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Vulnerability of forested habitats to invasion by unwanted vegetation

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Abstract. We sought features that indicate the vulnerability of forests to invasion by non-native plants such as Japanese barberry and Asian bittersweet, based especially on land use features, physical attributes, and fuel loads. If such features can be identified as vulnerabilities, then managers could better prioritize conservation activities in natural areas. Fuel data were collected in 110 plots at eleven study areas in MA, ME, NJ, NY, and VT, and were grouped into four common forest types – hardwoods (40 plots), mixed woods (20 plots), pitch pine (30 plots), and softwoods (20 plots). We interpreted joint plots from non-metric multidimensional scaling ordinations to determine the most important environmental variables associated with invasive plant populations for

Japanese barberry, Asian bittersweet, alder-leaved buckthorn, and 10 other invasive, non-native plants. In a 2-dimensional solution with 87% of the variance accounted for by the first two axes, the variable with the highest loading was distance from the boundary of the park or refuge; other important variables were three shrub variables (cover, height, and frequency), graminoid cover, and distance from trail. Invasive plants tended to be near the boundary except at a few sites, and are probably spread by birds from adjacent properties. Shrubs in natural areas often constitute the most visible invasive plant populations, while non-native grasses are common as well. Canopy opening, soil texture, aspect, slope, and abundance of some common native trees were not informative. Despite their popularity with some wildlife, we propose that domesticated apple and red raspberry should be considered for control in some situations.

Introduction

The degradation of natural areas by invasive, non-native plants has been well-documented for many types of ecosystems (Luken and Thieret 1997; McKnight 1993; Pysek et al 1995; Starfinger et al 1998). In the northeastern and mid-Atlantic U.S., Japanese barberry has been found to alter soil pH and other attributes of the habitat, and this makes conditions more conducive to barberry regeneration (Kourtev et al). Richburg et al (2001) focused on the potential difference in the fuels that might result when invasive plants are present.

Eradication of most invasive plant species is probably unattainable. Determination of the potential invasion capacity of plants has been attempted but Williamson (1996) concluded this was not fully effective. Another approach is to determine invasibility of an area so that invasive plant populations could be treated. Invasibility has been studied regarding habitat features (Kourtev et al), and regarding the interrelationships between plant life history traits and habitat type (Gerlach and Rice 2003).

Identification of the conditions under which northeastern forests are likely to be invaded would enable managers to increase the effectiveness of their monitoring and control efforts. The common assumption is that disturbed areas such as trails, roadsides, and around buildings will be especially prone to invasion. Global change is projected to bring about increased frequency and intensity of storms, and increased spread of insect pests, disease, and invasive, non-native plants. Canopy gaps that result could rapidly become occupied by invading species, and this would lead to long-term changes in forest composition.

The consequences of invasion are not fully known, but they might vary according to invasive species and forest type. For example, in pitch pine forests, invasion by black locust has led to conversion of a fire-adapted ecosystem to one that rarely burns, and pitch pine is lost as the dominant tree. This alteration of the disturbance regime is expected to be permanent unless black locust is controlled. With the demise of pitch pine, other fire-adapted plants and the animals which depend on them are imperiled. In other forest types such as mixed hardwoods, red spruce-balsam fir, and oak-pine, fuels comprised of invasive plants might lead to greater potential for wildfire, and invasive plants might recover quickly after a fire.

Our objective was to find factors that indicate vulnerability of forest habitats to invasion by unwanted invasive, non-native plants, based on duff and litter characteristics, land use, and geographic features across four forest types in the northeastern and mid-Atlantic states. Our goal was to identify features associated with invasion so that managers of natural areas would be able to better prioritize their invasive plant monitoring andcontrol activities and increase their effectiveness.

Methods

Study Sites – In 2000-2003 we established eleven study areas on federal, state, and private land in six eastern states (Maine, Massachusetts, New Jersey, New York, Vermont, and Virginia; Table 1; further details provided in Dibble and Rees, unpubl. data (paper to be submitted to International Journal of Wildland Fire). Priority was given to sites on federal land because the study was funded by the Joint fire Science Program, a federal cooperation between seven agencies. Some private lands were also included.

Sampling layout – At each study area we sought a forested stand that was invaded with at least one woody non-native species and a stand that was similar in overstory composition, history, soils, slope and aspect, but was uninvaded. Ideally, the uninvaded stands were mature forest and represented conditions toward which managers would seek to restore degraded stands. We categorized as uninvaded some stands that had invasive plants present but at low density and low stature. At ten of our sites, we found invaded and uninvaded habitats that were contiguous, within a single stand. At three of our sites we had to search for separate uninvaded stands. None of these comparison stands were more than 4.5 km apart. Average basal area in the stands of various forest types excluding pitch pine were 18 - 39 $m^2 ha^{-1}$, and in stands dominated by pitch pine were 6 - 32 $m^2 ha^{-1}$. We made this distinction because pitch pine is a fire-adapted forest type while the other types we studied were not.

Stand survey -- We used parallel, 4 m wide belt transects spaced 30 m apart to survey the vegetation in a stand. We compiled a species list along each transect and subjectively ranked portions of the transect as (1) heavily invaded, with invasive plants dense or common; (2) uninvaded (or in some cases slightly invaded), with invasive plants either absent or present at low numbers of seedlings or small individuals, and low density; and (3) transitional, and so excluded from sampling with plots. We also disqualified segments of each transect where conditions varied greatly such as where the transect crossed a road, trail or stream. Transects varied from 50-300 m long, depending on size of the stand, but we sampled a minimum of 100 m in each habitat condition.

Fuel sampling -- We randomly chose five locations each along the designated heavily invaded and uninvaded portions of the transects as sampling locations. Each location was to be a minimum of 10 m away from another or the end of the transect segment although this was not possible in all cases (one pair of locations were 5 m apart and another pair were 9 m apart). These locations represented plot centers and associated sampling locations. We excavated a 40 x 40 cm sample of litter and dead fuel down to duff at a previously specified location 1m from plot center. These samples were dried to constant temperature, sorted into nonwoody litter and hour size classes and weighed to the nearest 0.1 g.

At each plot we chose two random numbers between 1 and 360 associated with each plot to represent the bearing of planar intercepts (Brown Lines). We disqualified any bearing that would result in a Brown Line less than 10 degrees away from the bearing of the transect. At 1 m on each side of plot center, along the transect (Fig. 1), we established starting points for these randomly-radiating Brown Lines (except in some of the sites sampled in the first season where Brown Line origins were up to 25 m away from plot centers.)

On each Brown Line we recorded the random bearing of the line and the slope along the bearing. We tallied the number of dead, detached, woody fuels in each diameter size category (0-0.64 cm (1 hr fuels), 0.64-2.54 cm (10 hr fuels), 2.54-7.62 cm (100 hr fuels) (Brown 1974). We sampled 1 hr fuels for either 1.85 m or 3.7 m, 10 hr fuels for either 3.7 or 7.3 m and 100 hr fuels for 7.3 or 14.6 m. We doubled the length of the sampling plane in many cases to reduce variance in the data. We recorded fuel depth, litter depth and shrub height at three to eight points along the sampling plane and duff depth at two points. We measured fuels to a maximum height of 1.2 m and shrubs to a maximum height of 3 m.

We calculated fuel loads for each site according to Brown (1974). To obtain average diameter of hour size class fuels needed for these calculations, we averaged diameters of individual fuels collected on the 40 x 40 cm biomass plots. We estimated specific gravity for shrub species not listed in the Wood Handbook (USDA 1974) by measuring diameter of dried twigs at their midpoint, measuring their length and calculating their volume. We summed the volume of twigs of each species and divided by the total mass of each species. Throughout the study we encountered the majority of fuels either on the ground or parallel to it, so we did not use a correction factor to account for nonhorizontal fuels.

We collected live fuel materials at 6 sites on four or six Brown Lines per condition. We clipped all live vegetation in a plot 0.3 m wide by 1.85 m long and 1.2 m high. We labeled and bagged this material, dried it to constant weight and then sorted it into nonwoody and hour class sizes and weighed each portion. At sites where grasses were abundant we further sorted the nonwoody material into grass, forb, shrub or moss and weighed these individually.

Vegetation sampling – At each plot center we established overlapping fixed and prism plots. To estimate cover of forbs, grasses, low shrub, high shrub, tree, and slash we assigned each a cover class after Braun-Blanquet (Mueller-Dombois and Ellenberg 1974): <1%, 1-5%, 6-25%, 26-50%, 51-75%, 76-100% based on aerial cover within a 3 m radius from plot center. At plot center we used a 10 basal area factor prism to sample trees. We tallied all trees by species and designated them as alive or dead. Also at plot center we used a convex spherical densiometer to assess canopy cover from 1.2 m above the ground in the four cardinal directions. We used a Kelway soil tester to assess pH at plot center. We recorded aspect and slope of the plot using a compass, and recorded visible disturbances (e.g., stone wall, charcoal, or cut stumps evident nearby).

We set up a 2 x 8 m vegetation plot perpendicular to the transect. We recorded every vascular plant species in the plot and assigned a percent cover in these cover classes: rare (< 5 individuals, count), one clump of 5-10 individuals (or does not have to be in a single clump), occasional (numerous individuals, not common; must look around to find it); common (occurs

+/- everywhere you look, but covers < 5%), 5-25%, 26-50%, 51-75%, 76-100%, vicinity (not in plot but nearby, within about 20 m of plot), overstory tree could be overhanging plot, but is < 5% in plot. We also walked around the vicinity of the plot and recorded additional species not in the plot and collected voucher specimens for species that we couldn't readily identify in the field.

In three predetermined 1 x 1 m subplots within the vegetation plot we counted all woody plants greater than 0.5 m tall with an individual stem coming out of the ground. We identified species if possible and tallied them as alive or dead. When counting copious low shrub stems such as blueberry, we counted up to 50 stems and then recorded "more than 50". We counted individual tree seedlings and shrub seedlings which ranged to several hundred individuals per subplot.

Using the prism data obtained at the five plots per condition per site, we divided the data into various cover types (Appendix I). The pitch pine types were obvious. The softwood type had more than 50 percent of the basal area as softwoods (mainly white and red pine, red and white spruce). The mixed hardwood designation was assigned to sites that had over 25 percent softwoods, and the hardwood designation for sites with less than 25 percent hardwoods. Each datum in our summary dataset was the average of 4-15 measurements.

Data Analyses – We used Principal Components Analysis (PCA) in preliminary explorations of data structure. Ordinations with all 110 plots, 306 species, and 23 environmental variables had too much noise to be relevant to the question of what factors are associated with plant invasion. Because the data did not meet the assumptions of multivariate normality, and the dataset included many zeroes, we chose a nonparametric technique, non-metric multidimensional scaling (NMS) for ordination (McCune and Grace 2002; Peterson and McCune 2001). We used PC-ORD 4.0 software (McCune and Mefford 1999), in which NMS is based on an algorithm developed by Kruskal (1964) and refined by Mather (1976). The technique has provided repeatable results in numerous recent studies.

Selection of environmental variables -- Selection among the 23 untransformed environmental variables (Table 2) was based on a dataset that included 12 of the most abundant invasive, non-native species, and pitch pine. We conducted Discriminant Function Analysis (DFA) in SYSTAT 10.2.1 (SAS Institute 2000) with forward stepping, alpha-to-enter and alpha-to-remove set at 0.15, and tolerance of 0.1. This correctly classified 93% of the 55 invaded plots, and 100 percent of the 55 uninvaded plots. A rule of thumb is that each variable should have at least 10 plots available in the dataset (so, n=230 plots, over twice what we had available), thus our data were not appropriate for this technique as a determining analysis. However, informal use of DFA suggested that we could dismiss 12 variables as uninformative to our question, including most of the fuels variables. A subset of 11 environmental variables were used in subsequent analyses, nine were quantitative, and two were categorical (Table 2). The three shrub variables were linearly associated with each other but each reflected slightly different aspects of the shrub layer.

Selection of species -- Exploratory PCA by forest type and over all forest types suggested that most native species were not informative regarding vulnerability of habitat. For NMS, we included 22 species (Table 3) in an ordination of 110 plots. Plots that did not contain the invasive species of interest led to division by zero, an unworkable situation that was remedied by including some common native species so that all 110 plots could be incorporated in the ordination. Sixteen of the 22 species were invasive, non-native plants that occur in forests, including three trees, nine shrubs or vines, one forb, and four grasses. A seventeeth species, *Rubus idaeus,* was common but material available was of questionable nativeness based on Fernald (1950) and on Haines and Vining (1998). Three species were native, non-invasive trees that can be dominant in forests of the region (i.e., *Acer rubrum, Acer saccharum,* and *Pinus rigida*). Two genera with multiple species lumped for this analysis were *Carex*, (including especially *C. pennsylvanica*) and *Quercus* (including *Q. rubra, Q. illicifolia, Q. alba,* and *Q. prinoides*).

Data were not transformed or relativized (McCune and Grace 2002). The distance matrix used was Sorensen (Bray-Curtis), with 6 dimensions to start (maximum available). The initial configuration was a random number seed of 3-4 digits, and this was changed for each of ten runs once a stable solution had been reached. NMS parameters for these ten runs were a stability criterion of 0.00001, ending after 20 iterations without stability, an initial step length of 0.2, and maximum of 300 iterations. We evaluated the solution according to (1) a scree plot for each ordination, and mean values to compare the proportion of initial variation that was accounted for by the final NMS solution to that generated in Monte Carlo simulations; this was consistently lower than the resampling values, which is the desirable condition, (2) a plot of distance versus dissimilarity, in which we found distinct leveling off of stress as the number of runs increased, (3) comparison of joint plots resulting after each solution, in which local minima would have been detected by presence of odd patterns such as a line, sigmoid, or circle.

Results

Of 306 total species found among the 11 study areas, 98 species were non-native plants (Table 3). In the NMS, a 2-dimensional solution was reached consistently (Fig. 1), and the first two axes explained 86.6 percent variance of the variance, with 49.9 and 36.7 percent explained by the first and second axes respectively. The number of iterations for the final solution ranged from 59 - 115 (mean = 86.3, SD = 19.771). Distance from the boundary of the park or refuge had the highest loadings on the first axis, and the second highest on the second axis (Fig. 1, Table 4). Other variables with high scores on the second axis were shrub frequency and shrub cover. Lesser variables that contributed to the ordination were graminoid cover, distance from a trail, and shrub height.

Invaded plots, represented by circles in Figs. 1-3, were in several clusters, sometimes related to site but otherwise unrelated. Four more-or-less distinct groups are suggested

(Fig. 3), especially one large group of invaded plots with higher values on the 2nd axis, above the Boundary vector in the joint plot.

Species associated with high values for distance from Boundary include pitch pine. Most invasive plant species were nearer the centroid than the Boundary vector, suggesting that populations of Japanese barberry, Malus, and Asian bittersweet are associated with proximity to the Boundary at many sites. Sugar maple was especially prominent on the negative Boundary vector. Alder-leaved buckthorn, Japanese barberry, and red raspberry were associated with the three shrub variables. Associated with graminoid cover was Carex, and to a lesser extent, two of the three non-native grasses – sweet vernal grass and fine-leaved sheep fescue. Shrub frequency and cover were associated with honeysuckle, red raspberry, alder-leaved buckthorn, Japanese barberry, and to a lesser extent, apple. Species with low values on the shrub vectors include common speedwell, Norway maple, wood bluegrass, and common barberry. The ordination of Japanese versus common barberry could have to do with their relative abundance at several sites – common barberry was relatively rare.

Multiflora rose and common buckthorn were associated with the vector for distance from Trail, indicating that these species are found at several sites at a long distance from trail disturbance. Species for which these variables did not offer much explanatory power were common buckthorn, Eurasian highbush cranberry, and black locust. Variables that did not explain plots in species space included some environmental features that we had anticipated could be important, especially soil texture, distance from a mapped wetland, distance from a stream, canopy opening, basal area, and tree cover.

PCA ordinations by forest type could not be supported by rigorous adherence to assumptions of multivariate normality (figures not shown), but interpretation of joint plots from these ordinations mostly confirm the NMS results we obtained for all forest types together, reported above. In hardwoods, when only invasive, non-native species were included, we found that shrub cover was associated especially with Asian honeysuckle and to a lesser extent, with multiflora rose. For mixed woods, abundance of smooth buckthorn, and to a lesser extent, Asian honeysuckle, were associated with high values on the vectors for distance from road, distance from trail, distance from wetland, and 100-hour fuels. Where values for those vectors were low, abundance was high for Asian bittersweet and Japanese knotweed, and sweet vernal grass. Japanese barberry was associated with low values for percent canopy opening. For pitch pine, black locust was associated with higher values of shrub height, while an unknown grass (not identifiable from our material) was negatively associated with that vector. The data for 10 softwoods plots were insufficient to run a PCA.

Discussion

Of the 306 species of plants found in this study, one third are non-native. We think this could be typical in many forests of the wildland urban interface of northeastern and mid-Atlantic U.S. We consider 36 species or species groups to be especially aggressive invaders in forests that we have seen (see Table 3), though we did not encounter sufficient populations of all these that we could include them in the analyses. Some, such as daylily (*Hemerocallis*) are probably associated with edges or openings around old dwellings and spread vegetatively but not far from their original planting. Others with fleshy fruits spread by birds, such as Asian bittersweet and Japanese barberry, the honeysuckles, and multiflora rose, have spread deep into the forest and persist in the shady understory with little or no obvious herbivory by deer or insects.

Application of this research to actual management situations could take the following form:

1) When inventorying for invasive plants, do not ignore boundaries, but make these a priority to be searched in addition to roads, parking lots, trails, and building envelopes.
2) Identify grasses – so many that we found were non-native and persisting in forests that had once been pasture or plowed land. Invasive grasses such as Japanese stiltgrass, fine-leaved sheep fescue, and wood bluegrass, are capable of forming homogeneous fine fuels on the forest floor and have potential to increase the spread and intensity of a wildfire when dry.
3) Consider controlling apple and red raspberry. Although these plants provide high quality food for wildlife (and people), their propensity to spread and persist in forests suggests that they could become more problematic as global

warming continues to escalate disturbance and spread of non-native plants in the region.

In summary, we found several factors associated with forest vulnerability to the invasion by unwanted non-native plants. Proximity to a boundary, build-up of a dense shrub layer, and increase in graminoid cover were the three aspects of invasion in forests of the northeastern and mid-Atlantic U.S.

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Table 1. Eleven study areas at ten sites (two at Albany Pine Bush Preserve) where data were collected for this study.

State	Town	Name	Abbreviation for text
Maine	Bar Harbor	Acadia National Park	ACAD
Maine	Bradley	Penobscot Experimental Forest	PEF
Maine	Lyman	Massabesic Experimental Forest	MEF
Maine	Brooksville	Holbrook Island Sanctuary	HIS
Maine	Kittery	Rachel Carson National Wildlife Refuge	RCNWR (BBH)
Massachusetts	Wellfleet	Cape Cod National Searshore	CCNSS
New Jersey	Morristown	Morristown National Historical Park	MORR
New York	Albany	Albany Pine Bush Preserve (2 study areas)	APBP (L=Chubb and Locust; F= Firebrand and Friendly)
New York	Hector	Finger Lakes National Forest	FLNF
Vermont	Rupert	Merck Forest and Farmland Center	MERCK

Table 2. Environmental variables assessed in Discriminant Function Analysis. A subset (designated with *) were used in non-metric multidimensional scaling analysis to identify features associated with populations of non-native, invasive plants.

Variable	Abbreviation	Description	Units
*Plots invaded (1) or uninvaded (2)	Status	See Dibble and Rees IJWF paper	(category)
Aspect	Aspect	Measured in the field	degrees
Slope	Slope	Average slope for all fuel planar intercepts at a plot	degrees
Distance to nearest stream	Stream	Based on GIS or measured in the field	m
Distance to nearest mapped wetland	Wetland	Wetland mapped on National Wetland Inventory, based on GIS or measured in the field	m
Distance to nearest road accessible to 4 wheel drive vehicle	Road	GIS or measured in the field	m

*Distance to nearest footpath	Trail	GIS or measured in the field	m
*Soil texture	Soil_tex	Defined according to fineness	
*Distance from political boundary of natural area	Boundary	GIS or measured in the field	m
1 hour fuels	HR1	Sticks on the ground 0-0.64 cm	kg/ha
10 hour fuels	HR10	Sticks on the ground 0.64-2.54 cm	kg/ha
100 hour fuels	HR100	Sticks on the ground 2.54-7.62 cm	kg/ha
*Nonwoody litter biomass	Nonw	Leaves, cones, etc.	kg/ha
Duff depth	Duff	Depth of layer between undecomposed leaves and fungal mycelia	cm
Fuel depth	Fueldep	Depth of dead, detached woody fuels	m

*Graminoid cover	Gram	Braun-Blanquet cover class	percent cover
*Shrub cover	Shrubcov	Braun-Blanquet cover class	percent cover
*Forbs cover	Forbs	Braun-Blanquet cover class	percent cover
Slash cover	Slash	Braun-Blanquet cover class	percent cover
Tree cover	Tree	Braun-Blanquet cover class	percent cover
Basal areas	BA	10 Basal area factor prism	square m/ha
*Percent canopy cover	Canopy	Convex hemispherical densiometer	percent
*Shrub height	Shrub_ht	Average shrub height	m
*Shrub frequency	Shrub_freq	Average number of shrub data encountered on fuel intercept transects	count

Table 3. Non-native species encountered in forest habitats during this study. * = those we consider invasive in forests of the northeastern and mid-Atlantic U.S., and included in an ordination of plots, species, and environmental variables in non-metric multidimensional scaling. + = plants we observed to be aggressively invasive in forests we visited, but not present in sufficient quantity in our dataset to include in analyses. Nomenclature follows Haines and Vining 1998

Scientific name	Common name	Form	Family
*Acer platanoides L.	Norway maple	Tree-deciduous	Sapindaceae
Achillea millefolium L.	common yarrow	Herb	Asteraceae
Aconitum napellus L.	garden monkshood	Herb	Ranunculaceae
+Aegopodium podagraria	goutweed	Herb	Apiaceae
Aesculus hippocastanum L.	horse-chestnut	Tree-deciduous	Sapindaceae
Agrostis capillaris L.	Rhode Island bentgrass	Grass	Poaceae
Agrostis gigantea Roth	redtop	Grass	Poaceae
Agrostis scabra Willd.	creeping bentgrass	Grass	Poaceae
Agrostis stolonifera L.	creeping bentgrass	Grass	Poaceae
+Ailanthus altissima	tree ofheaven	Tree-deciduous	Simaroubaceae
+Alliaria petiolata (Bieb.) Cavara & Grande	garlic mustard	Herb	Brassicaceae
Ambrosia artemisiifolia	common ragweed	Herb	Asteraceae
Anaphalis margaritacea (L.) Benth. & Hook. f.	pearly everlasting	Herb	Asteraceae
*Anthoxanthum odoratum	sweet vernal grass	Grass	Poaceae
Aquilegia vulgaris	garden columbine	Herb	Ranunculaceae
*Berberis thunbergii	Japanese barberry	Shrub	Berberidaceae
*Berberis vulgaris	common barberry	Shrub	Berberidaceae

Bromus erectus Huds.	erect brome grass	Grass	Poaceae
*Celastrus orbiculata	oriental bittersweet	Shrub	Celastraceae
Cerastium fontanum ssp. vulgare	common mouse-ear chickweed	Herb	Caryophyllaceae
Clenopodium vulgare L.	wild basil	Herb	Lamiaceae
Commelina communis	asiatic dayflower	Herb	Commelinaceae
+Convallaria majalis	lily-of-the-valley	Herb	Convallariaceae
+Sedum telephium L.	live-forever, garden orpine	Herb	Crassulaceae
Dactylis glomerata	orchard grass	Grass	Poaceae
Daucus carota	Queen Anne's lace	Herb	Apiaceae
Digitaria ischaemum (Schreb.) Muhl.	smooth crabgrass	Grass	Poaceae
Digitaria sanguinalis (L.) Scop.	northern crabgrass	Grass	Poaceae
Echinochloa muricata (Beauv.) Fern.	barnyard grass	Grass	Poaceae
+Elaeagnus angustifolia L.	Russian-olive	Shrub	Elaeagnaceae
+Elaeagnus umbellata Thunb.	autumn-olive	Shrub	Elaeagnaceae
+Epipactis helleborine	helleborine	Herb	Orchidaceae
Euphorbia cyparissias L.	cypress spruge	Herb	Euphorbiaceae
+Euonymus alatus	burning bush	Shrub	Celastraceae
+Fallopia japonica	Japanese knotweed	Herb	Polygonaceae
*Festuca filiformis	fine-leaved sheep fescue	Grass	Poaceae
Fragaria vesca L.	woodland strawberry	Herb	Rosaceae
*Frangula alnus	alder-leaved buckthorn	Shrub	Rhamnaceae
+Galeopsis tetrahit L.	brittlestem hempnettle	Herb	Lamiaceae
Glechoma hederacea	gill over the ground	Herb	Lamiaceae
+Hemerocallis sp.	day lily species	Herb	Hemerocallidaceae
+Hesperis matronalis	dame's rocket	Herb	Brassicaceae

+Hieracium aurantiacum L.	orange hawkweed	Herb	Asteraceae
Hieracium caespitosum Dumort.	yellow king devil	Herb	Asteraceae
Hieracium murorum L.	wall hawkweed	Herb	Asteraceae
Hypericum perforatum L.	common St. Johnswort	Herb	Clusiaceae
+Hypericum prolificum L.	shrubby St. Johnswort	Shrub	Clusiaceae
Leonurus cardiaca L.	common motherwort	Herb	Lamiaceae
Ligustrum vulgare L.	common privet	Herb	Oleaceae
Linaria vulgaris	butter and eggs	Herb	Veronicaceae
+Lonicera japonica	Japanese honeysuckle	Vine	Caprifoliaceae
*Lonicera sp. (includes *L. morrowii*, *L.* x*Bella*, and *L. tatarica* hybrids)	Asian honeysuckle	Shrub	Caprifoliaceae
Luzula pallidula Kirsch.	woodrush	Sedge	Juncaceae
Lysimachia punctata L.	spotted loosestrife	Herb	Primulaceae
*Malus sp.	apple	Tree-deciduous	Rosaceae
*Microstegium vimineum	Japanese stiltgrass	Grass	Poaceae
Muhlenbergia racemosa (Michx.) B. S. P.	grass	Grass	Poaceae
Muscari botryoides	grape hyacinth	Herb	Liliaceae
Myosotis sp.	forget-me-not species	Herb	Boraginaceae
Narcissus sp.	narcissus	Herb	
Oxalis cf. stricta	common yellow wood-sorrel	Herb	Oxalidaceae
Pachysandra terminalis	pachysandra	Herb	Buxaceae
Persicaria maculosa S. F. Gray	lady's thumb	Herb	Polygonaceae
Phleum pratense	timothy	Grass	Poaceae
+Physocarpus opulifolius (L.) Maxim.	ninebark	Shrub	Rosaceae
Picea abies	Norway spruce	Tree-coniferous	Pinaceae
Plantago major	common plantain	Herb	Plantaginaceae
*Poa nemoralis	wood bluegrass	Grass	Poaceae

Poa pratensis L.	Kentucky bluegrass	Grass	Poaceae
Potentilla cf. recta L.	rough-fruited cinquefoil	Herb	Rosaceae
Prunella vulgaris L.	selfheal	Herb	Lamiaceae
Prunus cf. avium	sweet cherry	Tree-deciduous	Rosaceae
Ranunculus acris	common buttercup	Herb	Ranunculaceae
Ranunculus reptans	creeping spearwort	Herb	Ranunculaceae
*Rhamnus cathartica	smooth buckthorn	Shrub	Rhamnaceae
*Robinia pseudoacacia	black locust	Tree-deciduous	Fabaceae
*Rosa multiflora Thunb. Ex Murr.	multiflora rose	Shrub	Rosaceae
Rubus idaeus L.	red raspberry	Shrub	Rosaceae
Rubus phoenicolasius	wineberry	Shrub	Rosaceae
*Rumex acetosella	sheep sorrel	Herb	Polygonaceae
+Saponaria officinalis L.	bouncing bet	Herb	Caryophyllaceae
+Solanum dulcamara L.	bittersweet nightshade	Herb	Solanaceae
Solanum nigrum L.	black nightshade	Herb	Solanaceae
Sorbus aucuparia L.	European mountain-ash	Tree-deciduous	Rosaceae
Stellaria graminea	common stitchwort	Herb	Caryophyllaceae
Syringa vulgaris L.	lilac	Shrub	Oleaceae
Taraxacum officinale	common dandelion	Herb	Asteraceae
Trifolium pretense L.	red clover	Herb	Fabaceae
Trifolium repens L.	white clover	Herb	Fabaceae
Trifolium sp.	clover species	Herb	Fabaceae
Ulmus thomasi	rock elm	Tree-deciduous	Ulmaceae
Valeriana officinalis	garden-heliotrope	Herb	Caprifoliaceae
Verbascum thapsus	common mullein	Herb	Scrophulariaceae
*Veronica officinalis L.	common speedwell	Herb	Veronicaceae
*Veronica serpyllifolia L.	thyme-leaved speedwell	Herb	Veronicaceae
*Viburnum opulus L. var. opulus	Eurasian highbush cranberry	Shrub	Adoxaceae

Vicia cracca	cow vetch	Herb	Fabaceae
Weigela sp.	weigela species	Shrub	Caprifoliaceae

Table 4. Environmental variables in non-matric multidimensional scaling that consistently had r^2 values of 0.2 or greater. Values greater than 0.4 are considered to be robust.

Variable	Axis 1	Axis 2
Distance from boundary (m)	.758	.456
Graminoid cover (percent)	.200	.080
Distance from trail (m)	.185	.013
Shrub frequency	.005	.583
Shrub height (m)	.004	.218
Shrub cover	0.000	.416

Figure 1. Joint plot of a 2-dimensional solution in non-metric multidimensional scaling of 110 plots, 22 species (of which 16 are unequivocally invasive, non-native plants), with 11 environmental variables. Plots are represented by circles (invaded) and diamonds (uninvaded).

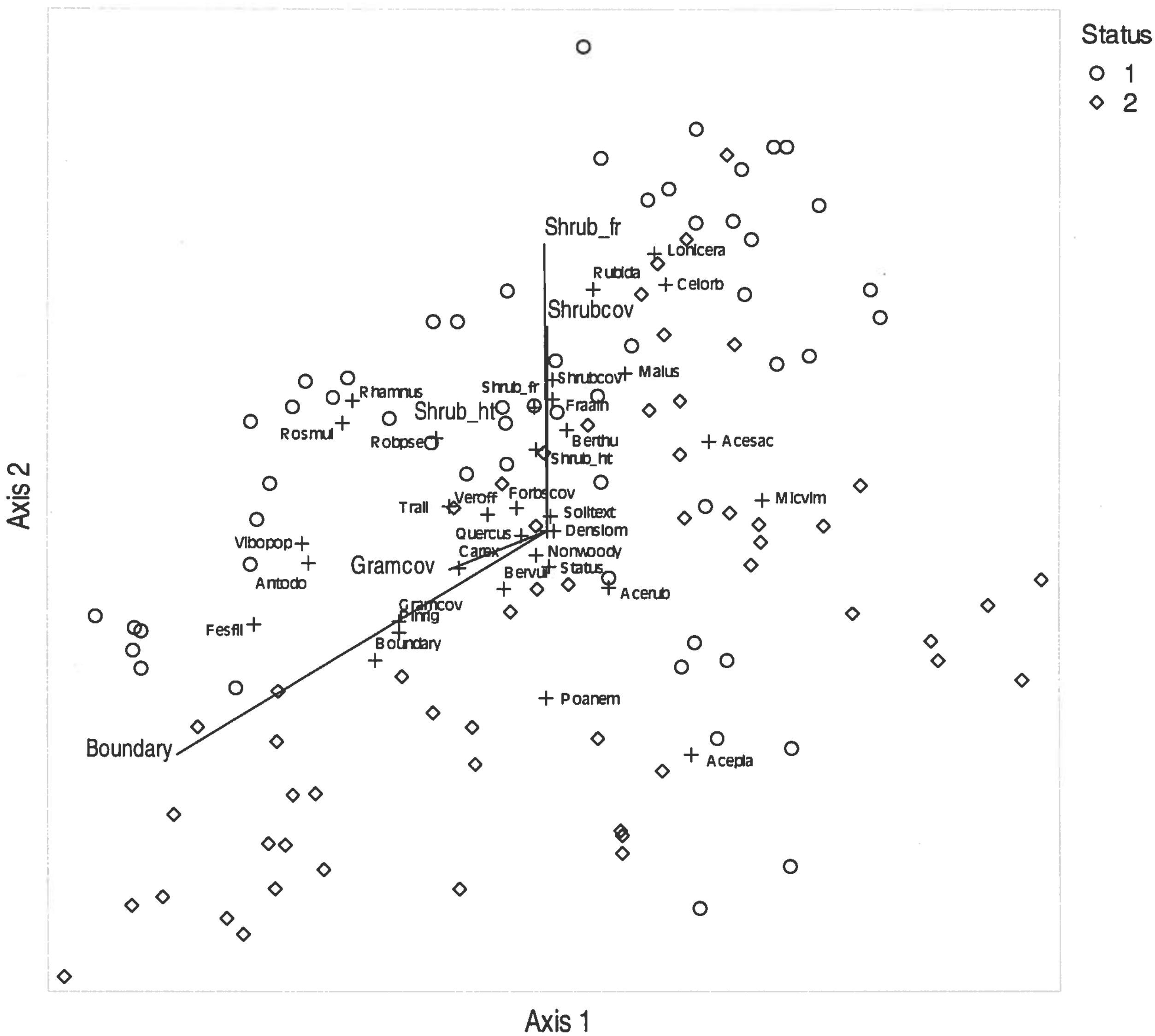

Figure 2. Joint plot of the ordination shown in Fig. 1, but with plots labeled. Plot circles with numbers 1-5 are invaded, diamonds with numbers 6-10 are uninvaded. Study areas are symbolized as a = Acadia National Park, b = Rachel Carson National Wildlife Refuge, c = Cape Cod National Sea Shore, f = Massabesic Experimental Forest, h = Holbrook Island Sanctuary, k = Merck Forest and Farmland Center, l = Albany Pine Bush Preserve, Chubb and Locust parcels, n = Finger Lakes National Forest, o = Morristown National Historical Park, p = Penobscot Experimental Forest, r= Albany Pine Bush Preserve, Firebrand and Friendly parcels.

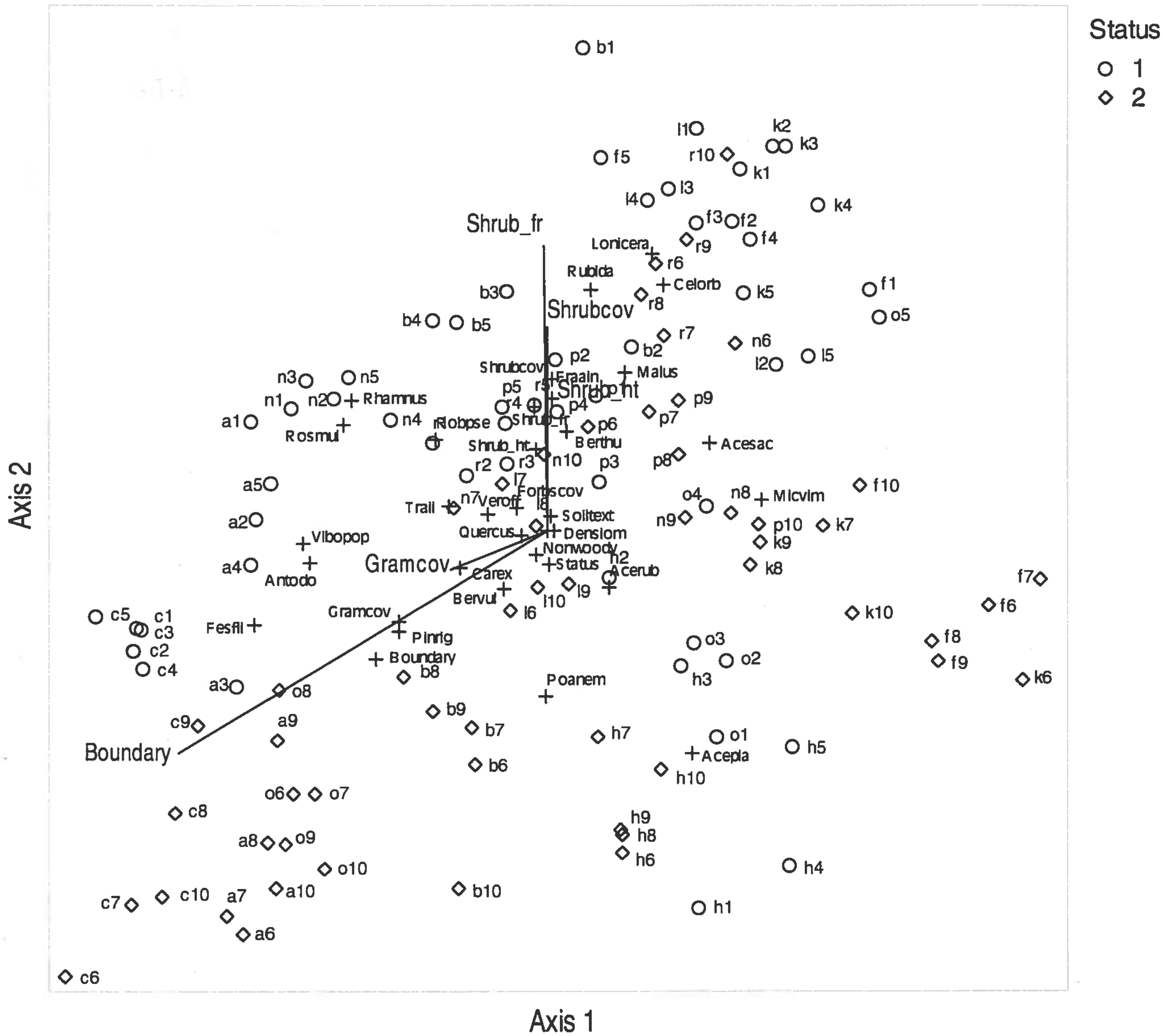
Status
1
2
Axis 1
Axis 2
Shrub_fr
Shrubcov
Shrub_ht
Gramcov
Boundary

Figure 3. Joint plot as in Figs. 1 and 2, but with lines drawn to indicate the groups discussed in the text.