Putting community data to work: some understory plants indicate red spruce regeneration habitat

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Abstract

When harvested, red spruce (*Picea rubens*) at low elevations is vulnerable to temporary displacement by balsam fir (*Abies balsamea*) and hardwoods. If indicator plants can be found by which to assess spruce regeneration habitat, then biota dependent on red spruce dominance could benefit. Associations between spruce seedlings (0.1–0.5 m tall) and understory plants, species life histories, and successional processes can be considered in managing for biodiversity; species richness alone is inadequate. Data from eight Maine sites in 50 permanent 0.0625 ha plots and 600 1 m^2 subplots along a disturbance gradient included 30 understory species and nine environmental variables. In a canonical correspondence analysis (CCA), the first two canonical axes accounted for 64.6% of the species–environment relationship; their eigenvalues accounted for 22% of the total variation. Spruce seedlings were sparse in clearcuts and most abundant in stands that were partially harvested at ≥20 year intervals and where Curtis' Relative density, softwood:hardwood ratio, and percent of understory plants visited by bees were all high. We propose a suite of common, widespread herbs and a liverwort as potential indicators, but recognize that parent trees probably influence red spruce seedling density more than does ground flora composition. © Published by Elsevier Science 1999.

Keywords: Biodiversity; Indicator plants; Red spruce; Regeneration; Understory; Forest succession

1. Introduction

Ecologically sustainable harvests in red spruce (*Picea rubens* Sarg.)–balsam fir (*Abies balsamea* [L.] P. Mill) forests in northeastern North America will ideally retain spruce as the dominant species because this long-lived species stabilizes the light environment in the understory, influences the texture and chemistry of forest litter, provides habitat for numerous birds and mammals, and is commercially

valuable for timber and pulp. Red spruce appears to be vulnerable to temporary displacement by balsam fir and other fast-growing pioneer species (including red maple, *Acer rubrum* L., trembling aspen, *Populus tremuloides* Michx., big-tooth aspen, *P. grandidentata* Michx., and paper birch, *Betula papyrifera* Marsh) across its range (Seymour, 1992; Smallidge and Leopold, 1994). Its seeds are short-lived and do not persist in the soil seed bank (Blum, 1990). Individual longevity can be longer than 300 years, and is considerably longer than that of balsam fir (about 70 years). Red spruce is less susceptible to spruce budworm (*Choristonenura fumiferana* [Clem.]) than is fir, but in

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openings that follow a budworm epidemic or other disturbance, seed dispersal differs between these species (Hughes and Bechtel, 1997), and small spruce trees grow more slowly than young fir. Since red spruce is economically valuable for timber and pulp (Seymour, 1992), and usually has better health and sizes than balsam fir, it has been harvested repeatedly on the same sites in Maine since the early 1800s. It has low genetic variability and may lack adaptability to environmental stress including global change (DeHayes and Hawley, 1992). Red spruce is in documented decline in some parts of its range (Adams and Stephenson, 1989; Klein et al., 1991; Battles and Fahey, 1995). On some private industrial forest lands in Maine this species is no longer favored over hardwoods because of a shift in market demand for printing papers with a smooth finish that offer crisper letters and pictures (S. Balch, pers. comm.). A diminishing incentive on the part of some managers to retain red spruce in the overstory might reduce the likelihood that red spruce will return to dominance in former red spruce stands, at least in the next 30–60 years. Any change in priority for red spruce as a timber or pulpwood species is unrelated to its ecological importance to understory species and associated animals.

In the earliest days of colonial New England, tree species were used as indicator plants for identifying soils suitable for agriculture. The trees themselves influenced soil quality (Cronon, 1983), although many early farmers did not realize this. Understory plants were recognized as 'indicator species' of potential timber productivity since the 1920s (Clements, 1928; Hunter, 1990). Westveld (1954) proposed three understory species pairs which could indicate the suitability of a site for red spruce with (1) yellow birch (*Betula alleghaniensis* Britt.): *Oxalis montana* with *Cornus canadensis* (see Table 1 for naming authorities of all herb and shrub species); (2) sugar maple (*Acer saccharum* Marsh), American beech (*Fagus grandifolia* Ehrh.): *Viburnum* spp. with *Oxalis montana*; and (3) balsam fir: *Cornus canadensis* with *Maianthemum canadense*.

The understory flora in a stand dominated by mature red spruce is characteristically species-poor (Blum, 1980; Griffin, 1980) and has received little attention between earlier studies (Oosting and Billings, 1951; Westveld, 1952; Westveld, 1954; Davis, 1964) and recent forest site classification projects in New Bruns-

wick, Canada (Bowling and Zelazny, 1992) and Quebec, Canada (Bergeron et al., 1992). The reproductive biologies of some understory plants associated with red spruce have been studied (e.g. Reader, 1977; Mirick and Quinn, 1981; Bierzychudek, 1982; Barrett and Helenurm, 1987), but many others are not yet investigated. The relative simplicity of the understory flora makes it attractive for exploration of some plant associations that could be pertinent to red spruce regeneration. From a plant conservation perspective, if there are herb or shrub species that depend on understory conditions associated with mature red spruce, they have not yet been identified as such.

Some understory plant species and suites of species are designated based on their relative abundances as 'indicator species' in some community ordination techniques used for ecological classification (e.g. Two-way indicator species analysis, TWINSPAN, as described in Gauch, 1982, p. 201). However, such species and groups do "... not necessarily represent ecological groupings or associations" (Kotar and Burger, 1996, pp. 1–11). The associations of such species with recognizable edaphic, hydrologic, and shade environments are often either stated or implied, but other aspects of their biologies receive little or no emphasis. We suggest that understory plants with potential as ecological indicators of forest conditions or cover-types should be examined not just for their floristic relationships, as species on a list (e.g. Coffman and Willis, 1977; Collins, 1988; Kirby, 1990; Scheiner and Istock, 1994; Burgess, 1996; Kotar and Burger, 1996) but with some consideration of reproductive biology and dependence on mutualists.

Aspects of the individual plant biologies could be as relevant to conservation of forest biodiversity as changes in understory species richness following harvest activities (e.g. Duffy and Meier, 1992; Reader and Bricker, 1992). Although native understory plants are components of forest biodiversity, their requirements for essential services such as pollinator availability may be unknown and are rarely heeded in stand prescriptions. Fruit set for many herbs and shrubs depends on the activity of various animal pollinators, of which bees are considered especially effective at inadvertently transferring pollen. Possibly the proportion of bee-pollinated (versus wind-pollinated) plants varies across a harvest disturbance. If the proportion is higher where red spruce regeneration is abundant, then

Table 1
Species codes for understory plants used in CCA (Fig. 3)

Code	Species
ANMA	*Anaphalis margaritacea* (L.) Benth and Hook. f., pearly everlasting
ARHI	*Aralia hispida* Vent., bristly sarsaparilla
ARNU	*Aralia nudicaulis* L., wild sarsaparilla
ASAC	*Aster acuminatus* Michx., white whorled wood aster
CLBO	*Clintonia borealis* (Ait.) Raf., blue bead lily
COCA	*Cornus canadensis* L., dwarf cornel or bunchberry
COGR	*Coptis trifolia* (L.) Salisb. ssp. *groenlandica* (Oeder) Hultén, goldthread
CYAC	*Cypripedium acaule* Ait., pink lady's slipper
DARE	*Dalibarda repens* L., Dalibarda or dewdrop
DILO	*Diervilla lonicera* P. Mill., fly honeysuckle
DRSP	*Dryopteris campyloptera* (Kunze) Clarkson, *D. carthusiana* (Vill.) H.P. Fuchs, and *D. intermedia* (Willd.) Gray, wood ferns
EPAN	*Epilobium angustifolium* L., fireweed
EPRE	*Epigaea repens* L., trailing arbutus
GAHI	*Gaultheria hispidula* (L.) Bigelow, creeping snowberry
GAPR	*Gaultheria procumbens* L., wintergreen or checkerberry
HISP	*Hieracium aurantiacum* L. and *H. caespitosum* Dumort. (syn. *H. pratense*), hawkweeds
KAAN	*Kalmia angustifolia* L., sheep laurel
LIBO	*Linnaea borealis* L. ssp. *longiflora* (Torr.) Hultén, twinflower
LOCA	*Lonicera canadensis* Marsh., Canadian honeysuckle
MACA	*Maianthemum canadense* Desf., wild lily-of-the-valley
MEVI	*Medeola virginiana* L., Indian cucumber-root
ORAS	*Oryzopsis asperifolia* Michx., a ricegrass
OXMO	*Oxalis montana* Raf., Common wood-sorrel
PTAQ	*Pteridium aquilinum* (L.) Kuhn v. *latiusculum* (Desv.) Heller, bracken fern
RUID	*Rubus idaeus* L., red raspberry
SOSP	*Solidago* spp. (includes *S. juncea* Ait. and others), goldenrods
TRBO	*Trientalis borealis* Raf., Northern starflower
TRUN	*Trillium undulatum* Willd., painted trillium
VASP	*Vaccinium angustifolium* Ait. and *V. myrtilloides* Michx., lowbush blueberry and sour blueberry
VISP	*Viola* spp. (includes *V. blanda* Willd. v. *palustriformis* Gray, *V. cucullata* Ait., and others), violets

Nomenclature follows Campbell et al. (1995).

the needs of beneficial insects could be accomodated simultaneously with management for timber production. Pollination ecology is an appropriate feature for inclusion in indicator plant studies because native pollinators are declining in many ecosystems (Buchmann and Nabhan, 1996). Forest management decisions could influence pollinator populations, especially if they involve aerial application of chemicals.

There is an inherent circularity in the concept of understory plants as indicators of either the overstory or of regeneration habitat. Maguire and Forman (1983) found that patches of understory plants affect tree regeneration, yet the influence of understory plants could be minor compared to the effects that the tree layer has on the understory environment in terms of light transmission and quality (Endler, 1993),

hydrology, root competition, litter depth, and the chemistry of throughfall, stemflow (Crozier and Boerner, 1984), and litter. The abundance and diversity of vertebrates and invertebrates that pollinate, disperse, and consume understory plants depend upon overstory structure and composition. Thus, trees might 'indicate' the understory composition more than bryophytes, herbs, and shrubs indicate overstory species. Add to this complexity the successional stages that are characteristic of any forest-type and it becomes problematic to identify plants as reliable indicators of regeneration conditions. It is difficult to separate causal factors from understory plant distributions in a forest ecosystem, especially where harvest intensity is the major disturbance. Timber species, not understory plants, continue to be emphasized in assessments of forest condition (Hagenstein, 1990) although bryo-

phytes and lichens are increasingly recognized as potential indicators of forest health (USDA Forest Service, 1997).

Given some limitations, there is the potential that understory species can be recognized as a characteristic of understory habitat in which a dominant tree is likely to regenerate successfully. Such indicators would be useful in predicting the likelihood of regenerating red spruce given stand structure and the harvest treatment proposed. Sustainability in Maine red spruce–balsam fir flats requires sufficient natural regeneration because the alternative, planting, is expensive.

Further knowledge of red spruce regeneration habitat is needed to improve decision making in forest management. For example, it is popularly assumed that mineral soil is the most desirable seedbed for red spruce (Blum, 1990). Hart (1959) thought that the seedling root system of red spruce dried out more quickly in forest litter than in bare ground. A controlled study that supported this supposition did not differentiate spruce to species and probably included both *P. rubens* and *P. glauca* ((Moench) Voss) (Davis and Hart, 1961). However, soil scarification could expose seeds of *Rubus idaeus* L., red raspberry, a shrub that is capable of temporarily outcompeting conifers especially on better soils (Lautenschlager, 1995). Except for studies of *R. idaeus*, the relationships between red spruce regeneration and understory plants have not been much examined.

A site classification for the red spruce–balsam fir flat forest-type is in progress for Maine (McLaughlin, 1997), and was not the focus of this study. Our objectives were to (1) characterize some features of red spruce regeneration habitat, (2) see if some common understory plant species can be used to indicate habitat quality for red spruce regeneration, and (3) detect possible patterns in distribution of understory plant species in relation to harvest disturbance.

2. Materials and methods

2.1. Study sites

Maine contains a large population of red spruce, and is toward the northern end of its range (Blum, 1990). The extent to which the red spruce–balsam fir flat-

type, as defined by Griffin (1980), covered Maine in pre-settlement times is difficult to determine but probably none of the original red spruce–balsam fir flat forest-type remains entirely unharvested (Cogbill, 1996). Soils in the glaciated region we sampled are usually thin, stony, and poorly-drained, and encompass a wide variety of types. Mapping of some areas in our sample has not been completed by the Natural Resource Conservation Service. The topography is rolling hills and mountains to 1597 m (Mt. Katahdin), with many river, lake, and peatland systems. Annual precipitation at nearby Bangor, ME is 1060 mm, 48% of which falls from May through October. Mean annual temperature is 6.6°C, with an average daily temperature in January of −7.7°C and in July of 20.0°C. The growing season averages 156 days.

Permanent plots set up for this study are coordinated with a long-term study at the Penobscot Experimental Forest (PEF) in Bradley on northern conifer response to various silvicultural treatments, which is ongoing since 1952. Eleven of 390 circular 0.081 ha plots in the PEF in Bradley were overlaid with the square 0.0625 ha plots of this study, and these represent 10 treatments and a control in the PEF. In addition, the Forest Service has 30 years of regeneration data from ca. 2000 4.05 m^2 subplots that are measured at about 5-year intervals (Brissette, 1996); 33 of these subplots are nested within 0.0625 ha plots established for this study.

In 1994–1996, eight sites in northern, western, and eastern Maine (Table 2; Fig. 1) were selected according to the presence of naturally regenerated red spruce–balsam fir stands, low elevation, flat topography, and accessibility. Sites vary in elevation (all are <200 m), slope (all are <15°), soil-type, stand history, and intended harvest schedule. To our knowledge, none has been plowed or pastured. We did not control the confounding of elevation, slope, or soil-type with harvest disturbance, but used multiple plots per location and paired plots (see below) to compensate for some between-site differences.

2.2. Field sampling

To study natural regeneration across a wide region, 50 paired plots, each 25×25 m^2 (0.0625 ha) were arbitrarily placed one each in a low elevation, intact mature stand and in a nearby, not necessarily adjacent,

Table 2
Study sites and their location, landowner or manager, and number of plots per site

| Name of site	Town	County	Landowner/manager	Number of plots
Penobscot Experimental Forest	Bradley	Penobscot	University of Maine/USDA Forest Service	11
Scientific Forest Management Area	Township (T) 6 Ranges (R) 9 and 10 WELS[a]	Piscataquis	Baxter State Park	6
Big Reed Pond Preserve	T 8 R 10 WELS	Piscataquis	Maine Chapter, The Nature Conservancy	3
Munsungan Lake	T 8 R 10 WELS	Piscataquis	Seven Islands Land Company	3
Third Machias Lake	T 42 MD BPP[b]	Washington	Champion International Corporation	8
Lobster Lake	T 3 R 14 WELS	Piscataquis	Bowater/Great Northern Paper Company	6
Round Pond	T 13 R 12 WELS	Aroostook	Maine Bureau of Public Lands	6
O. Young's Woodlot	Hope	Knox	Orvil Young	3
Richardson town Township	T 4 R 1 WBKP[c]	Franklin	Maine Bureau of Public Lands	4

[a] WELS: west of the Easterly Line of the State.
[b] MD BPP: middle division, Bingham's Penobscot purchase.
[c] WBKP: west of Bingham's Kennebec purchase.
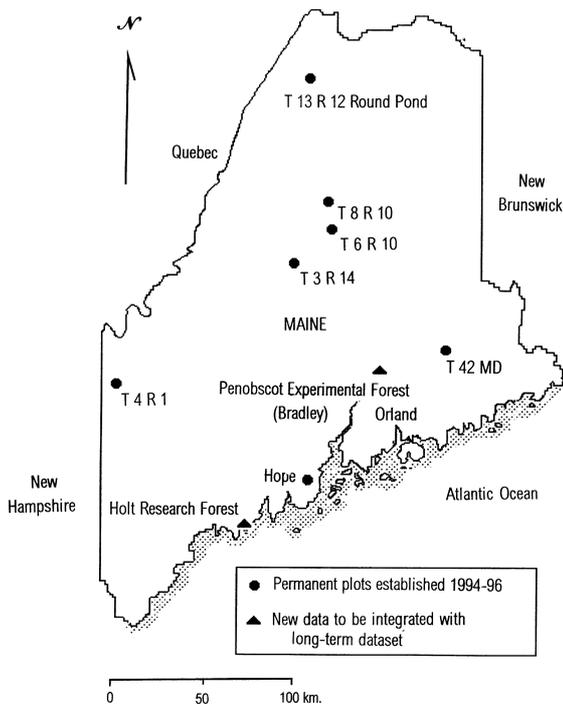
Fig. 1. Approximate locations of study sites in the state of Maine, USA. New data will be integrated with two large, existing databases.

harvested stand. The sample represents a disturbance gradient from relatively undisturbed mature forest to recent clearcuts. None of the older stands are completely unharvested old growth, which is extremely rare in Maine, though in some stands only a few white

pine and/or red spruce were harvested more than 100 years ago. Pairs were usually within 0.5 km of each other and ranged from 50 m to 5 km apart. At one site, the PEF, multiple harvested plots were paired with a single plot in a control stand. Within a site, aerial photos, records of harvest, soil maps, and ground reconnaissance were used to determine plot placement. Criteria for plot placement, in addition to elevation and slope considerations, were: current or recent dominance by red spruce (determined in harvest openings by identification of cut stumps), no herbicide yet applied, and distance from a forest edge or road of at least 50 m. Treatments included irregular shelterwood, single-tree selection, precommercial thinning, salvage clearcuts, and conifer release. To minimize bias, distance from the road and compass bearing to plot center were selected before entering a stand. Plots were assigned a posteriori to one of four harvest intensity levels based on stand history (Table 3). Sampling was conducted when leaves were fully expanded in June until leaf fall in October of 1994–1996. Spring ephemerals that disappear after flowering were not in our study so we considered a single observation per season to be adequate.

Within the 0.0625 ha plot, dbh (at 1.37 m) was recorded for all trees >2.5 cm. Basal area and quadratic mean diameter were used to calculate Curtis' relative density (Davis and Johnson, 1987). Each plot contained 12 1 m^2 circular subplots (radius 0.56 m; total 600 subplots) arranged at regular intervals along intersecting transects to make an 'x' pattern. For each

Table 3
Categories of harvest intensity levels, their characteristics, and sample size for groups of sampled plots established in eight study sites

Harvest intensity	Level 1	Level 2	Level 3	Level 4
Years since entry	>80	20–70	<15	<15
Harvest	Partial (or possibly none)	Partial	Shelterwood with retention, intensive selection, crop tree diameter limit, flexible diameter limit, unregulated harvesting, partial harvest on private woodlot	Unregulated clear cut
Number of plots in category	15	14	9	12
Number of sites in category	6	4	2	4

subplot, tree seedlings 0.1–0.5 m tall (h; referred to hereafter as 'small') were counted, and percent cover for understory species was scored according to relevé procedures of Witham et al. (1993) in four height classes (<0.25, 0.25–<0.5, 0.5–<1.0, and ≥1.0 m from the ground). Number of stems for understory plants was recorded per species except for prostrate creepers such as *Oxalis montana*, *Gaultheria hispidula*, and *Linnaea borealis*, which were scored as percent cover only. Percent cover in bryophytes on the forest floor was estimated for each subplot; bryophytes were identified to species if common and abundant or placed in one of 11 species groups if infrequent.

In addition to subplot data on ground cover and understory plants, the relative abundances of understory plant species within each 0.0625 ha plot were scored according to these classes: 1=≤5 individuals; 2=6–25 individuals; 3=common but ≤20% of total cover in the herb or shrub stratum; 4=≥25% cover in the herb or shrub stratum. For some species, decisions regarding placement into these abundance classes were reinforced from the average percent cover for 12 subplots per plot and/or average number of stems/m^2.

For the data matrix used in canonical correspondence analysis (CCA), only the 30 most common understory plant species were included (Table 1), because rare species (i.e. those that occurred in fewer than five of the 50 plots) were expected to have little influence on patterns of red spruce regeneration. All 30 understory plant species are native except *Anaphalis margaritacea* and the two species of *Hieracium* (Table 1; Campbell et al., 1995). No tree seedlings were included in the species data matrix, although many small trees were present in some plots. Nomenclature follows Campbell et al. (1995).

Our environmental variables (abbreviated and defined in Table 4), so-called because of their use as such in the ordination technique, characterize harvest intensity, amount of time since last harvest, stand density, overstory composition, abundance of small red spruce and balsam fir (not included in the herb and shrub species data matrix used in CCA), abundance of bryophytes on the forest floor, number of herb species per plot, and percent of understory plants in a plot that are known to be visited by native bees rather than wind-pollinated. Bryophyte cover was included because some mosses contribute to Norway and white spruce regeneration (*Picea abies*, Hörnberg et al., 1997; *P. glauca*, Parker et al., 1997). The use of a variable for plant associations with pollen vectors is unusual in studies of forest understories but was consistent with our interest in uncovering a feature of understory plant biology that (1) might be descriptive of red spruce regeneration habitat and (2) is likely to be affected by disturbance. Bees in the genera *Bombus*, *Andrena*, *Osmia*, *Halictus*, and *Dialictus* have been collected in some of the study plots (Dibble, unpublished data). Data were summarized in notched-box plots using SYSTAT 5.2.1 for Macintosh (Wilkinson, 1992) with harvest intensity level as the grouping variable. These were used especially as visual comparisons and include confidence intervals at $\alpha=0.05$ in that the lack of overlap on the y-axis for the notched portion of any box with that for another indicates that the groups are significantly different. Such plots provide comparisons of groups that contain unequal sample sizes. Two variables were not summarized with the others because of their influence as grouping variables: harvest intensity and years since harvest.

Table 4
Environmental variables used in CCA, sample size, mean, SD, and range

Variable mnenomic and definition	N	Mean	SD	Min	Max
SMPI (average number of red spruce trees 0.1–0.5 m h per 1 m^2 for 12 subplots per plot)	50	1.02	2.36	0	16.0
SMAB (average number of balsam fir trees 0.1–0.5 m h per 1 m^2 for 12 subplots per plot)	50	1.19	1.73	0	7.67
CURT (Curtis' relative density for plot, a relative index value[a])	50	6.32	3.68	0	13.5
SWHW (softwood:hardwood ratio for overstory trees >2 cm dbh)	50	0.76	0.30	0	1.00
MOSS (percent cover of ground in bryophytes; average of 12 subplots per plot)	50	0.38	0.26	0	0.90
HERB (number of herb and shrub species in 25×25 m plot)	50	22.2	12.1	8.0	64.0
BEEV (percent of understory species that have been observed to be visited by bees in these and/or other locales)	50	0.73	0.14	0.42	1.00

Two qualitative variables, estimated years since harvest (estimated or recorded) and harvest intensity category (Table 3), are not listed.
[a] See Davis and Johnson (1987).

2.3. Ordination methods

For exploratory purposes, vegetation data for the 50 plots were ordinated with nine environmental variables (Table 4) in a CCA using CANOCO of ter Braak (1992; Version 3.2). This direct gradient analysis technique was used to seek patterns of distribution for species along a disturbance gradient (Palmer, 1993). The first two axes for canonical coefficients and intra-set correlations were used to examine the relative contribution of the environmental variables to the ordination. Vectors for environmental variables, in which the mean passes through the origin and the positive end is shown, were evaluated in relation to species distributions in the ordination scatterplot (Anderson et al., 1996).

3. Results

The average number of small red spruce (Fig. 2(a)) was greatest in association with mature stands that are partially harvested on >80-year intervals (Level 1; Table 3), but did not differ significantly among the four harvest intensity levels at $\alpha=0.05$. Variance, also, was greatest among plots in Level 1. Few red spruce in the 0.1–0.5 m h size class were found in most of the clearcuts, which suggests that harvest was conducted before advanced regeneration had become well established. The median for small balsam fir (Fig. 2(b)) was slightly higher in Levels 1 and 2 than was the median for small red spruce (Fig. 2(a)), though the difference was not significant at $\alpha=0.05$. Curtis' relative density was significantly highest in Level 1; Levels 2 and 3

were not significantly different (Fig. 2(c)). Ratio of softwoods to hardwoods was similar for Levels 1 and 2, and was lowest in the clearcuts (Fig. 2(d)). Bryophyte cover was similar for Levels 1–3 but significantly lower in the clearcuts (Fig. 2(e)); in recent clearcuts dead bryophytes were in evidence but most of these apparently disappear within a few years of overstory removal and some pioneer bryophyte species become established. A leafy liverwort, *Bazzania trilobata* (L.) S. Gray, was often common and abundant where small red spruce was also abundant; its presence was more consistent than any other bryophyte species or species group observed. The median number of herb species per plot was highest in the clearcuts and was significantly higher than in Levels 1 and 2 (Fig. 2(f)). The percent of bee-visited plants was highest in Levels 1 and 2, and was significantly higher there than in the clearcuts (Fig. 2(g)). Summary statistics for environmental variables except harvest intensity level and years since harvest are listed in Table 4.

In the CCA ordination, the first canonical axis accounted for 45% of the species–environment variation (eigenvalue=0.21), and the second for 19.6% (eigenvalue=0.09). Such a low percentage of variation explained by the first few axes is typical of many community ordination studies and is not necessarily considered too noisy for ecological interpretation (Gauch, 1982; ter Braak, 1987). Species–environment correlations were 0.87 and 0.71 for the first two axes, respectively. The first two CCA axes accounted for 64.6% of the total variation in the species–environment relationship. The canonical coefficients, intra-set correlations (Table 5), and a biplot of species and
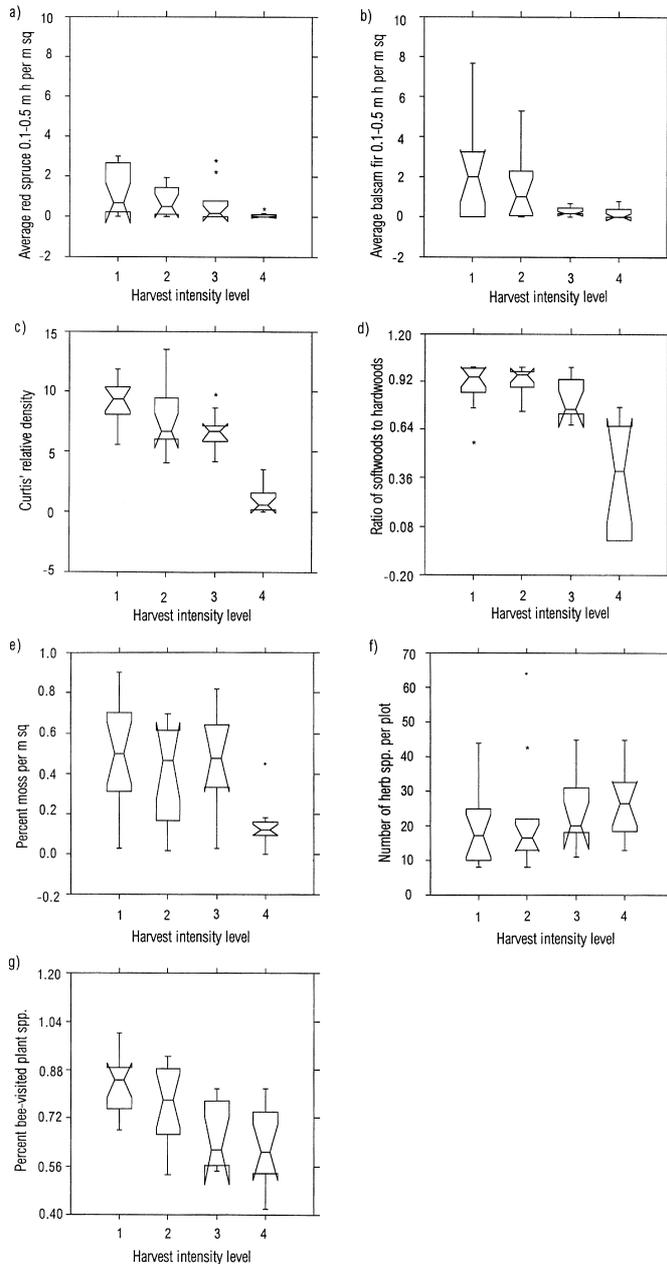
Fig. 2. Notched-box plots with harvest intensity as the grouping variable. (a) Average number of red spruce 0.1–0.5 m per m² for 12 subplots per plot; (b) average balsam fir 0.1–0.5 m per m² for 12 subplots per plot; (c) Curtis' relative density; (d) ratio of softwoods:hardwoods; (e) average percent cover in bryophytes per m² for 12 subplots per plot; (f) number of herb species per plot; (g) percent of bee-visited understory species per plot. The central box shows the median (short horizontal line in central box) and the upper and lower quartiles, with a confidence interval (α=0.05) indicated by the notched portion. If the notched portion of the central box does not overlap with that of another box on the vertical axis, then that group is significantly different from all others. Also provided are the hinges (longer horizontal lines at top and bottom of central box), whiskers (vertical lines) or inner fences which are approximately comparable to three standard deviations, and stars as outliers. When sample size is small, the confidence interval can extend beyond the limits of the upper or lower quartile, creating a pronged appearance.

Table 5
Canonical coefficients and intra-set correlations resulting from CCA

Variable	Canonical coefficients Axis 1	Canonical coefficients Axis 2	Intra-set correlations Axis 1	Intra-set correlations Axis 2
YEAR	−0.62	−0.96	−0.71	0.08
INTE	−0.39	−0.55	0.64	−0.17
SMPI	−0.03	−0.09	−0.22	0.15
SMAB	−0.08	1.13	−0.44	0.48
CURT	−0.50	0.59	−0.77	0.01
SWHW	−0.42	−0.94	−0.63	−0.05
MOSS	−0.22	−0.27	0.05	−0.13
HERB	−0.003	0.26	0.16	0.16
BEEV	0.058	−0.18	0.04	−0.23

Variables are described in Table 4.

environmental variables (Fig. 3) indicated that the variables that most influenced understory species composition along the first ordination axis were years since harvest, Curtis' relative density, softwood:hardwood ratio, and harvest intensity level. The second ordination axis was influenced especially by abundance of small balsam fir, secondarily by the same variables that influenced the first axis (these vary only slightly along the y-axis), and also by the percent of plants visited by bees, number of herb species, and percent cover in bryophytes. The abundance of small red spruce had minor influence on the second ordina-
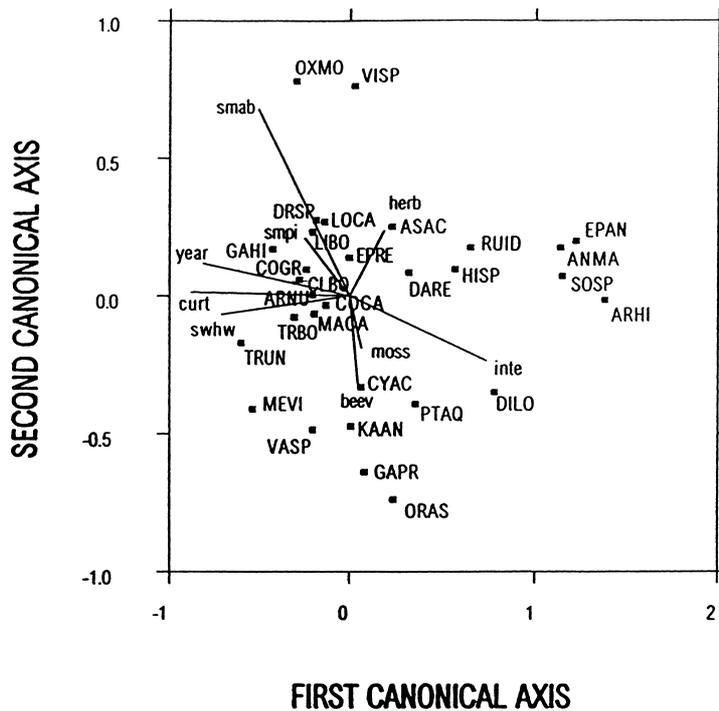

Fig. 3. Biplot of first and second canonical correspondence axes for an ordination including 50 plots, 30 understory plant species, and nine environmental variables. Only the species (abbreviations in Table 1) and environmental variables (abbreviations in Table 4) are shown. See also Fig. 4, which is the same ordination, presented separately to minimize clutter.

tion axis and little or none on the first; this vector was closely correlated with that for abundance of small balsam fir but was not as long, hence did not influence the ordination as much.

Despite the minor influence of small red spruce on the ordination (Fig. 3), understory species that associated most closely with it are of interest as possible indicators, and included especially *Linnaea borealis* ssp. *longiflora*. *Dryopteris* spp. and *Lonicera canadensis* also associated with the abundance of small balsam fir. Other species that were near these vectors in the ordination were *Gaultheria hispidula*, *Coptis trifolia* ssp. *groenlandica*, *Clintonia borealis*, and *Epigaea repens*. A species negatively correlated with small red spruce is *Pteridium aquilinum*, which has allelopathic influences (Nava et al., 1987). Species that were uncorrelated with small red spruce are those of large, recent clearcuts: *Epilobium angustifolium*, *Aralia hispidula*, *Anaphalis margaritacea*, *Rubus idaeus*, *Solidago* spp., and *Hieracium* spp. *Cypripedium acaule* was closely associated with the vector for bee-visited plants.

The 50 plots, symbolized according to their harvest intensity (Table 3), were ordinated in a biplot (Fig. 4), that is, the same ordination as Fig. 3. The two less-intense harvest categories (Levels 1 and 2) did not separate from each other on the *x*-axis. All but one mature plot (Level 1) were discrete from the cloud of clearcut (Level 4) plots. Partial harvests on 5–15-year intervals (Level 3) formed a narrow column between the less-disturbed (Levels 1 and 2) and clearcut plots. No separation could be seen on the *y*-axis. Clearcuts featured low values for basal area, softwood:hardwood ratio, percent cover in bryophytes, and percent of bee-visited understory plants. The total number of herb species (Fig. 2(f); 'herb' in Fig. 3) increased with disturbance, was high in Levels 3 and 4, and was especially high if plots contained moist depressions with skid trails through them.

To clarify some of the associations indicated in Fig. 3, we examined understory plant abundance from plots where the average number of small red spruce per m^2 is greater than one. There were 13 such plots, with in descending order by relative abundance, *Maianthemum canadense*, *Trientalis borealis*, *Trillium undulatum*, *Clintonia borealis*, *Cornus canadensis*, *Dryopteris* spp., and *Gaultheria hispidula*.

We found no herb or shrub species present in all plots. Species that occurred in at least 25 of the 50 plots include, in descending order, *Maianthemum canadense* (present in 42 plots), *Trientalis borealis*, *Cornus canadensis*, *Clintonia borealis*, and *Vaccinium* spp., *Dryopteris* spp., *Gaultheria hispidula*, *Linnaea borealis*, *Coptis trifolia* spp. *groenlandica*, and *Rubus idaeus*. When present, *Pteridium aquilinum* often dominated the understory vegetation. *Rubus idaeus*
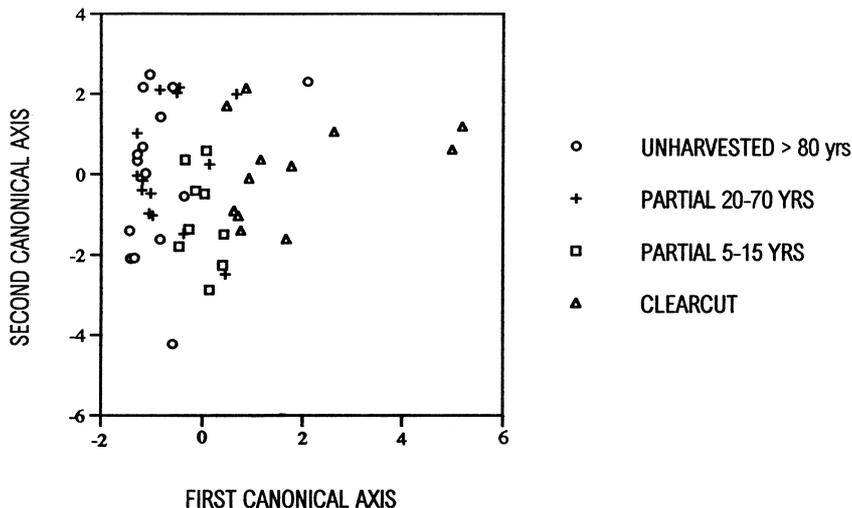

Fig. 4. Biplot of first and second canonical correspondence axes for an ordination including 50 plots, 30 understory plant species, and nine environmental variables. Plots are coded according to harvest intensity level, described in Table 3. See also Fig. 3, which is the same ordination.

was present in 32 plots and was unusual in the extent to which it can fill the understory stratum in a dense, continuous mass. This species was present at low densities in three of the six stands we categorized as Level 1, unharvested for more than 80 years.

Species represented in the data matrix from <15 of the 50 plots were, in descending order: *Oryzopsis asperifolia*, *Epigaea repens*, *Medeola virginiana*, *Hieracium* spp., *Solidago* spp., *Aralia hispidula*, *Aster acuminatus*. All of these are widely distributed, common species in Maine and sometimes occur in large populations.

Two suites of understory plant species were associated with vectors that relate to the disturbance gradient (Fig. 3). The first of these, associated with higher values for Curtis' relative density, softwood:hardwood ratio, and abundance of both small red spruce and small balsam fir, includes *Gaultheria hispidula*, *Oxalis montana*, *Linnaea borealis*, *Trillium undulatum*, and *Trientalis borealis*. The second, associated with low values for these same four environmental variables, includes *Epilobium angustifolium*, *Aralia hispidula*, *Anaphalis margaritacea*, *Rubus idaeus*, and *Solidago* spp. Except for *Rubus idaeus* and some *Solidago* spp., species in this second suite were present only in clearcuts.

Indicators of red spruce regeneration habitat can be considered from the CCA ordination and from those understory plant species that grow where the abundance of red spruce is greatest. Based on the above results and additional field observations from these plots and other sites, we propose the following as potential (not absolute) indicators of conditions suitable for red spruce regeneration within low-elevation forests where this tree species already grows: *Linnaea borealis*, *Trientalis borealis*, *Trillium undulatum*, *Gaultheria hispidula*, and the liverwort *Bazzania trilobata*. None of these species associate exclusively with red spruce or with one particular successional stage in Maine.

4. Discussion

4.1. What makes a good indicator of regeneration habitat?

Ideally, understory plant indicators of regeneration habitat for a particular dominant tree (1) overlap in habitat preferences with the desired tree species, (2) occur commonly across the geographic range of the desired tree species, (3) are not dependent upon a particular successional stage, (4) can be measured with accuracy so that comparisons can be made over time, and (5) are readily recognizable by non-specialists. The species we propose as potential indicators qualify according to all five of these characteristics, but are of limited effectiveness because they all appear to have a much broader niche than does red spruce. All are also found in other forest cover-types, and in the case of *Gaultheria hispidula*, in sphagnum-dominated bogs. We expected to find few or no species that grow only in red spruce understories, partly because the Maine flora has relatively few habitat specialists and those tend to be calciphiles or are restricted to alpine zones or wetlands (Dibble et al., 1989). Smith (1995) found that most understory plants of upland northern hardwoods in Vermont had broad ecological niches, but some were useful for site classification when ordinated with physiography and soils variables.

Some species that were frequent in low-elevation red spruce regeneration habitat, including *Clintonia borealis*, *Dryopteris intermedia*, and *Oxalis montana* are also present in old-growth red spruce stands above 1000 m in southwestern Virginia and central West Virginia (Adams and Stephenson, 1989). Another, *Cornus canadensis*, was recognized by Tappeiner and Alaback (1989) to be important in the western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) – Sitka spruce (*Picea sitchensis* (Bong.) Carr.) ecosystem, and by Coffman and Willis (1977) to be an indicator of eastern hemlock (*T. canadensis* (L.) Carr.) stands in Michigan. Thus, these species might have limited utility as indicators in red spruce–balsam fir flats because their geographic ranges and habitat preferences are broad.

Maianthemum canadense is almost ubiquitous under red spruce in Maine, though often at low densities and in a mostly vegetative state. However, it is too much of a generalist to be considered an indicator of red spruce regeneration habitat. This species was considered an indicator of climax eastern hemlock sites in Michigan by Coffman and Willis (1977), and can be common in hardwood stands (MacLean and Wein, 1977; Crowder and Taylor, 1984). The niche widths of other species that occur

in habitat conducive to red spruce regeneration, such as *Trientalis borealis*, *Trillium undulatum*, *Clintonia borealis*, *Cornus canadensis*, *Dryopteris* spp., *Gaultheria hispidula*, *Linnaea borealis*, *Oxalis montana*, and *Coptis trifolia* spp. *groenlandica*, are not yet fully explored. None is restricted to red spruce stands and all but two (*G. hispidula* and *O. montana*) were understory components in mixed hardwoods and/or jack pine stands in New Brunswick (MacLean and Wein, 1977).

4.2. Circularity of the indicator plant concept

Causal factors are not revealed in our data. The associations between understory species and red spruce regeneration could be due to the light quality, which differ in coniferous understories from those in mixed woods or hardwoods (Endler, 1993), or pH, soil nutrients, hydrology, other habitat features, or stochasticity, and we suspect that a combination of factors is likely. Abiotic factors were found to explain little of the variation in the distribution of seedling black spruce (*Picea mariana* [P. Mill] B.S.P.) (defined as <1 cm dbh) and balsam fir in the southwestern boreal forest of Quebec, although there appeared to be some preference for fine soil texture (Kneeshaw and Bergeron, 1996). Red spruce litter probably contributes to acidification of the understory; thus, red spruce may limit plant associations and influence the composition of the herb and shrub layers. Further, the understory plants themselves might contribute to red spruce establishment at the microhabitat scale by serving as nurse plants, loosening soil, and by concentrating throughfall nutrients around the dripline of the understory plants.

Kneeshaw and Bergeron (1996) found the presence of seed trees to be a significant factor in explaining the distribution of conifer seedlings in boreal forests of southwestern Quebec, although they did not score the herb layer. We regard seed trees in this study as more important indicators of red spruce regeneration habitat than any understory species. Because red spruce seed is short-lived, a seed source is vital to the continuing appearance of new cohorts (Frank and Safford, 1980). In harvested stands, if advanced regeneration was sparse at the time of the disturbance, then wind dispersal into a disturbed site is essential to the robust regeneration of the stand. In almost all the clearcuts

we studied, few or no small red spruce were in the plots (Fig. 2(a)), and few or no red spruce were in the remaining overstory (data not shown). The distance between a clearcut and a cone-bearing spruce is expected to affect recolonization by red spruce in heavily disturbed stands (Randall, 1974; Hughes and Bechtel, 1997) unless advanced regeneration is present at harvest or planting is undertaken.

4.3. Bryophytes and bee-visited plants in relation to red spruce regeneration

While red spruce does not require the presence of a bryophyte layer to germinate and grow, there appears to be a link between bryophyte cover, percent of understory plants that are visited by bees, and the abundance of small red spruce (Fig. 2(a),(e) and (g)); this is probably attributable to the shady environment under mature red spruce. Bryophytes provide a rich source of nutrients, especially under the growing portion of the mat, to red spruce seedlings and shallow-rooted herbs and shrubs. The liverwort *Bazzania trilobata* was associated with high levels of P and Fe in Maine peatlands (Anderson et al., 1996). In a black spruce (*Picea mariana*) forest in Quebec, Canada, this layer contained N, P, K, Ca, and Mg (Weetman, 1967). Many of the herb and shrub species in our study have shallow root systems and thus might benefit from the nutrients under the bryophyte mat.

A high proportion of plants that are found in shady, bryophyte-carpeted understories are also visited by bees and bear fleshy fruits (e.g. *Aralia nudicaulis*, *Clintonia borealis*, *Cornus canadensis*, *Gaultheria hispidula*, *G. procumbens*, *Lonicera canadensis*, *Maianthemum canadense*, *Rubus idaeus*, and *Vaccinium angustifolium*). Fruit production may vary across silvicultural treatments, and tends to increase with available light for most species. In turn, when the canopy is opened during harvest, certain trends are well known: the number of herb species increases (Fig. 2(f)), more flowers become available temporally, forest bees have increased foraging opportunities for pollen and nectar, more fruits are produced, and patches of some understory plant species increase in size and density. There could be a fine balance: if the stand is opened too much, then perhaps the early-successional species obtain an advantage and outcompete red spruce for regeneration habitat.

4.4. Beyond species richness

Managers trying to meet the criterion of maintaining forest biodiversity need reliable indicators by which the ecological sustainability of timber management can be assessed (Kangas and Kuusipalo, 1993). Species richness, a crude metric, is subject to worker bias when measured as percent cover. It is often the measure by which changes in forest understory composition are attributed to harvest activities, and these changes are studied for their relevance to conservation (examples and discussion: Reader and Bricker, 1992; Duffy and Meier, 1992; Duffy, 1993a, b; Elliott and Loftis, 1993; Elliott et al., 1997). The concept of biodiversity, ''the diversity of life in all its forms and at all levels of organization'' (Hunter, 1996), is sometimes confused with species diversity (Schlesinger et al., 1994), which is often expressed as an index of species richness and evenness (relative abundance) (Magurran, 1988). However, species diversity offers scant opportunity to weight a species according to its global rarity, influence on other species, vulnerability to disturbance, habitat specificity, or genetic variability, and does not address some concerns in maintaining biodiversity such as species dependent on old forests (Pielou, 1996). Furthermore, a change in understory species richness may poorly relate to the broader issue of protection of a dominant species that influences habitat for many other species, for example, red spruce.

The potential usefulness of ordination techniques in biodiversity-related research is not well explored (exception: Dufrêne and Legendre, 1997). Ordinations such as those output by CCA reveal structure in datasets and permit examination of the relationships between environmental variables and species composition (ter Braak, 1987; Anderson and Davis, 1997; Anderson et al., 1996). Community data have much to offer in forest conservation studies because manipulation of the overstory is relatively easy, and canopy openings could be adjusted to favor a rare understory species. In the reductionist approach, changes in species composition with forest succession are associated with reproductive, physiological, or other characteristics that increase potential for colonization of disturbed habitat or persistence in a shady understory (Roberts and Gilliam, 1995). The life histories and life spans of the species involved should be considered whenever there is sufficient information.

4.5. Rubus idaeus and red spruce regeneration

The rate at which a stand will return to dominance by red spruce can be greatly influenced by *Rubus idaeus*, for which some aspects of species biology have been studied. Our results parallel those of Lautenschlager (1995) who found this shrub to vigorously outcompete regenerating *Picea glauca*, white spruce. Probability of *R. idaeus* germination appears to increase with time (Lautenschlager, 1997) to some undetermined threshold, thus, a conifer stand in which *R. idaeus* is sparse or absent in the understory might harbor beneath the humus layer a cohort of *R. idaeus* seeds that responds quickly to harvest disturbance. When the overstory is disturbed, these seeds germinate because of higher temperatures, increased temperature fluctuation (Lautenschlager, 1997), increased light (Roberts and Dong, 1993), or other influences. A site might become increasingly predisposed to colonization by *R. idaeus* during subsequent disturbances because of the build-up of the seedbank. Overstory removal not only spurs *R. idaeus* germination but leads to vigorous vegetative reproduction by stolons. The germination rate of *P. glauca*, was found to be inhibited by the presence of *R. idaeus* shoots and soil in which this shrub had been growing (J.R. Steinman, unpublished data); this suggests that an unidentified agent in *Rubus* seed, litter, or rhizomes might contribute to an allelopathic effect. Vast areas of the red spruce–balsam fir flat forest-type in Maine were recently logged for salvage following the spruce budworm episode of 1970–1985 (MacLean, 1996). Some large canopy openings have filled with *R. idaeus* and it appears that succession to a red spruce-dominated stand will be delayed. Although *R. idaeus* attracts beneficial insects such as bees (Hansen and Osgood, 1983) and provides forage and cover for animals, its dominance is economically undesirable where spruce is the intended crop, and ecologically undesirable because mature forest habitats are proportionately few compared to early successional habitats in Maine. Lautenschlager (1997) thought that there is little managers can do to reduce germination of *R. idaeus* after harvest, so preventive measures should be considered. Our results suggest that managing for red spruce regeneration habitat could keep the *R. idaeus* population at an acceptable level.

4.6. Implications for management

Our results do not confirm the recommendation to provide mineral soil for red spruce germination (Blum, 1990) and are contrary to results of Davis and Hart (1961) who thought that a substantial humus layer dried too quickly for adequate spruce establishment. Harvest methods that minimize disturbance to the forest litter layer, such as harvest during winter and/or low-impact processors, are likely to allow red spruce to dominate the overstory on red spruce–balsam fir sites. If forest openings are kept small through single tree or group selection, patch cuts, strip cuts, or other partial harvest methods, desired conditions should result. This would also allow bryophytes and shade-adapted understory plants to continue to dominate the lowest stratum.

When large openings are necessary, advanced regeneration of red spruce will ideally be in place at the time of harvest, or planting may be required. Islands of mature red spruce can be left standing here and there in a large opening as a seed source and to provide cover and vertical structure for animals. On thin soils, these islands might blow down within few years but could provide a seed crop before they do so. All of these measures are expected to minimize (1) competition with balsam fir, even on poor sites, and (2) a predisposition toward rapid colonization by *R. idaeus*. The common understory plants we found as potential indicators should be observed further, in diverse sites, to test their applicability across the geographic and habitat range of red spruce.

At the landscape scale, inferences regarding changes in understory species composition might be possible from information on aerial photos of forested areas in Maine. This study suggests that predictable understory changes are likely where the canopy has been disturbed, given similarities in topography and soil-type. If ground-truthing follows the understory vegetation-type mapping proposed by Westveld (1954), then models might be developed to test scenarios under which red spruce regeneration could be enhanced.

5. Conclusions

Our proposal of potential indicators of red spruce regeneration habitat includes no species that are diagnostic for ideal regeneration conditions or are limited to red spruce–balsam fir flats or mature seral stages. However, we suggest that where cone-bearing red spruce trees are present in the overstory, the following understory characteristics, separately or in combination, may indicate habitat conducive to red spruce regeneration: (1) abundant ground cover in bryophytes (especially the liverwort *Bazzania trilobata*), (2) a high proportion of insect- versus wind-pollinated understory plant species, and (3) presence of one or more of the following vascular plant species: *Linnaea borealis*, *Trientalis borealis*, *Trillium undulatum*, and *Gaultheria hispidula*. Other species that are common in red spruce stands but that appear to have lower potential as indicators of red spruce regeneration habitat because of their wide niches include *Clintonia borealis*, *Cornus canadensis*, *Dryopteris* spp., *Oxalis montana*, and *Coptis trifolia* spp. *groenlandica*. Early successional plants that fill forest openings, such as *Rubus idaeus*, *Epilobium angustifolium*, *Aralia hispida*, and *Anaphalis margaritacea*, can be considered indicators of poor quality habitat for red spruce on the short term but in most cases if a seed source is nearby, we think that red spruce is likely to recolonize the stand eventually.

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