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PREDICTION OF RARITIES FROM HABITAT VARIABLES: COASTAL PLAIN PLANTS ON NOVA SCOTIAN LAKESHORES[1]

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Abstract. Predictive models relating species richness of rare plants to measured habitat variables were developed using data from the shoreline vegetation of lakes in southwestern Nova Scotia. These lakes contain large disjunct populations of many Atlantic Coastal Plain plant species whose main ranges are along the eastern seaboard of the United States. The richness of rare coastal plain herbs was easier to predict than richness of the "background flora" of wide-ranging species from noncoastal plain elements. Multiple-regression models using habitat variables accounted for 83% of the variability in species richness of rare coastal plain species but only 45% of that for the background flora. Richness was best correlated with the two inter-related variables, watershed area and shoreline width. The mechanism underlying this pattern appears to be that flooding kills woody plants, thereby reducing competition from shrubs and creating open expanses of shoreline.

Key words: Atlantic coastal plain plants; conservation; flooding; predictive ecology; rare species; shrubs; watershed area; wetlands.

INTRODUCTION

The prediction of species richness from environmental factors is not only a goal of theoretical ecology (e.g., May 1986, Currie and Paquin 1987), but is of obvious importance for conservation biology as well. The ability to forecast areas of greatest species richness could facilitate the preservation of genetic diversity, a major objective of the World Conservation Strategy (IUCN 1980). Predictions of species richness of plants can be made at a variety of scales ranging from the continental (Currie and Paquin 1987, Adams and Woodward 1989) to the local level, where richness is often predictable from the community biomass (McNaughton 1967, Grime 1979, Wheeler and Giller 1982, Moore et al. 1989, Wisheu and Keddy 1989). Our objective is to explore predictive models made at an intermediate scale, within a single biogeographic region (e.g., White and Miller 1988, Baker 1990), and to place particular emphasis on predicting the occurrence of rare and endangered plant species at that scale.

There is no guarantee that rare species will obey the same rules as the common ones. Indeed, White and Miller (1988) demonstrated that different regression models were generated for the different components of the plant species richness of southern Appalachian high peaks. In contrast with Miller's work (1986) showing the possibility of predicting species richness of the rare and endangered Appalachian plants, Nilsson et al. (1988) found that rare riparian plants could not be predicted from habitat variables, and they advocated extensive field work in order to locate sites of interest for conservation. Scott et al. (1987) point out that it is the rarest species for which we have the poorest powers of prediction; conservation of many of these species is pursued on a site-by-site basis. In remote areas, there is frequently too large an area of potential habitat to allow full documentation of the distribution of species on an individual basis; to do so, Keddy (1991) suggests would leave biologists outnumbered by species to be monitored. Thus, we decided to take the empirical approach; regression techniques are used to explore relationships among selected state variables that characterize communities and environments (e.g., Peters 1980, Rigler 1982, Keddy 1987). Recent examples of this approach include Miller et al. (1987), Currie and Paquin (1987), Nilsson and Keddy (1988), White and Miller (1988), Adams and Woodward (1989), Wisheu and Keddy (1989), and Baker (1990). In this paper, the dependent variable is the species richness of different components of the vegetation; the independent variables are environmental factors.

Our model system is the Atlantic Coastal Plain flora, which is increasingly endangered because its range largely overlaps the industrialized eastern seaboard of the United States (Keddy and Wisheu 1989). The present study focussed on disjunct assemblages of these species, which occur among remote lakes in Nova Scotia and asked two questions: (1) can environmental factors be used to predict plant species richness? (2) do predictions differ among rare and common groups of species?

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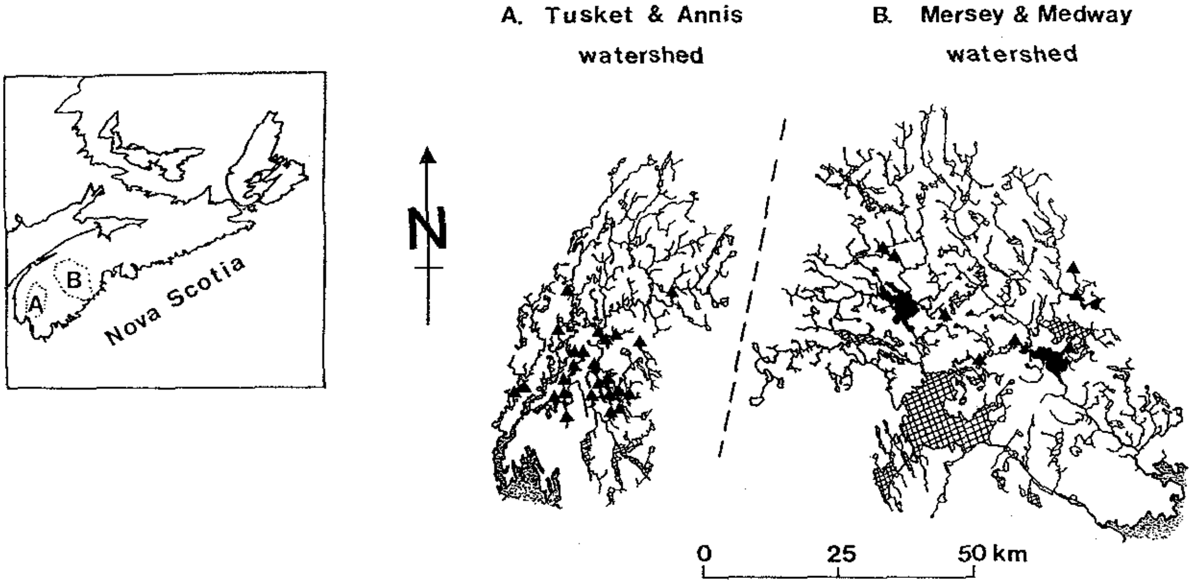

FIG. 1. Location of 35 of the lakes studied in Nova Scotia in the watershed of the Tusket and Annis Rivers and in the watershed of the Mersey and Medway Rivers. Lakes studied are designated with ▲ except for large lakes, which are blackened in. The two study lakes not shown in this figure lie between areas A and B. Cross-hatched areas represent dammed lakes.

MATERIALS AND METHODS

Study areas

Thirty-seven lakes were chosen from two regions within Nova Scotia noted for their coastal plain vegetation. The first region included 24 lakes of the Tusket and Annis river systems (Fig. 1A, center of area, 44°00′ N, 65°50′ W), and the second included 10 lakes of the Mersey and Medway river systems (Fig. 1B, center of area, latitude 44°22′, longitude 65°00′). In addition, two lakes between these two regions were included because they contain the only known populations of *Eleocharis tuberculosa* in Canada. Lakes were chosen in a nonrandom manner to ensure that a wide range in lake surface area and in watershed area was represented in the final list of lakes studied. In addition, final selection of lakes excluded dammed lakes or those known to have been dammed in the past.

Species richness

Since there is well known within-lake variation in vegetation resulting from effects of exposure to waves (Hutchinson 1975), species richness of littoral zone vegetation was recorded for 100-m stretches around an exposed headland, a sheltered bay, and a straight shoreline from each side of each lake in order to include the full range of exposure conditions. These positions were chosen a priori from topographical maps. The two sides of a lake were taken as the opposing shorelines from inflow to outflow on each lake; however, at lakes where inflow and outflow positions were in close proximity, the two lake sides were simply the opposite shorelines on either side of the long axis of the lake. The three positions from each side of a lake were chosen to maximize the between-site variability in vegetation, hence the most sheltered bay, the most exposed headland, and the longest uninterrupted stretch on each lake side were chosen. The vegetation was sampled from 1 m below the waterline to 1 m above the beginning of the upper shrub layer. The width of this littoral zone, here taken as the waterline to the shrub layer, ranged from 0 to 8 m. All species of the vegetation were censussed except forest herb species above the shrub layer (e.g., *Cornus canadensis, Maianthemum canadense,* and *Trientalis borealis*). (Species nomenclature follows Roland and Smith [1968], except in the cases where authorities appear.)

Species lists were divided into five species groups: (1) shrubs, (2) rare coastal plain herbs, (3) common coastal plain herbs, (4) "background" noncoastal plain herbs (that is, all remaining herbs) and (5) all herbs (total herbaceous species richness). Coastal plain designations followed Roland and Smith (1968). The rare species designations came from the list of rare species in Nova Scotia (Maher et al. 1978), the list of Canadian nationally rare species (Argus and Prior 1990) and the list of endangered and threatened species published by the Committee on the Status of Endangered Wildlife in Canada. Ranked in order of their rarity on a global basis, the rare coastal plain herbs found during this study consisted of provincially (Nova Scotia) rare *Panicum dichotomiflorum,* nationally (Canada) rare *Eupatorium dubium, Platanthera flava* (L.) Lindl., *Lachnanthes caroliniana* (Lam.) Dandy, *Dicanthelium*

TABLE 1. Correlations (r) between species richness of vegetation groupings and physical characteristics of 37 lakes in Nova Scotia, eastern Canada.

		Independent variables						
Vegetation groups		*Lake surface area*	*Watershed area*	*Shore width*	*% sand of shore*	*Water alkalinity*	*% poorly drained shore*	*Elevation*
Herbs								
Rare coastal plain	r	0.32	0.82**	0.79**	0.45**	−0.38*	0.38*	−0.34*
	P	0.06	<0.01	<0.01	<0.01	0.03	0.02	0.04
Common coastal plain	r	0.39*	0.62**	0.60**	0.58**	−0.32	−0.22	−0.33*
	P	0.02	<0.01	<0.01	<0.01	0.05	0.19	0.04
Noncoastal plain	r	0.21	0.56**	0.59**	0.32	0.04	0.12	−0.22
	P	0.21	<0.01	<0.01	0.05	0.84	0.46	0.18
All herbs	r	0.28	0.64**	0.66**	0.40*	−0.08	0.19	−0.27
	P	0.10	<0.01	<0.01	0.01	0.62	0.27	0.10
Shrubs								
All shrubs	r	−0.44**	−0.14	−0.06	−0.11	−0.001	−0.01	−0.17
	P	<0.01	0.42	0.74	0.53	0.99	0.96	0.31

* Correlations significant at the .05 level; ** correlations significant at the .01 level.

rigidulum Nees var. *pubescens* and *Woodwardia areolata,* nationally imperilled *Eleocharis tuberculosa, Hydrocotyle umbellata* and *Utricularia subulata,* nationally imperilled and globally rare *Coreopsis rosea, Lophiola aurea,* and *Sabatia kennedyana* and globally imperilled *Scirpus longii.*

Independent variables

The aquatic vegetation of lakes of the Mersey River (see Fig. 1B) was earlier studied for its relationship with water chemistry variables, showing relative acidity to separate lakes into two main groups (Catling et al. 1986). In this study, we performed analyses of color, pH, conductivity, alkalinity, and concentrations of Ca, Cl, and Fe in water from each lake. During a 4-d period in the last week of August 1988, 200-mL water samples were collected from the center of each lake.

Watershed area was calculated from unpublished maps (Land Registration and Information Services, Amherst, Nova Scotia) and the proportion of poorly drained soils around lakes (0.4 km wide rim) was estimated by planimetry from soil maps (Nova Scotia Department of Agriculture). Presence or absence of quartzite, granite, and slate around lakes was deter-

TABLE 2. Correlation matrix among 19 habitat variables ($n = 37$ lakes; $P < .05$ for $0.32 < r < 0.41$; $P < .01$ for $r > 0.41$).

	Physiography*			Shoreline*				
Habitat variables	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Physiography								
(1) Lake surface area	1.00							
(2) Watershed area	0.27	1.00						
(3) Elevation	0.24	−0.23	1.00					
Shoreline								
(4) % poorly drained	−0.21	0.20	−0.35	1.00				
(5) Quartz	0.09	0.16	−0.42	0.13	1.00			
(6) Granite	0.29	−0.13	0.42	0.10	0.11	1.00		
(7) Slate	0.38	−0.03	0.58	0.02	−0.37	0.15	1.00	
(8) Shore width	0.26	0.77	−0.18	0.33	0.17	−0.01	−0.01	1.00
(9) % stone	−0.13	0.01	−0.02	−0.19	0.01	0.11	−0.06	0.04
(10) % sand + gravel	0.30	0.42	0.12	0.13	0.12	0.36	0.12	0.56
(11) % boulder + cobble	0.06	−0.23	−0.03	0.23	0.21	0.09	0.05	0.30
(12) % peat	−0.14	−0.08	−0.07	0.16	−0.18	−0.26	−0.08	−0.11
Water chemistry								
(13) pH	−0.06	−0.32	0.12	−0.28	−0.12	−0.32	0.25	−0.34
(14) Alkalinity	−0.20	−0.40	0.13	−0.18	−0.18	−0.28	0.13	−0.39
(15) Conductivity	−0.29	0.09	−0.65	0.38	0.26	−0.26	−0.39	−0.29
(16) Ca	−0.29	0.21	−0.31	−0.02	0.11	−0.51	−0.16	−0.04
(17) Cl	−0.17	−0.10	−0.54	0.43	0.18	−0.20	0.08	−0.06
(18) Fe	−0.06	0.12	0.01	0.21	−0.34	−0.03	0.09	0.08
(19) Color	−0.25	0.22	−0.18	0.22	−0.03	0.02	−0.29	0.12

* Individual habitat variables corresponding to numbers listed for each class of variables are given in first column.

mined from geological maps (Department of Energy, Mines, and Resources, Ottawa, Ontario) and entered into multiple-regression analyses as dummy (qualitative) variables.

To quantify shoreline characteristics, the proportion of each 100-m stretch of shoreline consisting of organic matter (peat and vegetation), boulder, cobble, stone, gravel, and sand was estimated by eye. The minimum and maximum shoreline width for each stretch was measured and was the distance from the current waterline to the beginning of the shrub line. The average was taken between minimum and maximum widths at each within-lake site, with the exception of sheltered bay sites, and an average of these values was taken as the mean shoreline width for a given lake. Sheltered bay data were not included in these calculations because these are uniformly peaty shores where widths may be quite unrelated to shoreline widths at the other four stations.

Mean values and units of measurement for habitat variables may be found in the Appendix.

Data analysis

Relationships between species richness and lake environmental factors were assessed using Pearson correlation coefficients and stepwise (forward) multiple regression in the Statgraphics software package (1991). Models were generated at two probability levels, $P < .05$ and $P < .01$; F values determining whether variables were accepted into the model or removed from the model were identical. Data were intentionally gathered in a nonrandom manner; study lakes and within-lake study sites were selected from topographic maps to ensure that the full range in lake surface and watershed areas was represented for the region and that sites including the maximum range of exposure conditions were sampled in each lake systematically.

RESULTS

Species richness of all groups of herbs was positively correlated with watershed area and shoreline width (Table 1). Rare and common coastal plain herbs also showed strong positive correlations with the percentage of shoreline area as sand. Lake water chemistry variables were weakly related to species richness; only the inverse relationship between water alkalinity and rare coastal plain species richness was significant. Species richness of shrubs, which occupy the upper part of the littoral zone, was related to none of those variables that were correlated with richness of herbs, the dominants of the lower shoreline region. Whereas common coastal plain herb richness was positively correlated with lake surface area, shrub richness showed an inverse correlation with lake area. In addition, there was a negative correlation between the richness of these two life-form groups ($r = -0.44$, $P < .05$). The multiple correlations referred to in this study are not corrected for Type II error, therefore, care has been taken not to over-interpret data significant only at the .05 level.

The two variables most strongly correlated with species richness of rare coastal plain plants (Table 1), watershed area and shoreline width, are highly correlated with one another ($r = 0.77$, Table 2). Watershed area is the total area of run-off that ultimately funnels into a lake, thus it is a major factor influencing lake hydrology. Variation in spring flood levels, determined

TABLE 2. Continued.

Shoreline				Water chemistry*						
(9)	(10)	(11)	(12)	(13)	(14)	(15)	(16)	(17)	(18)	(19)
1.00										
0.33	1.00									
0.23	0.30	1.00								
−0.66	−0.35	−0.73	1.00							
−0.02	−0.23	0.22	−0.05	1.00						
−0.06	−0.33	0.05	0.15	0.89	1.00					
−0.11	−0.13	−0.25	0.31	−0.01	0.13	1.00				
−0.05	0.11	−0.17	0.21	0.30	0.31	0.66	1.00			
−0.13	−0.14	−0.04	0.17	0.24	0.28	0.72	0.42	1.00		
−0.14	0.03	−0.39	0.31	−0.45	−0.35	0.02	−0.06	−0.02	1.00	
−0.08	−0.02	−0.34	0.31	−0.75	−0.56	0.35	0.11	−0.01	0.45	1.00

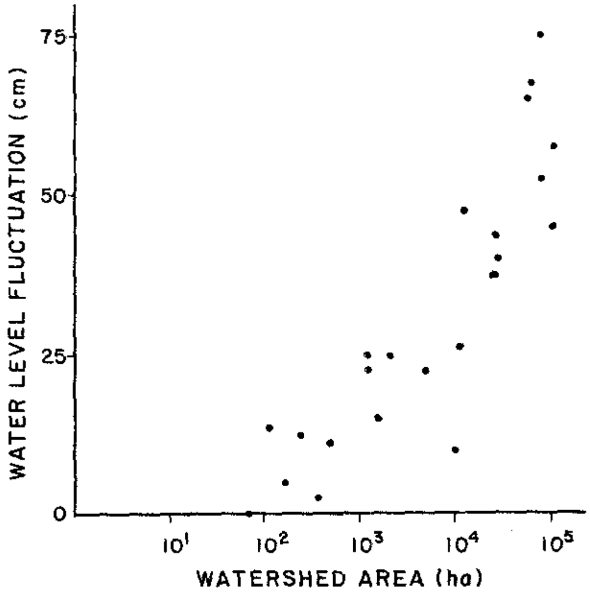

FIG. 2. Relationship between the increase in water level over winter (fall 1988 to spring 1989) for 20 accessible lakes of the Tusket and Annis River watersheds and the watershed area (log scale) upstream of each lake ($r^2 = 0.75$, $P < .0001$).

for 20 accessible lakes in the Tusket region, was largely accounted for by the lake watershed area ($r^2 = 0.66$, $P < .0001$) and by the log of lake watershed area (Fig. 2, $r^2 = 0.75$, $P < .0001$).

Watershed area was positively correlated with the percent of sand and gravel of lake shorelines, which may reflect a greater degree of flooding and erosion of shores of high watershed area lakes. Lake water chemistry was also related to watershed area; alkalinity was negatively correlated with watershed area. As might be expected, many significant correlations were observed among water chemistry variables, including those between water pH and alkalinity, pH and color, pH and iron, and color and iron content (Table 2).

In simple regression analysis, watershed area alone accounted for most of the variation ($r^2 = 0.67$, $P < .0005$) in rare coastal plain herb richness but less than a third of the richness of herbs of the background flora ($r^2 = 0.31$, $P < .005$). In multiple-stepwise regression, the environmental factors were taken into models generated at $P < .01$ and $P < .05$ for species richness of each vegetation type (Table 3). The best model was generated for rare coastal plain species alone and accounted for 83% of the variation at the .05 cut-off level. In contrast, a much weaker model was generated for species richness of the "background" flora, a collection of species from various noncoastal plain floral elements, which accounted for only 45% of the variation (Table 3). Lake environmental factors could not account well for species richness of shrubs in the upper littoral zone; the sole significant factor, lake surface area, accounted for 17% of the variation in richness.

DISCUSSION

Predicting rare species

In a paper entitled "The ecology of rare plants," Griggs (1940) concluded that studies of rarities should concentrate on the reasons behind their persistence in their current habitats. The complex of rare plants of the Atlantic coastal plain flora appears to have invaded postglacial Nova Scotia ≈11 000 yr BP (Roland and Smith 1968, Roland 1982) and to have survived mainly on the shorelines of a small subset of lakes. Our study on the distribution of these rarities supports Griggs' contention, for >80% of the variability in the present-day pattern of species richness of rare and endangered members of this flora can be accounted for by contemporary environmental factors. Two-thirds of this variation in species richness is accounted for by the watershed area of lakes; lakes with large watershed areas have diverse littoral plant communities containing many rare coastal plain species; in contrast, the flora of neighboring lakes with small drainage basins is depauperate.

Our results are similar to those of studies on the montane flora of the southern Appalachians (Miller 1986, White and Miller 1988): here "elevational diversity" accounted for 74% of variation in log rare species richness/log area (Miller et al. 1987). These data indicate that communities exposed to high levels of environmental stress are often responsible for increasing local species diversity, and point to the need to include such habitats in nature reserve systems (Miller et al. 1987, Moore et al. 1989, Keddy 1991).

It is apparent from our data that as one moves from small to high watershed lakes, rare species do not replace the common species but rather co-occur with them. Rare coastal plain species (including *Dicanthelium rigidulum* var. *pubescens*, *Sabatia kennedyana*, *Lachnanthes caroliniana*, and *Utricularia subulata*) are restricted to large watershed area lakes and co-occur with a set of common, noncoastal plain species (viz. *Aster nemoralis*, *A. tradescanti*, *Lycopus uniflora*, *Lysimachia terrestris*, *Triadenum virginicum* (L.) Raf., *Agrostis perennans*, and *Calamagrostis canadensis*), which grow over the entire watershed gradient and occur in >95% of lakes.

Pattern and putative mechanism

It is one thing to demonstrate a correlation, it is quite another to demonstrate the underlying mechanism (Cale et al. 1989). Two-thirds of the variation in rare coastal plain species richness was accounted for by watershed area alone, but what is the cause? The gradient of flooding from small-to-large watershed lakes entails a complex of environmental factors, just as altitude does (Austin and Smith 1989). In summer, excess water during prolonged flooding will reduce light and oxygen availability to plants. In winter, the larger fluctuations

TABLE 3. Multiple-regression models predicting species richness of herbaceous plants and shrubs. Independent variables (with their units) are listed in order fitted by stepwise variable selection ($n = 37$ lakes). e = error.

Species groups	P	Independent variables (Xi)	Regression model
Rare coastal plain herbs	.01	(1) watershed area (10^3 ha) (2) shore width (m) $r^2 = 0.72$	$Y = 0.23 + 0.02X1 + 0.28X2 + e$
	.05	(1) + (2) + (3) poor drainage (%) (4) water color (TCU†) (5) sand (%) (6) alkalinity (mg/L) $r^2 = 0.83$	$Y = 3.89 + 0.033X1 + 0.24X2 + 0.023\,X3 - 0.0080X4 - 0.13X5 - 0.72X6 + e$
Common coastal plain herbs	.01	(1) watershed area (10^3 ha) (2) sand + gravel (%) $r^2 = 0.48$	$Y = 2.94 + 0.040X1 + 0.14X2 + e$
	.05	(1) + (2) + (3) elevation (m) $r^2 = 0.56$	$Y = 4.23 + 0.030X1 + 0.18X2 - 0.026X3 + e$
Noncoastal plain herbs	.01**	(1) shore width (m) (2) water pH (units) $r^2 = 0.45$	$Y = -13.6 + 3.06X1 + 10.7X2 + e$
All herbs	.01	(1) shore width (m) $r^2 = 0.42$	$Y = 48.5 + 3.80X1 + e$
	.05	(1) + (2) granite (+/−) (3) water color (TCU†) $r^2 = 0.54$	$Y = 54.1 + 3.98X1 - 10.3X2 - 0.044X3 + e$
All shrubs	.01 and .05	(1) lake area (10^3 ha) $r^2 = 0.17$	$Y = 64.3 - 8.91X1 + e$

† TCU = total color units (APHA 1985).
** Correlations significant at the .01 level.

in water levels result in increased disturbance from ice scouring, which means greater losses of nutrients as plant residues are removed from site. In this case, however, we hypothesize that the underlying mechanism maintaining high species richness on lakeshores is the reduction of competition from shrubs by flooding.

Watershed area is the area of land surrounding a lake from which the water is shed and ultimately reaches the lake basin. According to the "rational formula" of engineering hydrology, peak discharge or flooding is directly related to watershed area: $Q = CIA$, where Q is peak discharge, C, a runoff coefficient determined by drainage basin characteristics, I, rainfall intensity, and A, the drainage area or watershed (Chow 1964). We have since confirmed for the lakes accessible in spring in the Tusket region, that spring flood levels are strongly correlated with watershed area (Fig. 2). Because synchronous measurements of flooding over many widely separated wetlands is time consuming, a physiographic variable, such as watershed area, which largely determines hydrological events may be more useful in predictive modelling of vegetational patterns than the actual hydrological events, which change from year to year and are not synchronized between regions due to seasonal differences in weather. Moreover, since watershed area is easily measured from topographic maps, field work can be easily focussed on high watershed area lakes that have a good likelihood of supporting rare species.

The relationship between large fluctuations in lake levels and the occurrence of coastal plain species has already been shown in Ontario (Keddy and Reznicek 1982). Similarly, in a preliminary study of 12 Nova Scotian lakes, four rare coastal plain species were largely restricted to the shores of lakes of the Tusket River, where water levels show wide seasonal and year-to-year fluctuations (Keddy 1985).

The mechanisms relating flooding and species richness are probably related to how stress and disturbance in general reduce the intensity of competitive interactions (Grime 1979, Sousa 1984, Keddy 1989*a*). In particular, since woody plants are often sensitive to flooding (Kozlowski 1984), high water periods probably eliminate shrubs and create open shoreline. A century ago, Thoreau (1854) observed that flooding of Walden Pond killed shrubs and maintained open shorelines. This process has been illustrated for coastal plain shorelines (Keddy and Reznicek 1982), and the negative effects of shrubs on coastal plain plants documented both descriptively (Keddy 1985) and experimentally (Sharp and Keddy 1985, Keddy 1989*b*). Regeneration of herbaceous species from buried seed allows recolonization of shorelines after shrubs are killed (Keddy and Reznicek 1982, McCarthy 1987).

Keddy and Reznicek (1986) proposed that, in general, occasional high water periods are essential for maintaining wet meadow vegetation on shorelines, the upper limits of wet meadow species being set by the lower limits of shrubs. A 4-yr field experiment (Keddy 1989*b*) showed that when shrubs were experimentally removed from a shoreline, herbaceous wet meadow species expanded their distributional limits landward. We therefore propose that a decline in intensity of competition along a flooding gradient from small-to-large watershed lakes in this study is responsible for the observed correlation between rare species richness and watershed area. The majority of the rare coastal plain species in this study (12/14) are small, slow-growing species, which under more productive conditions would doubtless be outcompeted by more robust species. Work by Gaudet and Keddy (1988) confirms that two of these rare species (*Sabatia kennedyana* and *Dicanthelium rigidulum* var. *pubescens*), and small species in general, have low competitive abilities. Although it is logical that stresses associated with flooding reduce competitive interactions in these low-biomass communities, one cannot, and we do not, discount the role of disturbance. As flooding is correlated with lake watershed area, so too may be the over-winter scouring by ice of the shores of these lakes. The upheaval and disruption of vegetated peat shorelines can be observed in early spring, and is especially apparent at high watershed area lakes. Further study is needed to determine whether flooding and ice scour act synergistically to reduce competition.

Finally, our data on shrubs are consistent with the above evidence. Unlike herb species, shrub richness in the upper littoral zone was not correlated with any of the same factors linked to herb species richness. In fact, the sole significant correlation, lake surface area, was negatively correlated with shrub species richness, while common coastal plain herb richness was positively correlated with surface area.

CONCLUSION

While it is important to be able to predict the species richness of ecological communities, our results show that one cannot necessarily treat members of a community collectively, since quite different models are fitted for the four classes of littoral zone herbs (rare and common coastal plain, noncoastal plain, and all herbs) and upper littoral zone shrub species (Table 3). Unlike the unpredictable nature of rare riparian species (Nilsson et al. 1988), we can make fairly accurate predictions of where rare coastal plain species should occur most frequently among lakes. This prediction has two benefits. The first is that it may be possible to move from a total reliance on extensive field surveys to field surveys directed by model predictions, which should result in a more practical and efficient method for selecting sites to conserve rare plant habitats. The second is that identification of a habitat shared by a complex of rare species leads to the understanding of their common life history strategy; once species can be considered as members of a functional group, management guidelines can be drawn up at the group level and the problems of integrating multiple management strategies for each species of concern in a single habitat are avoided. The empirical/predictive methods used here have been discussed elsewhere (Peters 1980, Rigler 1982, Keddy 1987). Our results (and those of White and Miller 1988) suggest that they should work for other species and habitats where the scientific bases for habitat selection and management are urgent priorities. By identifying key predictors of species distributions, such methods should also assist in the search for mechanistic causes of plant distributions.

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APPENDIX

Values and units of measurement for habitat variables in $n = 37$ lakes in Nova Scotia, Canada.

Habitat variable (units)	Mean	Range
Physiography		
Lake surface area (ha)	259	8–2453
Watershed area (10^3 ha)	24.0	0.07–108
Elevation (m)	48.5	9.15–114
Shoreline		
Poorly drained (% of area)	20	0–70.0
Shore width (m)	8.54	0–53.0
Stone (% of area)	18.6	0–29.1
Sand + gravel (% of area)	13.2	0–33.5
Cobble and boulder (% of area)	46.8	4–71.2
Peat (%)	20.7	1.5–96.0
Water chemistry		
pH	5.25	4.53–6.00
Alkalinity ($CaCO_3$, mg/L)	0.69	0.1–2.24
Conductivity (μS/cm)	33.3	23.0–49.7
Ca (mg/L)	1.10	0.56–2.59
Cl (mg/L)	6.19	3.6–18.5
Fe (mg/L)	0.32	0.02–1.58
Color (total color units)*	90.6	2.5–300

* Follows method 2120 of APHA standard methods (APHA 1985).