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Lakeshore diversity and rarity relationships along interacting disturbance gradients: catchment area, wave action and depth

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Abstract

Diversity patterns of riparian plant communities have been associated with disturbance. Populations of a diversity of Atlantic Coastal Plain plants occur as disjuncts on shores of large catchment area lakes in Nova Scotia. These lakeshore communities contain rare plants with local, national and global rankings. The populations of rare plants are dynamic and their management requires an understanding of the relationship between disturbance and the survival of rare plants. This present study measured (overwinter wooden dowel removal) and observed disturbance along gradients of catchment area (CA), exposure and depth. In three separate experiments ranging from the landscape to the lake, to the single shoreline level, disturbance was linked to lake CA, exposure and depth, respectively. At all scales, disturbance was positively associated with the presence of rare species. The pattern of rare species richness over the river system was complex; at the within-lake level, the frequency of rare species per site was greatest in the intermediate CA lake while the pool of rare species was greatest in the largest CA lake. The findings focus field efforts on wide, exposed shorelines of large CA lakes where new rare plants continue to be discovered. In addition, the discrepancy between highest frequency of rare plants on intermediate CA lakes and highest species pools of rarities on large CA lakes, reinforces the need for larger protected area systems for the most naturally disturbed ecosystems which often support populations having a high turnover rate but a low site to site frequency.

Keywords: Disturbance gradients; Lake catchment area; Shoreline plant communities; Rare Atlantic Coastal Plain plants; Species pools; Protected areas; Turnover rate

1. Introduction

Riparian zone communities are non-equilibrium systems whose dynamics largely follow hydrological disturbance regimes (Gawler et al., 1987; Naiman et al., 1992; Decamps, 1993; Nilsson et al., 1993; Scarsbrook and Townsend, 1993; Bornette et al., 1998b; Ward, 1998). A full understanding of any of these communities involves a mechanistic understanding of the disturbance regime. In river systems, disturbances are expected to mirror flow rates and thus increase from headwater to higher order streams and rivers. Indeed, the diversity values for a variety of organism types follow expectations of the intermediate disturbance hypothesis and maximum values have been recorded at mid-reach sections of rivers (invertebrate patterns: Vannote et al., 1980; vascular plant patterns: Nilsson et al., 1989; Planty-Tabacchi et al., 1996; Pollock et al., 1998), although in other cases, maximum richness has coincided with maximum flood disturbance (e.g. vascular plants: Gould and Walker, 1997; Bornette et al., 1998a, b; amphibians: Real et al., 1993; and fish: Guegan et al., 1998).

In many temperate regions, shoreline communities of lakes in river systems are the hot spots of vascular plant diversity. In Nova Scotia, lakeshores support diverse plant communities which are especially rich in populations belonging to the more southerly Atlantic Coastal Plain (ACP) flora (Fernald, 1921). Species of this flora have ranges that overlap the Atlantic Coastal Plain (ACP) geological province, made up of Appalachian Mountain sediments eroded during Triassic time and laid down by rivers along the eastern seaboard of the United States (Christensen, 1988). Many species of this flora extended their ranges beyond the geological province during low sea level periods of the Pleistocene and migrated northward along wetlands on the Continental

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Shelf. Upon glacial retreat, populations became established in southern Nova Scotia (Roland and Smith, 1968; Sorrie, 1998) and today these disjunct populations are a significant global reserve for many rare species of the ACP flora (Hill and Keddy, 1992). Although Nova Scotian lakeshore ecosystems may be less affected by industrialization (Wisheu et al., 1994) than are their counterparts along the Atlantic seaboard of the United States (Schneider, 1994; Sorrie, 1994), their status is by no means secure. The natural hydrological regime in approximately one half of the most important lake shoreline habitats for rare ACP plants in Nova Scotia (lakes of catchment area greater than 50,000 ha) has been significantly modified by damming (Hill et al., 1998) and recreational activities threaten to undermine the integrity of the remaining communities. The most valued lakes for recreation lie near the coast and these are the large catchment area lakes at the ends of river systems also prized for their biodiversity value (Hill et al., 1998). With this background of change, there is a need to establish benchmark research on the disturbance dynamics of healthy, unmodified systems. To protect these communities, we will need to understand the mechanics of disturbance and its relationship to diversity patterns.

The present study set out to determine how disturbance was related to three lakeshore gradients that have been shown to be associated with changes in the composition of the shoreline plant community. At the landscape level, a catchment area gradient drives water level fluctuations (Chow, 1964); this relationship has been documented for Nova Scotian lakes (Hill et al., 1998) and furthermore, empirical evidence shows a strong relationship between rare plant species richness and lake catchment area (Hill et al., 1998). At the individual lake level, an exposure gradient determines wave energy and has been related to shoreline fertility (Keddy 1984), competitive interactions (Wilson and Keddy, 1986) and the proportion of ACP species (Keddy, 1985). Finally, at the single shoreline level, depth determines the length of the terrestrial phase of the growing season and sediment organic matter content, plant community biomass (Holt et al., 1995) and the intensity of competition (Lennssen et al., 1999). In a series of three experiments conducted at the landscape, lake and single shoreline levels, we test whether significant disturbance and rarity relationships are associated with each of these gradients and we discuss the implications of the findings for the conservation of the flora.

2. Materials and methods

2.1. Study area

The lakes in this study were chosen because while they varied greatly in size of catchment area, they were in close proximity to one another along a river continuum and had similar geological features (Fig. 1). The lakes belong to the Christopher River system (44° 20′ N, 64° 55′ W to 44° 20′ N, 65° 05′ W), and show little evidence of anthropogenic influence. The geological history and nature of the area as well as other background information can be found in Holt et al. (1995). This earlier study on these lakes revealed strong catchment area: biomass and substrate fertility patterns suggestive of the impact of disturbance. A study of conservation priorities for the lake with the largest catchment area in this river, revealed the presence of globally rare Atlantic Coastal Plain plants (Wisheu et al., 1994).

2.2. Assessment of disturbance

Shoreline disturbance was assessed by an experimental method and by simple observation. The experimental method scored overwinter disturbance by recording in the spring the fates of wooden dowels (20 cm length, 0.6 cm diameter) inserted at 10 cm depths the previous fall. Dowels were designed to mimic woody shrubs whose growth is known (through removal experiments) to suppress rare lakeshore plants (Keddy, 1989). The removal or damage of dowels reflects the role of disturbance processes that prevent shrub domination and help to maintain species rich herbaceous shoreline communities (Wisheu and Keddy, 1989). Details of dowel placements are given in Experiments I–III below.

Observed disturbance was defined as moved sods or undercut and sheared vegetation occurring within 5 m on either side of the dowel lines. While we suspect most of the observed disturbance occurred the previous winter, some of these disturbances may have occurred in previous years and therefore, this method may integrate over a longer time period than the experimental method.

Data for measured and observed disturbance were processed independently.

2.3. Catchment area level, Experiment 1

The four lakes chosen from the Christopher River system represented the following differences in lake catchment area sizes: Appletree Lake ($10^{2.1}$ ha), Telfer Lake ($10^{3.4}$ ha). Second Christopher Lake ($10^{3.9}$ ha) and St. Mary Bay (10^{5} ha; Fig. 1). Thirty random points were selected along the shoreline of each lake using 1:50,000 scale topographic maps. These shoreline sites were then determined on the lake by canoe using shoreline perimeter features. Orientation of the shoreline with respect to the prevailing winds (i.e. windward versus leeward) and whether the shoreline was sheltered (i.e. within a bay) or exposed were noted. The shoreline width was measured from the tree/shrub line to the waterline. Five wooden dowels were spaced evenly along a transect by dividing the shoreline width by five

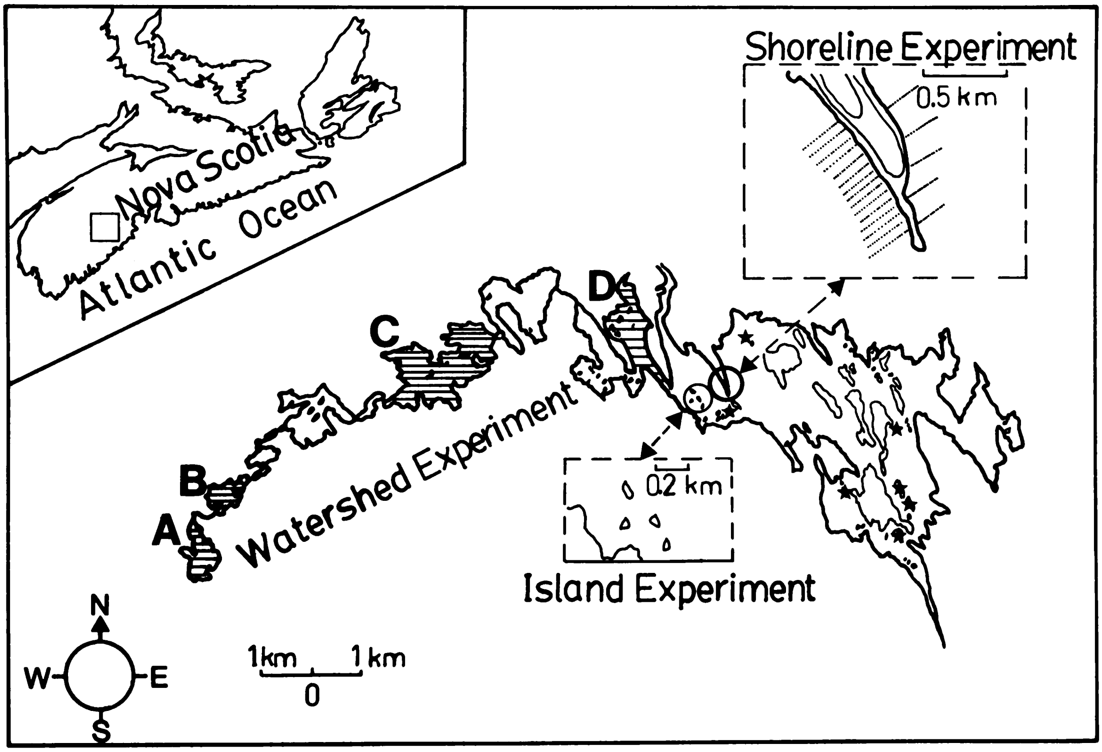

Fig. 1. Map of the Christopher River system indicating its location in southwestern Nova Scotia (insert in upper left corner) and sites of the watershed, island and shoreline experiments. Lakes included in the watershed experiment are indicated with hatching and labeled as A (Appletree Lake), B (Telfer Lake), C (Second Christopher Lake) and D (St. Mary Bay). The dotted lines in the insert for the shoreline experiment indicate the position of the dowel lines. Stars indicate sites included in the Ponhook Lake Nature Reserve.

to obtain the required distance between dowels. The first dowel was then placed at the waterline and each succeeding dowel at the required distance from the previous dowel proceeding towards the shrub line. In cases where the tree/shrub line occurred at the water's edge, dowels were arbitrarily placed at 10-cm intervals starting at the waterline and proceeding into the lake. Dowel lines were established in the field between 26 October and 1 November 1992. In the Spring of 1993, dowels were checked for damage (severed or cracked dowels) or removal, and if one or more of the dowels were removed or cracked, the site was considered disturbed. In addition, for each dowel placement, a corresponding visual assessment of disturbance (observed method) was made, so that sites were deemed disturbed if observed disturbance was associated with any of the dowels in a given line.

Vegetation surveys were conducted between 9 August and 7 September 1993. The location and percent cover of each species along dowel lines was recorded using the line intercept method (Hawley, 1978). Seasonal water level fluctuation was estimated by determining the vertical distance between the August waterline (it was assumed this was the low water mark) and the tree/shrub line (the high water mark) for each dowel line.

Vegetation data were summarized by calculating species richness (number of species per site), species density (number of species per m of transect length), total coverage (sum of the intercept lengths of all species divided by transect length) and by noting the presence or absence of rare species at each transect site. Multiple regression was used to examine the impact of topographic variables on the various vegetation parameters and the two measures of disturbance. Linear least squares regression was used for species richness, species density and total coverage, while logistic regression was used for the presence or absence of rare species and for disturbance. In both sets of analyses the independent (predictor) variables consisted of: shore width, shoreline exposure (sheltered = 1, exposed = 2), orientation (windward = 1, leeward = 2) and log watershed area. A preliminary analysis revealed that there were no significant correlations among any of the independent variables. Analysis of variance was used to examine the difference between disturbed and undisturbed sites in species richness, species density and total coverage. Log linear analysis was used to examine the relationship between disturbance and the presence or absence of rare species.

2.4. Within-lake level, Experiment II

To more efficiently determine what shore types are most disturbed at the within-lake level, islands were chosen as model systems since they provide both windward and leeward exposure in small, geologically homogenous areas. A series of transects were constructed on six islands located in Ponhook Lake (adjoining St. Mary's Bay and having similar catchment area, CA, size). All islands were approximately the same shape and were a similar distance from the mainland. On 23–25 October 1992 eight dowel lines were established as described above on each of six islands, placing four on the eastern shore and four on the western shore of each island. Dowels were checked for signs of disturbance in the spring of 1993. The percentage of dowels damaged or removed was calculated separately for each of the 48 transects.

To examine the relationship between the degree of exposure and vegetation, three transects were established on the windward and leeward shores on each of five additional islands in Ponhook Lake Nature Reserve between 17 and 18 August 1993. Transects ran from the tree/shrub line to the waterline. All vegetation crossing the transect was identified and plant species cover and position recorded.

The vegetation data were summarized by calculating species richness, total cover and cover of shrubs, herbaceous dicots, monocots and rare plants for each transect. Leeward and windward transects were compared using unpaired *t*-tests for normally distributed data (species richness, total cover and cover of herbaceous dicots and monocots) and Mann–Whitney *U*-tests for non-parametric data (percentage dowels removed, shrub cover and rare plant cover).

2.5. Shoreline level, Experiment III

To investigate the role that disturbance plays in the vertical distribution of coastal plain species, plant zonation was compared to shoreline disturbance. Disturbance was measured at different vertical positions on the shore of an exposed point where the diversity of coastal plain plants was known to be high (Hill and Keddy, 1992). Dowel lines were placed as in the watershed experiment except for the following changes. Fifteen dowel lines were set up on the windward side of Maplesue point between 16 and 24 October 1992. Fifteen dowels were spaced evenly along a transect from the waterline up to the tree/shrub line. In the spring of 1993 the dowels were checked for signs of disturbance or removal. From 29 July to 1 August 1993, plant distribution patterns were measured using belt transects with 25×25 cm quadrats. The number of species and individuals and their positions were noted and percent cover was estimated.

To determine whether wave action alone without the presence of ice scour could remove dowels, an additional five dowel lines were placed on the leeward side of Maplesue point in May 1993 and re-enumerated on 29 July 1993. It was assumed that any dowels removed over the months of May, June and July, were removed by wave action. We chose this particular site for this experiment because it had a sandy substrate that we suspected would maximize dowel removal by wave action. Therefore, this experiment can only demonstrate that dowel removal by wave action is possible, and was not intended to estimate the actual proportion of dowels removed by wave action across all sites.

To describe the relationship between vegetation parameters and vertical distance down the windward shore, species richness and number of rarities per quadrat were plotted as a function of relative distance down the shore where 0 represented the established shrub line and 1 represented the July waterline (i.e. the transects were normalized to a transect length of 1). Lines were fitted to these plots using a distance weighted least squares method (Wilkinson, 1990). Proportion of dowels removed at each of the 15 positions along the transects was also plotted as a function of relative distance down the shore for comparison. To assess the relationship between disturbance and vegetation parameters, each quadrat was classified as disturbed versus undisturbed on the basis of whether the closest dowel was damaged or not. Mann–Whitney *U*-test were then used to compare species richness, number of rarities, number of individuals, total cover, rare plant cover and shrub cover of "disturbed" versus "undisturbed" quadrats.

2.6. Plant identification

Taxa were identified to the species level following Roland and Smith (1968). Voucher specimens are stored at the Nova Scotia Museum and in the E.C. Smith Herbarium at Acadia University. Nomenclature followed Argus and Pryer (1990). Using the list of nationally significant and rare taxa in the Medway River listed by Wisheu et al. (1994), the following taxa were classed as rare: *Lachnanthes caroliniana*, *Lophiola aurea*, *Scirpus longii*, *Euthamia galetorum*, *Panicum rigidulum* var. *pubescens*, *Rhexia virginica*, *Xyris difformis* and *Utricularia subulata*.

3. Results

3.1. Watershed level, Experiment 1

Disturbance was assessed through observation of shoreline disruption, the observed method, and by monitoring fates of experimentally placed wooden dowels, the experimental method. In both cases, a trend showing disturbance increasing with increasing lake catchment area was noted, however, a reversal in this trend occurred for the two smallest catchment area lakes (Fig. 2). For both disturbance data sets, a small surface area lake of intermediate catchment area size

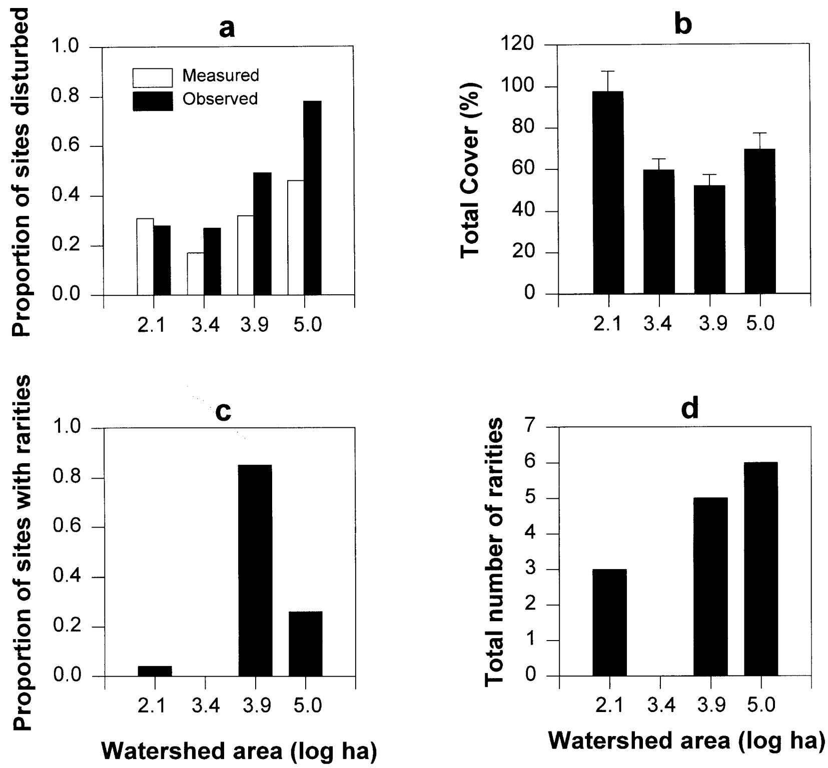

Fig. 2. Effect of watershed area on (a) proportion of sites disturbed, (b) total cover, (c) proportion of sites with rarities, and (d) total number of rarities per lake.

was less disturbed than the smallest catchment area lake of larger surface area. Overall, the association between disturbance and catchment area was significant for the observed disturbance but not for the measured disturbance data (Table 1). None of the other topographic variables were significantly associated with disturbance at the 0.05 level.

Vegetation parameters were also related to topographic variables (Table 1). Variation in species richness per transect and species density (richness m^{-1}) were partly accounted for by shoreline width (Table 1). Species richness increased with shore width up to 800 cm after which, shore width had little impact (Fig. 3a). Species density decreased sharply with shore width up to 500 cm after which it declined more gradually (Fig. 3b). Total cover was linked to catchment area (Table 1), but this relationship was largely due to the high cover values of the lake with the smallest catchment area, there being little difference in the cover values of the other three lakes (Fig. 2). The presence of rare species at the site level was linked to both shore width and watershed area, the two variables being of approximately equal importance (Table 1). The average shore width of sites with rare species was 719 ± 78 compared to 381 ± 25 cm for sites lacking rare species. The proportion of sites with rare plants reached its maximum at the $10^{3.9}$ ha CA lake and declined thereafter (Fig. 2). It should be noted however, that the total number of rare species per lake was greatest for the two lakes with the largest catchment areas (five and six rare species in the $10^{3.9}$ and the $10^{5.0}$ ha CA lakes, respectively) and lowest in the smallest catchment area lakes (three and nil in the $10^{2.1}$ and the $10^{3.4}$ ha CA lakes, respectively).

Vegetation parameters were analyzed using disturbance indicators as independent variables (Table 2). Neither variation in species richness nor density could be accounted for by either disturbance indicator. Variation in total cover and rare species cover was inversely related to measured disturbance. Both types of disturbance indicators were potential predictors of the presence of rare species at lakeshore sites; in both cases, disturbance was positively correlated with rare species presence.

3.2. Within-lake level, Experiment II

Overwinter forces removed the majority of dowels placed on the windward shores of islands but less than a third of those placed on leeward shores (Table 3). There was greater plant cover and fewer species on lee shores, however, these differences and others were not significant (Table 3). There were equivalent amounts of dicot herbaceous cover on lee and windward shores and significantly more monocot cover on the windward sides of islands (Table 3). Rare plant cover was more than three-fold greater on windward shores than on lee shores (Table 3).

Table 1
The effect of topographic variables on vegetation parameters and disturbance in four lakes of the Christopher River system in Nova Scotia[a]

Topographic variables	Estimate	Sums of squares	Chi-square	Level of significance
Species richness				
Intercept	6.56	–	–	0.0016
Shore width	0.011	1418.95	–	<0.0001
Shoreline indentation	−0.461	4.87	–	0.5473
Shoreline orientation	−0.020	0.01	–	0.9777
Watershed area	0.326	11.47		0.3565
Species density				
Intercept	4.59	–	–	<0.0001
Shore width	−0.00212	55.79	–	<0.0001
Shoreline indentation	0.058	0.079	–	0.8103
Shoreline orientation	−0.178	0.810	–	0.4433
Watershed area	−0.105	1.186	–	0.3538
Total coverage				
Intercept	132.07	–	–	<0.0001
Shore width	−0.013	2120	–	0.2382
Shoreline indentation	−10.98	2760	–	0.1788
Shoreline orientation	−1.009	2596	–	0.8958
Watershed area	−10.09	10964	–	0.0082
Presence of rare species				
Intercept	−7.295	–	13.63	0.0002
Shore width	0.0039	–	14.71	<0.0001
Shoreline indentation	0.639	–	1.24	0.2662
Shoreline orientation	−0.925	–	2.91	0.0879
Watershed area	1.243	–	13.67	0.0002
Observed disturbance				
Intercept	−3.958	–	8.95	0.0028
Shore width	0.0002	–	0.09	0.7588
Shoreline indentation	0.843	–	3.18	0.0747
Exposure	−0.706	–	2.42	0.1199
Watershed area	0.949	–	15.18	<0.0001
Dowel disturbance				
Intercept	−1.698	–	1.82	0.1777
Shore width	−0.0004	–	0.45	0.5031
Shoreline indentation	0.686	–	2.03	0.1539
Exposure	−0.674	–	2.37	0.1240
Watershed area	0.272	–	1.66	0.1978

[a] In the case of species richness, species density and total coverage multiple linear regression was used to describe the relationship with topographic variables, while logistic regression was used for the presence or absence of rarities, observed disturbance and measured disturbance. There were no significant correlations among any of the topographic (i.e. independent) variables used in the analyses.

3.3. Shoreline level, Experiment III

The windward side of Maplesue Point had a higher percentage of disturbed dowels (49%) than the leeward side (38%; $P<0.05$). The windward, eastern shore was wide and gently sloping and supported a diverse Atlantic Coastal Plain plant community. At the top of this shore in the shrub zone, there was little overwinter dowel loss (Fig. 3a). Dowel losses increased steadily from the top of the shore (7% loss) down to just above the summer low waterline (92% loss) and thereafter dowel loss rates declined, to slightly lower levels (50% loss). Species richness and the total number of rarities per quadrat increased from low values at the top of the shoreline to maximum values at transect positions below the zone of maximum recorded disturbance (Fig. 3b, c).

Overall, disturbed areas on the windward shore of Maplesue Point supported more rare plants ($P<0.001$), species ($P<0.001$) and individual stems ($P<0.001$; Table 4). Disturbed areas also had greater cover of rare plants ($P<0.001$) and lower cover of shrubs ($P<0.001$) in comparison with undisturbed shore areas.

Re-enumeration of dowel lines on the leeward side of Maplesue Point indicated that wave action alone without ice scour was an important form of disturbance.

Table 2
Differences in community composition between disturbed and undisturbed sites on four lakes of the Christopher river system in Nova Scotia[a]

	Observed disturbance			Measured disturbance		
	+	–	*P*-value	+	–	*P*-value
Species richness	12.6±0.7	11.7±0.7	0.3756	11.8±0.9	12.3±0.6	0.6489
Species density	2.79±0.19	3.20±0.18	0.1313	2.95±0.24	3.04±0.16	0.7507
Total coverage	6.23±5.6	76.0±5.4	0.0799	5.68±6.8	75.3±4.6	0.0264
% Sites with rare species	45.1%	20.0%	0.0057	52.9%	22.2%	0.0016

[a] Levels of significance for differences in species richness, species density and total coverage were determined using a one-way analysis of variance. Error terms represent one standard error. Level of significance for the difference in percentage of sites with rare species was obtained from a log linear analysis.

Between the original census in May 1993 and the final census in late July of the same year, 20% of the remaining dowels were removed (Fig. 4).

4. Discussion

The importance of disturbance in maintaining populations of rare Atlantic Coastal Plain plants in these river systems is clear. Regardless of the scale at which it was assessed, disturbance was positively associated with the presence of rare species. In the catchment area study, roughly half of the disturbed sites supported rare plants in comparison with less than a quarter of those undisturbed sites. At the within-lake level, in our island study, we found that cover of rare ACP species was three times higher and disturbance was more than twice as frequent on exposed shores than on the leeward sides. At the single shoreline level, cover of rare plants was 2.5 times greater on those portions of the shoreline subject to disturbance as compared to those portions of the shoreline that were not disturbed.

Disturbed sites tended to have lower total cover values (Table 2) and in particular, lower shrub cover (Table 4). As the rare ACP species are thought to be poor competitors (Keddy, 1985; Wisheu and Keddy, 1994), the reduction in cover after disturbance probably facilitates colonization by rare species. Experimental study confirms the requirement for disturbance; neither flooding nor reduced fertility treatments were adequate to maintain small and slow-growing plants in experimental microcosms (Weiher et al., 1996). The vertical zonation of rare ACP species on shorelines (Fig. 2; see also Keddy, 1984) suggests that increased competition at higher shoreline stations restricts rare ACP species to low shoreline positions. Indeed, the competitive release of small herbs such as the rare *Xyris difformis* in upper shoreline areas following experimental removal of shrubs supports this (Keddy, 1988).

To understand how to manage an assemblage of rare species that is dependent on disturbance for its continued survival, we both measured and observed disturbance along topographic gradients that we expected

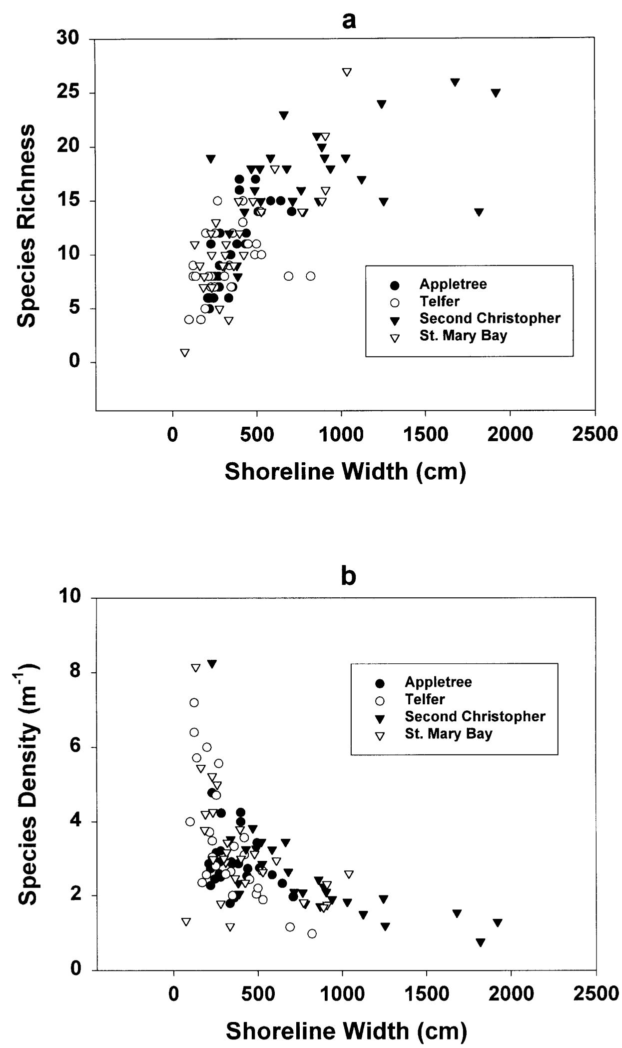

Fig. 3. Effect of shoreline width on (a) species richness and (b) species density in the catchment area experiment.

would influence the degree of disturbance. At the among lake level, our results generally supported expectations; we observed that disturbance was greatest where peak flooding is greatest (rational formula, Chow, 1964, and field measurements), in the lake with the largest catchment area. However, the overall catchment area: disturbance relationship was significant only

Table 3
Differences in community composition and disturbance on the windward and leeward sides of a series of islands in Ponhook Lake, Nova Scotia[a]

Variable	Windward	Leeward	*P*-value
% of dowels removed	71.3	29.2	0.001[b]
Number of species	20.2±1.0	16.5±1.6	0.060
% Cover			
Total	50.1±4.9	60.9±3.3	0.194
Shrubs	23.2	28.1	0.382[b]
Herbaceous dicots	10.1±1.0	9.3±1.9	0.671
Monocots	13.9±1.7	8.6±1.4	0.025
Rare plants	3.1	0.9	0.003[b]

[a] The *P*-value is the level of significance for the difference between windward and leeward means. Unless otherwise noted, data were normally distributed and means were compared by unpaired *t*-tests. Mann–Whitney *U*-tests were used for non-parametric data.

[b] Non-parametric data.

Table 4
Changes in the plant community and physical characteristics of the shoreline with disturbance on Maplesue point, Ponhook Lake, Nova Scotia[a]

Variables	Undisturbed	Disturbed	*P*-value
Number of			
Rarities	0.3	1.0	0.001
Species	2.7	7.0	0.001
Individuals	11.1	36.4	0.001
Percent cover			
Rare plant	0.9	2.3	0.001
Shrub	5.6	0.2	0.001
Total	16.0	16.2	0.939

[a] Disturbance was measured using dowel removals. The *P*-value is the level significance for the difference between disturbed and undisturbed areas. Data were analysed using Mann–Whitney *U*-tests.

when observed scour disturbance data were used, suggesting that the observation method and the experimental dowel method may differ in their sensitivity to different disturbance processes. In the observation method, an area was recorded as disturbed only if sods were overturned or were sheared to their roots. This type of disturbance is most likely associated with ice scour. The significant observed disturbance:catchment area relationship makes sense since ice movement is driven by water level fluctuations and river currents through lakes which are both catchment area related processes (Chow, 1964; Hill and Keddy, 1992). In the experimental method, both dowel breakage and dowel removal were recorded as disturbances, thus this may record both the effects of wave wash and ice scour. The fact that dowels were removed during the summer months as well as the winter months, clearly illustrates that wave wash is an important factor in dowel removal. Wave wash in contrast to ice scour is likely to be less dependent upon catchment area and more dependent upon lake surface area which will influence fetch, and within lake topographic variables such as exposure and susceptibility of the substrate to erosion. Given that the lakes used in this study were chosen in part because they were of a similar size (Fig. 1), it is unlikely that slight differences in lake surface area can explain the differences in measured disturbance among sites rather, it is within lake variables that were responsible for these differences.

In experiment 1 there was little evidence that the within lake topographic variables we examined (i.e. shoreline orientation and exposure) had much effect on disturbance. However, this may only reflect the fact that we did not control for substrate composition in this experiment. Substrate composition will determine the susceptibility of the substrate to erosion (e.g. a sandy beach will be more easily eroded than a rocky shore). Indeed, Keddy (1982, 1983,1984) has argued that substrate composition is a good proxy for degree of exposure. The island experiment demonstrated the importance of shoreline orientation for disturbance in that significantly more disturbance occurred on the exposed sides of islands than on their lee shores. Islands are ideal to test for differences in exposure effects since islands provide large differences in exposure on quite similar geological material. Between shoreline geological variation can be wide in this region due to differences in the history of glacial deposition (Keddy and Wisheu, 1989).

Given that disturbance was associated with catchment area, it is not surprising that catchment area was also closely associated with the presence or absence of rare species. A previous study of 37 lakes found that catchment area of lakes accounted for 67% of the variation in the richness of rare shoreline ACP species at the among-lake level (Hill and Keddy, 1992). Although the presence or absence of rare species was clearly associated with catchment area in the present study, the pattern of this association was more complex than that suggested by the Hill and Keddy study. The proportion of sites with rare species was highest at the second largest catchment area lake (Fig. 3d) while the greatest number of rarities occurred at the largest catchment area as in the previous study (Hill and Keddy, 1992). These data suggest rare species may be more common on lakes of intermediate disturbance, but they have lower total pools of rare species than lakes of the highest disturbance.

A higher frequency of rare species on lakes of intermediate disturbance is in accord with the intermediate disturbance hypothesis (Connell, 1978; Huston, 1994). Further support for this hypothesis is provided by the single shoreline experiment, in which we documented how rare species richness increased with depth and attained maximum levels just below the maximum zone

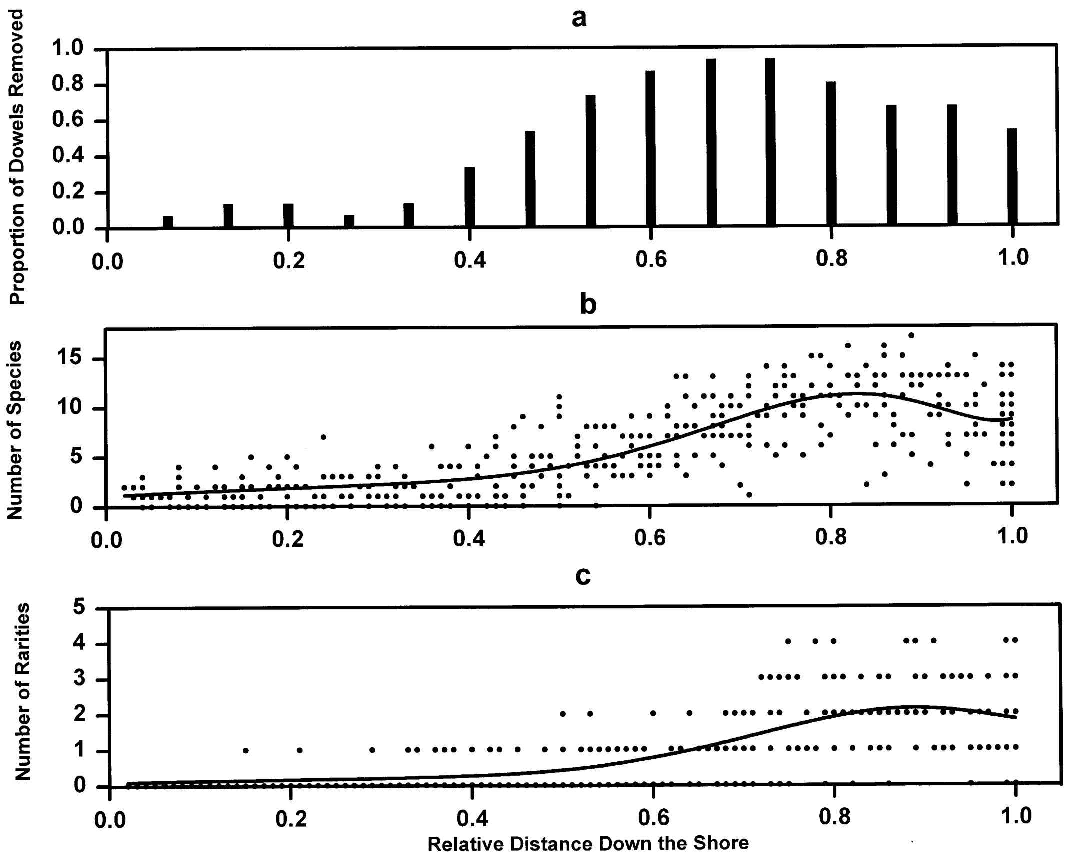

Fig. 4. The relative distance down the shore on the windward side of Maplesue Point and (a) proportion of dowels removed, (b) number of species and (c) number of rarities. Relative distance goes from the established shrub line (0) down to the July waterline (1.0). Lines were plotted using a distance weighted least squares method (Wilkinson, 1990).

of measured disturbance. It should be noted however, that the peak in richness was one-sided and occurred only at the low water side of the maximum disturbance zone, suggesting other factors may be limiting growth at higher shoreline positions. Similarly, Keddy (1985) has shown that richness of ACP species is highest at intermediate levels of wave exposure. However, how can you reconcile the predictions of the intermediate disturbance hypothesis with the observation that the greatest number of rarities occurs on the lake where disturbance is most frequent?

A larger pool of rare species in the downstream lake could simply be the result of an accumulation of propagules from rare species populations in upstream lakes, dispersed by hydrochory to the downstream, larger catchment area lake (Nilsson et al., 1993). This is a logical mechanism since there are many small catchment area lakes above fewer large catchment area lakes, however, this mechanism can not explain the results of the present study in that it predicts that the rare species pool in the large catchment area lake is simply the sum of the species pools in the small catchment area lakes upstream. This was not the case; the large catchment area lake had a larger rare species pool because it contained species that were not present in the upstream lakes.

The disparity between the greater frequency (Fig. 2) of rare species on the shores of the intermediate disturbance lake and the larger total pool of rare species in the lake with greatest disturbance indicates that different classes of rare species have different abilities. On shores of the intermediate disturbance lake, lower disturbance may result in greater competition at the patch level and less frequent gap formation so that species with the lowest competitive ability fail to persist. In the present study, this lost group would include the rarest of the rare Atlantic Coastal Plain plants in Canada, species that are listed by COSEWIC (Committee on the Status of Endangered Wildlife in Canada) and include *Lachnanthes caroliniana*, *Lophiola aurea* and *Scirpus longii* well represented in the largest catchment area lake (CA $\sim 10^5$ ha) of the river system of the present study (species mapped in Wisheu et al., 1994) but scarcely present on the shores of intermediate CA lake in this study. This distinction in the distribution of the rarest rarities is also evident in another Nova Scotian river system, the Tusket, notable for housing rare and endangered Atlantic Coastal Plain species. The COSEWIC listed species occur more frequently in the six lakes of large catchment area ($>50{,}000$ ha) in the Tusket River than in six lakes of intermediate catchment area (10–50,000 ha) in the Tusket and Annis Rivers (100 versus 50% for *Sabatia kennedyana*, 33 versus 17% for *Coreopsis rosea*, 33 versus 0% for *Scirpus longii* and 17 versus 0% for *Hydrocotyle umbellata*; Hill and Keddy, unpublished data). Although frequent disturbance on the largest catchment lakes may allow these species to persist in that it allows them to avoid competition, it also means that any one site has a high probability of being destroyed by disturbance in the near future. The end result is that there will be fewer sites with rare species present due to constant destruction, but a wider variety of rare species will be able to grow on those sites that do exist. Note, however, that with this explanation, those sites that support rare species will not necessarily be permanent. The next disturbance event will eliminate the rare species as well as their potential competitors and unless there is a nearby source of propagules (e.g. seeds dispersed from an adjacent site or rhizomes buried below the depth of scour) to re-colonize the site, rare species may be eliminated from the system.

In addition to a lower competive ability, the rarest COSEWIC plants may be poor at regenerating through seed. COSEWIC species were either uncommon or absent from the seed bank of a large catchment area lakeshore in Nova Scotia (Wisheu and Keddy, 1991). For many COSEWIC listed ACP species, it appears that their reproductive ability is limited. *Scirpus longii* has only sporadic seed set (Schuyler, 1963). In Nova Scotia, *Hydrocotyle umbellata* produces mostly empty pods (Vasseur, Personal Communication).

Shoreline width was also important in predicting the presence or absence of rare species. Shoreline width is determined by fluctuations in water level as well as the slope of the shoreline. As fluctuation in water level is in part a function of catchment area (Chow, 1964) one would expect a correlation between catchment area and shoreline width as has been observed in previous studies (Hill and Keddy, 1992). The lack of such correlation in the present study probably results from both within and among lake variation in the slope of the shoreline and provides us with the opportunity to examine the direct effects of shoreline width on the presence or absence of rarities. The positive effect of increased shoreline width on the presence of rarities was not due to any increase in disturbance on long shorelines. Shoreline width was not correlated with either of the two measures of disturbance used in the present study. Rather, shoreline width probably has a direct impact on the occurrence of rare coastal plain species in that the wider the shoreline, the larger the area of suitable habitat for the lakeshore species.

4.1. Implications for conservation

How can these findings be put to practical use? Most immediately, the various models can be used as guides to locate areas richest in rare species; field searches for rare plants should be concentrated on wide, exposed shorelines on large catchment area lakes. Rare species populations may be best developed at low shoreline stations below areas of maximum disturbance. In the summer of 2000, a population of an annual (*Cyperus diandrus*), rare in eastern Canada was discovered in Nova Scotia for the first time in just such a position in a large catchment area lake of the Tusket River (Hill, 2001).

Only a minority (5%) of lakes in Nova Scotia have the large catchment areas (ca. 50,000 ha) required to sustain long-term populations of the rarest Atlantic Coastal Plain plants on lakeshores. We have provided data that suggest that despite the greater species richness of rare plants at the whole lake level on large catchment area lakes, at the site level, rare plants may be less frequent here than in less disturbed systems. This argues that proportionately more lakeshore will need to be safeguarded to preserve populations of the rarest plant species on large catchment area lakes than is needed on lakes that are less disturbed. Since these large catchment area lakes are in the minority and since the rarest species are often widely distributed over such lakes, the current reserve system on the Medway and Tusket Rivers that conserves less than 1% of the total length of large catchment area shoreline is wholly inadequate.

Our disturbance data strongly suggests that plant communities are more dynamic on large catchment area lakes than on lakes of smaller catchment area; both sets of disturbance data showed that the large catchment area lake was the most disturbed of all of the four lakes investigated. In spite of the fact that the large catchment area lakes are the principal habitats for COSEWIC-listed rare plants, the frequency of sites that supported rare plants was three times lower on the largest catchment area lake than on the lake of intermediate catchment. Given the national status of the rare species that they support and the apparently higher probability that patches of populations of rare plants on large catchment area lakes will be disrupted, the existing few, small reserves on large catchment area lakes of the Tusket and Medway Rivers will not be adequate to maintain populations of nationally rare species in the long term. Small patches are vulnerable to the local disturbance processes that maintain the necessary conditions for rare species on the whole lake level and to larger factors such as between-year variation in water levels. A series of high water years would elevate the band of maximum ice scour disturbance and could reduce deep water patches of plants that occur mainly at low shoreline stations such as the threatened *Coreopsis rosea*. Populations of these rare species will persist only if there are multiple patches and multiple suitable sites for regeneration. The fate of *Scirpus longii* on Wilson's

Lake in the Tusket River is such a case. In 1992, it was represented by a single population of eight, 1 m wide clones in a bay bog (Hill and Johansson, 1992). This was decimated in 1994 by muskrat herbivory and by 2000 there were only a few individual shoots remaining that had not succumbed to competition from shrubs. The fate of the species in this river system now rests on two populations in a large catchment area lake upstream that has no formal protection. It is clear that for the Tusket River and other rivers that have large catchment area lakes supporting endangered species, multiple site reserves are needed that anticipate that local populations will be founded and eradicated with similar frequencies. Without a system of committed reserves, the addition of multiple anthropogenic disturbances in the face of the natural disturbance regime will lead to the loss from these rivers of the most restricted and vulnerable group, the COSEWIC listed plant species.

In Nova Scotia, the shoreline habitat of large catchment area ($>50{,}000$ ha) lakes has been reduced by roughly 50% in terms of total shoreline length as a result of damming for hydroelectric generation. While there is much capital investment in dams, the cases of dam removal or flow mitigation to accommodate wildlife needs are increasing. Conservationists increasingly will be called upon to guide restoration or rernediation attempts and will need to have an understanding of the relationship between hydrology and ecological process that is equivalent to that of hydrology:power relationships held by dam proponents. Our understanding of landform:disturbance:vegetation relations is not complete but it is adequate to understand that alteration of hydrology will disrupt complex communities that rely on continual disturbance within bounds that need to be determined.

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