disturbance. *Ecology*, **86**: 476–486.
- Harrington, R.A., Brown, B.J., and Reich, P.J. 1981. Ecophysiology of exotic and native shrubs in southern Wisconsin. I. Relationship of leaf characteristics, resource availability and phenology to seasonal patterns of carbon gain. *Oecologia*, **80**: 356–367.
- Havel, J.E., Eunmi Lee, C., and Vander Zanen, M.J. 2005. Do reservoirs facilitate invasions into landscapes? *BioScience*, **55**: 518–525.
- Hierro, J.L., Maron, J.L., and Callaway, R.M. 2005. A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native ranges. *Journal of Ecology*, **93**: 5–15.
- Hill, N.M., Patriquin, D.G., and VanderKloet, S.P. 1989. Weed seed

- bank and vegetation at the beginning and end of the first cycle of a 4-course crop rotation with minimal weed control. *Journal of Applied Ecology*, **26**: 233–246.
- Hill, N.M., Keddy, P.A., and Wisheu, I.C. 1998. A hydrological model for predicting the effects of dams on the shoreline vegetation of lakes and reservoirs. *Environmental Management*, **22**: 723–736.
- Hinds, H.R. 1986. *The Flora of New Brunswick*. Primrose Press, Fredericton, NB.
- Hunter, J.C. 2002. The spread of woody exotics into the forests of a northeastern landscape, 1938–1991. *The Journal of the Torrey Botanical Society*, **129**: 220–227.
- INVADERS Database System [online]. 2005. Division of Biological Sciences, University of Montana, Missoula, MT. Available from <http://invader.dbs.umt.edu/> [accessed July 2006].
- Jenkins, C.N., and Pimm, S.L. 2003. How big is the global weed patch? *Annals of the Missouri Botanical Garden*, **90**: 172–178.
- Keddy, P.A. 2001. *Competition*. Kluwer Academic Press, Boston, MA.
- Leakey, R., and Levin, R. 1995. *The Sixth Extinction*. Doubleday, New York.
- Leckie, S., Vellend, M., Bell, G., Waterway, M.J., and Lechowicz, M.J. 2000. The seed bank in an old-growth, temperate deciduous forest. *Canadian Journal of Botany*, **78**: 181–192.
- Leishman, M.R., and Thompson, V.P. 2005. Experimental evidence for the effects of additional water, nutrients and physical disturbance on invasive plants in low fertility Hawkesbury Sandstone soils, Sydney, Australia. *Journal of Ecology*, **93**: 38–49.
- Leopold, A. 1949. *A Sand County Almanac*. Oxford University Press, New York.
- Lundgren, M.R., Small, C.J., and Dreyer, G.D. 2004. Influence of land use and site characteristics on invasive plant abundance in the Quinebaug Highlands of southern New England. *Northeastern Naturalist*, **11**: 313–332.
- MacDougall, A. 2001. Conservation status of Saint John River Valley hardwood forest in western New Brunswick. *Rhodora*, **103**: 47–70.
- MacDougall, A. 2003. Did Native Americans influence the northward migration of plants during the Holocene? *Journal of Biogeography*, **30**: 633–647.
- MacDougall, A.S., and Turkington, R. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology*, **86**: 42–55.
- Mack, R.N. 2003. Plant naturalizations and invasions in the eastern United States: 1634–1860. *Annals of the Missouri Botanical Garden*, **90**: 77–90.
- Makepeace, W., Dobson, A.T., and Scott, D. 1985. Interference phenomena due to Mouse-ear and King Devil Hawkweed. *New Zealand Journal of Botany*, **23**: 77–79.
- Malecki, R.A., Blossey, B., Hight, S.D., Schroeder, D., Kok, L.T., and Coulson, J.R. 1993. Biological control of purple loosestrife. *BioScience*, **43**: 680–687.
- Marris, E. 2005. Shoot to kill. *Nature*, **438**: 272–273.
- McAlpine, D.F., Bishop, G., Ceska, O., Moody, M.L., and Ceska, A. 2007. Andean watermilfoil, *Myriophyllum quitense* (Haloragaceae), in the Saint John River estuary system, New Brunswick, Canada. *Rhodora*, **109**: 101–107.
- McGrory Klyza, C. 1994. The Northern Forest: problems, politics and alternatives. In *The Future of the Northern Forest*. Edited by C. McGrory Lyza and S.C. Trombulak. Middlebury College Press, University Press of New England, Hanover, NH.
- McLachlan, S., and Bazely, D.R. 2001. Recovery patterns of understory herbs and their use as indicators of deciduous forest regeneration. *Conservation Biology*, **15**: 98–110.
- Mitchell, C.E., and Power, A.G. 2003. Release of invasive plants from fungal and viral pathogens. *Nature*, **421**: 625–627.
- Morash, R., and Freedman, B. 1983. Seedbanks in several recently clear-cut and mature hardwood forests in Nova Scotia. *Proceedings of the Nova Scotian Institute of Science*, **33**: 85–94.
- Patriquin, D.G., Hill, N.M., Baines, D., Bishop, M., and Allen, G. 1986. Observations on a mixed farm during the transition to biological husbandry. *Biological Agriculture and Husbandry*, **4**: 69–154.
- Perrings, C., Dehnen-Schutz, K., Touza, J., and Williamson, M. 2005. How to manage biological invasions under globalization. *Trends in Ecology & Evolution*, **20**: 212–215.
- Prinzinger, A., Durka, W., Klotz, S., and Brandl, R. 2002. Which species become aliens? *Evolutionary Ecology Research*, **4**: 385–405.
- Raup, D.M. 1991. *Extinction: Bad Genes Or Bad Luck?* W.W. Norton & Company, New York.
- Reid, C. 1899. *The Origin of the British Flora*. Dulau and Co., London, England.
- Rejmanek, M. 2004. *Book Review: Plant Invasions: Ecological Threats and Management Solutions*. Edited by L. Child, J.H. Brock, G. Brandu, K. Prach, P. Pysek, P.M. Wade, and M. Williamson. 2003. Backhuys Publishers, Leiden, The Netherlands. *In Madrono*, **51**: 400–401.
- Roberts, K.J., and Anderson, R.C. 2001. Effect of garlic mustard [*Aliaria petiolata* (Beib. Cavara and Grande)] extracts on plants and arbuscular mycorrhizal (AM) fungi. *American Midland Naturalists*, **146**: 146–152.
- Robichaud, L., and Catling, P.M. 2003. Potential value of glume length in differentiating native and alien races of Common Reed, *Phragmites australis*. *Botanical Electronic News* [online], **310**: 1–3. Available from <http://www.ou.edu/cas/botany-micro/ben/ben310.html> [accessed July 2006].
- Roland, A.E., and Smith, E.C. 1969. *The Flora of Nova Scotia*. Nova Scotia Museum, Halifax, NS.
- Scott, J.A., and Panetta, F.D. 1993. Predicting the Australian weed status of South African plants. *Journal of Biogeography*, **20**: 87–93.
- Swearingen, J. 2005. *Alien plant invaders of natural areas* [online]. Available from <http://nps.gov/plants/alien/fact/map/pisy1.htm> [updated 5 May 2005].
- Thoreau, H.D. 1854. *Walden; Or, Life in the Woods*. Ticknor & Fields, Boston. (First Penguin Edition, 1942, New York.)
- Torchin, M.E., Lafferty, K.D., Dobson, A.P., McKenzie, V.J., and Kuris, A.M. 2003. Introduced species and their missing parasites. *Nature*, **421**: 628–630.
- Vitousek, P.M., and Walker, L.R. 1989. Biological invasions by *Myrica faya* in Hawaii — plant demography, nitrogen fixation, ecosystem effects. *Ecological Monographs*, **59**: 247–265.
- Wesley, S.L., Hill, N.M., and VanderKloet, S.P. 1986. Seed banks of *Vaccinium angustifolium* on managed and unmanaged barrens in Nova Scotia. *Naturaliste Canadienne*, **113**: 309–316.
- White, D.J., Haber, E., and Keddy, C. 1993. Invasive plants of natural habitats in Canada: an integrative review of wetland and upland species and legislation governing their control. *Canadian Wildlife Service*, Ottawa, Canada. 121 p.
- Wilcox, D.A. 1995. Wetland and aquatic macrophytes as indicators of anthropogenic hydrologic disturbance. *Natural Areas Journal*,

Species Diversity in the Atlantic Maritime Ecozone

- 15:** 240–248.
- Wilson, E.O. 2002. *The Future of Life*. Vintage Books, New York.
- Wilson, S.D., and Gerry, A.K. 1995. Strategies for mixed-grass prairie restoration: herbicide, tillage and nitrogen manipulation. *Restoration Ecology*, **3**: 290–298.
- Wolfe, B.E., and Klironomos, J.N. 2005. Breaking new ground: soil communities and exotic plant invasion. *BioScience*, **55**: 477–487.
- Xiang, Q.J., Soltis, D.J., and Soltis, P.S. 1998. The eastern Asia and east and west North American floristic disjunction: congruent phylogenetic patterns in seven diverse genera. *Molecular Phylogenetic Evolution*, **10**: 178–190.
- Zinck, M. 1998. *Roland's Flora of Nova Scotia*. Nimbus Publishing, Halifax, NS.