Pitch pine (*Pinus rigida* Mill.) invasion of Cape Cod pond shores alters abiotic environment and inhibits indigenous herbaceous species

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Abstract

Invasion by pitch pine (*Pinus rigida* Mill.) on coastal plain pond shores may have direct impacts on the herbaceous community, or may merely indicate changes in hydroperiod, which are the actual cause of community change. We compared abiotic conditions and community composition of sites that had been invaded by *P. rigida* and those that had not on two Cape Cod ponds. Soil under living pines had lower pH and water content, reduced net nitrification, and increased rates of ammonification. Dense stands of pine saplings reduced PAR penetrance by 94% and excluded virtually all herbaceous species. To determine if pines alone can change community composition, we imposed artificial shade and added pine needle litter to experimental plots. In the course of one growing season, both litter and shade significantly reduced the frequency of herbs in the herbaceous zone of the pond shore. Litter had the greater effect (significant for six of seven taxa), while shade reduced the frequencies of three taxa significantly.

Keywords: Coastal plain pond shores; Disturbance regime; Mechanisms of competition; Native invasives; *Pinus rigida*

1. Introduction

Habitats shaped by periodic abiotic disturbances frequently support species-rich communities (Connell, 1978; Huston, 1994). Reduction of disturbance frequency and/or intensity in these systems may facilitate the invasion of species not normally part of the community (Sher et al., 2000). Furthermore, such invasions are usually associated with a decline in the local flora (Mack et al., 2000). It is often unclear, however, if the loss of diversity in the indigenous community is a direct result of changes in abiotic conditions or if the invasive species play an intermediary role in this process (Chambers et al., 1999; Lenssen et al., 1999; Farnsworth and Ellis, 2001).

The herbaceous community of coastal plain pond shores on Cape Cod, Massachusetts, USA, is an example of a disturbance-driven system that is susceptible to invasion. The coastal plain ponds of New England are small, shallow bodies of open fresh water with gently sloping, sandy shores and no surface inlets or outlets (Sorrie, 1994). The water levels in these ponds are dependent on precipitation in a very limited catchment area and on the depth of the underlying aquifer (Barbour et al., 1998). This hydrological sensitivity, together with rainfall variability, results in large fluctuations in pond levels from season to season and from year to year (Letty, 1984). The frequent but unpredictable flooding of the shore creates a broad zone between the permanent shrub line and the variable waterline in which neither upland nor aquatic plants can persist (Keddy and Reznicek, 1982; Menges and Waller, 1983; Keddy, 1984; Wilcox, 1995). Plant species that can survive the fluctuating conditions in this zone can escape competition from other plants, including upland woody species, that might exclude them from a more stable environment (Wilson and Keddy, 1986; Wisheu and Keddy, 1994). The coastal plain ponds of Cape Cod support a distinctive flora, including globally listed species, such as *Sabatia kennedyana* Fern. (Gentianaceae) (Plymouth gentian) and *Coreopsis rosea* Nutt. (Asteraceae) (rose...
coreopsis) (Sorrie, 1994). Other regionally rare taxa are confined to small areas on a handful of pond shores, making their survival vulnerable even to small-scale events (Craine, 2002).

Private and municipal water wells draw down the water table in the spring and early summer, when ponds would otherwise be most likely to flood (McHorney, 1998). In the late 1980s and early 1990s, abnormally low rainfall, coupled with human use of underground water resources, led to very low water levels on many Cape Cod ponds. During this time, dense stands of even-aged pitch pine saplings became established on some pond shores in the region (Simmons, 1996). Although P. rigida is the dominant tree species in upland Cape Cod, it is unusual for large numbers of pitch pines to mature on pond shores. Thus, the invasion of pitch pines is an indicator of changes in flooding regime. However, it is also possible that these invaders cause further alterations in the environment and that these changes are responsible for the reduced growth of pondshore herbs, perhaps posing a threat to the survival of some rare species.

This study uses correlative observations and manipulative experiments to examine the effects of pine saplings on the pondshore environment. We hypothesized that the presence of pitch pines causes changes in abiotic conditions that could, in turn, affect the herbaceous community. In this context, we asked: (1) how much litter and shade are created by a stand of pine saplings after approximately 10 years of growing on the pond shore, (2) how does soil chemistry differ in areas with living and dead pitch pines in comparison to areas that have not been invaded, and (3) is the pondshore flora different in species composition or density following pitch pine invasion? Because we observed large differences in litter accumulation and shade, we manipulated both litter cover and shade to test the hypothesis that P. rigida saplings inhibit the growth of pondshore herbaceous species.

2. Materials and methods

2.1. The study sites

We collected data in natural conditions at two coastal plain ponds in central Cape Cod, Massachusetts in 2000 and 2001. Campground Pond is one of the Mary Dunn group of ponds in the town of Barnstable, at approximately 41° 41’ N, 70° 17’ W. This group is recognized as including some of the best examples of the coastal plain pondshore flora (Sinnott, 1912). All these ponds experienced pitch pine invasion around 1990, and large stands of pines (as dense as 4.75 stems m⁻²) grew on several ponds until most were killed by two consecutive summers of exceptionally high water in 1997–1998. The only remaining dense stand of pines (4.35 stems m⁻²) is on Campground Pond.

Our second natural site, Grassy Pond, is in the town of Dennis, 10 km northeast of the Mary Dunn group, at approximately 41° 43’ N, 70° 09’ W. Grassy Pond experienced some pitch pine invasion in the dry years around 1990, but the densities nowhere approach those on the Mary Dunn ponds. Furthermore, the high-water years of 1997–1998 killed many of the trees but also left some alive. An area was chosen on the southwest shore where three adjacent quadrats (3×5 m each) could be located that encompassed, respectively, mostly living pines, mostly dead ones, and no pines. In the live pine quadrat, there were 34 trees (26 living and eight dead) for an average density of 2.26 stems m⁻². In the dead pine quadrat, there were 20 dead and three living trees for an average density of 1.53 stems m⁻². The average relative elevations of five haphazardly chosen points within each quadrat were measured. The dead pine quadrat was found to be 0.102 m higher, and the living pine quadrat 0.180 m higher, than the open quadrat. However, it is unlikely that these small differences in elevation alone could account for the large differences in the abiotic environment and the herbaceous community found in this study (see Results).

2.2. Differences in soil chemistry

Soil samples were taken on September 17, 2000, in the three quadrats established on the shore of Grassy Pond. Two adjacent 15-cm soil cores (2 cm in diameter) were extracted at each of five random locations within each quadrat. Each 15-cm core was divided between the upper 7.5 cm and the lower 7.5 cm, and pairs of cores from each location and depth were combined. Soil moisture was determined gravimetrically after drying sub-samples of 5 g each at 60 °C for one week, followed by 2 h at 100 °C. Separate sub-samples of 10 g each were dissolved in 10 ml of deionized water and the pH of the mixture measured with an Orion Model 410A pH meter. Two additional 10-g sub-samples were taken for nitrogen analysis. One set of sub-samples was extracted immediately with a 2M solution of potassium chloride, and the extract frozen for later analysis. The other set was stored in 200 ml, screw top, Nalgene bottles to incubate for 28 days in the dark at room temperature (Weaver et al., 1994). Quantities of available nitrogen (NO₃⁻ and NH₄⁺) in both sets of samples were measured with an automated ion analyzer system (Lachat QuickChem 8000, Lachat Instruments, Milwaukee, WI, USA).

For all the soil chemistry measurements, the results are reported for both the upper 7.5 cm and the lower 7.5 cm. Differences among the three types of plots at each depth were analyzed using one-way analysis of variance (ANOVA).
2.3. Differences in the herbaceous community

To measure differences in the plant communities based on the natural presence of *Pinus rigida*, we used counts of taxon frequency. Sampling grids—25 x 25 cm, divided into 25, 5 x 5 cm squares—were placed randomly within each quadrat representing differing degrees of pitch pine influence. The presence or absence of all species in each of 25 small squares in the grid was recorded. Each plant was assigned to the square in which it was rooted. Thus the data reported for community comparison are the percent of small squares occupied by any particular taxon averaged over all sampling grids in that quadrat type.

On August 20, 2001, community sampling was carried out at Campground Pond using five randomly placed sampling grids in both a 4 x 4 m quadrat in the center of the pitch pine stand and in another 4 x 4 m quadrat immediately outside the stand, toward the center of the pond, and less than 10 m from the center of the first quadrat. The second quadrat was still above the maximum water level reached by the pond in the previous 2 years. The frequencies of species encountered in the sampling grids, as well as the frequencies of totally unoccupied squares, were compared.

Community composition was compared among the same three quadrats at Grassy Pond that were used for soil sampling. On August 24 and 31, 2000, a frequency census was carried out for five randomly placed sampling grids within each of the quadrats. Average frequencies of each taxon encountered at levels sufficient to be analyzed were calculated for each quadrat type and compared. The frequencies of squares not occupied by any living plant were also compared. For the frequency of each species (or unoccupied squares), the significance of area effect was analyzed using the Kruskal–Wallis test.

2.4. Simulation of pitch pine litter and shade

This manipulative experiment was carried out on the shore of Israel Pond, another member of the Mary Dunn group. In 2000, a total of 1183 dead pitch pines, many as tall as 2 m and at a maximum density of 4.35 stems m⁻², were counted on the shore of this pond.

Eight replicates of a 2 x 2 factorial design manipulating pine litter and shade were established on May 1, 2001. Each of the eight replicate blocks included four 1 m² treatment plots—one with litter, one with shade, one with litter and shade, and one unmanipulated. The replicate blocks were situated in pairs around the pond, including a variety of exposures and soil conditions (Fig. 1). All were at elevations that placed them well within the pondshore herbaceous zone, where both flooded and exposed conditions had occurred over the past decade.

Shade plots were covered with 95% shade cloth (International Tela-Com, Inc., Asheville, NC, USA) suspended on a frame of PVC pipes 75 cm above the soil surface. On July 6, 2001, average PAR penetrance at noon was determined to be 6.07% (±0.245 SE, N=8) of ambient PAR. This approximated the actual PAR penetrance previously measured under the stand of living *P. rigida* saplings on Campground Pond (6.74% ±1.60, N=10). Pitch pine needles were collected from the upland forest just north of Israel Pond, and 2.45 kg of dry needles were spread on each 1 m² litter treatment plot. This density was based on the finding of 2.45 kg m⁻² in the stand of living pines on Campground Pond.

Species richness was determined on September 12, 2001, by enumerating every species (or higher taxon) observed within a 0.25 m² sample area in the center of each treatment plot (N=8 per treatment). Differences in the total number of species present (species richness) were compared to determine the effects of litter and shade using a two-way analysis of covariance (ANCOVA), with block as the covariate. Total species lists were also compared using Sørensen’s Similarity Index (S1) (Brower et al., 1998). A multi-response permutation procedure (McCune and Mefford, 1999) was then used to determine the significance of differences in
community composition among treatments in all possible pairwise combinations.

Species frequency was recorded on August 22 and 24, 2001, using one sampling grid of 25 squares (as described above) placed at random within the central 0.25 m² of each treatment plot. The percent of these 25 squares occupied by each taxon was considered its frequency for that block and treatment. A taxon was considered common enough for meaningful analysis only if its frequency exceeded 15% in all the unmanipulated plots taken together and if it was present in more than half of these eight plots. Differences in frequencies for each common taxon among treatments were compared by means of two-way analysis of covariance (ANCOVA), with litter and shade as the main effects and block as the covariate.

3. Results

3.1. Soil chemistry

Of the three adjacent quadrats on the shore of Grassy Pond, soil moisture was highest in the area that was free of pitch pines, lowest in the area dominated by living pines, and intermediate in the area containing mostly dead ones. In the upper 7.5 cm of soil cores, this relationship was statistically significant (Table 1). In the same three quadrats, pH was highest in the open area and lowest under the living pines. However, the difference was statistically significant only in the deeper half of the soil cores (Table 1). Available nitrate and available ammonium were also highest in the area free of pines. This trend was not significant, but in the case of ammonium it was nearly so ($P = 0.07$) (Table 1).

Net nitrification (incubated NO₃⁻ minus initial NO₃⁻) was greatest in the uninvaded area and lowest in the area dominated by dead trees or the open area (Fig. 2). Within the living $P. rigida$ stand, nearly half (48.8%) of sample squares had no living plant rooted in them. An additional 26.4% had no vascular plants, being occupied only by $Sphagnum$ spp. There were no unoccupied squares in the dead pine quadrat, and only two (1.6%) in the open one (one of these coincided with the opening to an animal burrow). The frequencies of $Panicum lanuginosum$ Ell. (Poaceae), other grasses, $Euthamia tenuifolia$ Pursh. (Asteraceae), $Lachnanthes tinctoria$

### Table 1

<table>
<thead>
<tr>
<th>Soil chemistry variable</th>
<th>Depth</th>
<th>No pines</th>
<th>Dead pines</th>
<th>Live pines</th>
<th>$F$ ratio</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>% water by weight</td>
<td>Upper</td>
<td>0.080±0.005 (a)</td>
<td>0.066±0.003 (ab)</td>
<td>0.056±0.006 (b)</td>
<td>7.032</td>
<td>0.010</td>
</tr>
<tr>
<td></td>
<td>Lower</td>
<td>0.188±0.045</td>
<td>0.148±0.060</td>
<td>0.130±0.054</td>
<td>0.293</td>
<td>0.752</td>
</tr>
<tr>
<td>pH</td>
<td>Upper</td>
<td>5.264±0.579</td>
<td>4.650±0.119</td>
<td>4.424±0.088</td>
<td>1.587</td>
<td>0.245</td>
</tr>
<tr>
<td></td>
<td>Lower</td>
<td>4.514±0.050 (a)</td>
<td>4.460±0.102 (ab)</td>
<td>4.050±0.152 (b)</td>
<td>5.382</td>
<td>0.021</td>
</tr>
<tr>
<td>NO₃⁻ ($\mu g \cdot g^{-1}$)</td>
<td>Upper</td>
<td>0.121±0.017</td>
<td>0.094±0.039</td>
<td>0.077±0.022</td>
<td>0.993</td>
<td>0.399</td>
</tr>
<tr>
<td></td>
<td>Lower</td>
<td>0.107±0.035</td>
<td>0.046±0.016</td>
<td>0.057±0.014</td>
<td>0.790</td>
<td>0.476</td>
</tr>
<tr>
<td>NH₄⁺ ($\mu g \cdot g^{-1}$)</td>
<td>Upper</td>
<td>1.181±0.228</td>
<td>0.689±0.196</td>
<td>0.562±0.082</td>
<td>3.288</td>
<td>0.073</td>
</tr>
<tr>
<td></td>
<td>Lower</td>
<td>0.680±0.150</td>
<td>0.409±0.054</td>
<td>0.377±0.020</td>
<td>3.220</td>
<td>0.076</td>
</tr>
<tr>
<td>Net nitrification ($\mu g \cdot g^{-1} \cdot 28 \text{ d}^{-1}$)</td>
<td>Upper</td>
<td>2.818±0.710 (a)</td>
<td>0.661±0.300 (b)</td>
<td>0.471±0.190 (b)</td>
<td>8.104</td>
<td>0.006</td>
</tr>
<tr>
<td></td>
<td>Lower</td>
<td>0.434±0.069</td>
<td>0.305±0.152</td>
<td>0.242±0.205</td>
<td>0.083</td>
<td>0.921</td>
</tr>
<tr>
<td>Net ammonification ($\mu g \cdot g^{-1} \cdot 28 \text{ d}^{-1}$)</td>
<td>Upper</td>
<td>5.331±2.676</td>
<td>3.038±1.460</td>
<td>4.103±1.328</td>
<td>0.358</td>
<td>0.706</td>
</tr>
<tr>
<td></td>
<td>Lower</td>
<td>-0.269±0.089 (a)</td>
<td>-0.167±0.040 (ab)</td>
<td>0.017±0.071 (b)</td>
<td>4.310</td>
<td>0.039</td>
</tr>
</tbody>
</table>

* Mean values (±SE) and results of ANOVA, with $n = 5$ for each condition. Statistically different variables are in bold and among-treatment differences (Tukey’s multiple comparison) designated by letters.
(Walt.) Ell. (Haemodoraceae), and Viola lanceolata were all lowest in the quadrat with living pine saplings (Fig. 2). However, for V. lanceolata and E. tenuifolia frequencies were highest in the plots dominated by dead pitch pines. The only taxon more common under the trees than in the open area was Sphagnum spp.

3.3. Simulation of pitch pine litter and shade

Both litter and shade reduced the total number of species present. The mean number of species (or higher taxa, such as Panicum spp. and Sphagnum spp., that were not identified to the species level) was highest in the eight no litter/no shade plots (Fig. 3). Richness was ranked as follows: no litter/no shade > shade only > litter + shade. Litter accounted for 37.88% of total variation in richness, shade for 8.99% of total variation, and the interaction for 0.22%. Block effects were not significant ($F = 1.168$, $P = 0.289$). Community composition of the litter-only plots was significantly different from that of the no litter/no shade plots, while the difference between litter + shade and no litter/no shade was nearly significant ($P = 0.058$) (Table 2). No other pairs of treatments showed significant differences.

Seven plant taxa met the criterion of at least 15% frequency in the unmanipulated plots, and all seven were also present in over half these plots. One additional category—unoccupied squares—was analyzed because it was very frequent in the litter, shade, and litter + shade plots even though there were no such squares in any of the no litter/no shade plots. For six of the seven plant taxa, litter significantly decreased their frequency; for three of these, shade also caused a significant reduction; and for one there was also a significant interaction.

Table 2
Community similarity among four treatments.$^a$

<table>
<thead>
<tr>
<th>Treatment</th>
<th>No Litter/No Shade</th>
<th>Litter</th>
<th>Shade</th>
</tr>
</thead>
<tbody>
<tr>
<td>Litter</td>
<td>S1 = 66.8 ± 3.075</td>
<td>S1 = 69.9 ± 2.489</td>
<td>S1 = 71.5 ± 4.840</td>
</tr>
<tr>
<td>Shade</td>
<td>S1 = 77.5 ± 2.435</td>
<td>S1 = 71.5 ± 3.951</td>
<td>S1 = 71.5 ± 4.840</td>
</tr>
<tr>
<td>Litter + Shade</td>
<td>S1 = 56.9 ± 5.795</td>
<td>S1 = 71.5 ± 3.951</td>
<td>S1 = 71.5 ± 4.840</td>
</tr>
</tbody>
</table>

$^a$ S1 = Sørensen’s Similarity Index (with SEM). $P$ = probability of S1 as small or smaller.
effect (2-way ANCOVA) (Table 3, Fig. 4). In seven of the eight categories, litter had a bigger effect on frequency than did shade, as indicated by F-values in Table 3. The only exception was Euthamia tenuifolia, for which none of the treatments had a significant effect. Both treatments and their interaction significantly increased the frequency of unoccupied squares.

4. Discussion

Pitch pine presence on the pond shore is both an indicator of hydrologic changes and an agent of change in the herbaceous community. In naturally occurring pondshore stands of *Pinus rigida*, we observed increased litter and shade, decreased soil pH and moisture, and decreased frequency of several plant species in comparison with uninvaded areas. We did not detect differences in available nitrogen, but net nitrification appears to be inhibited, while net ammonification may be accelerated by the presence of pitch pines. While each of these significant differences in soil chemistry was obtained in only one of the two depths analyzed, in most cases the same pattern was apparent at the other depth as well. Furthermore, dense growth of pitch pines appears to be incompatible with the survival of most indigenous herbaceous species. The stand of *P. rigida* at Campground Pond contains virtually no herbaceous plants in its understory, while the thinner group of saplings at Grassy Pond has lower frequencies of most taxa by a factor of between three and eight. The added litter and shade from pitch pine saplings make the most dramatic differences in community composition. Within one growing season, litter accounted for 38% and shade for 9% of total variation in species richness among plots in the center of the occasionally flooded herbaceous zone.

4.1. Changes in soil chemistry

The lower pH and decreased net nitrification found in the area dominated by living *Pinus rigida* is consistent with other published results. Pine needle litter is known to immobilize nitrogen (Conn and Dighton, 2000), and conifers generally promote acidification of the soil, which reduces rates of nitrification and lowers organic content in the A horizon (Miles, 1985). Lower pH under living pines at Grassy Pond also correlated with increased frequency of *Sphagnum* spp. *Sphagnum* is not only an acid-loving moss, but can also increase soil acidity where it grows (van Breemen, 1995), so it may be partly responsible for the lower pH found in the living pine plots.

4.2. Effects on the herbaceous community

The presence of pitch pines is strongly correlated with reduced frequency of herbaceous plants. A sharp discontinuity between the shrub zone and the herbaceous community has been noted in several different environments with fluctuating water levels: on the coastal plain ponds of Cape Cod (Graham and Henry, 1933) and Long Island (Zaremba and Lamont, 1993); on much larger Canadian lakes (Bégin and Filion, 1995); in salt marshes (Hacker and Bertness, 1999); in riverine floodplains (Menges and Waller, 1983); and in interdunal swales (Rheinhardt and Faser, 2001). In a similar way, the boundary line between stands of invasive pitch pines on pond shores and the surrounding herbaceous vegetation is often quite distinct (personal observation). In all these cases, the lower limit of the woody plants coincides with the upper limit of a well-defined herbaceous community.

There are two fundamentally different possible explanations for this coincidence. Either both communities are determined by abiotic factors alone (such as water availability, soil conditions, and flooding frequency), or, where they are not excluded by environmental factors, woody plants outcompete other species that could otherwise survive in the environment. We need to be able to distinguish between these two possibilities in order to assert that the presence of an invader like *P. rigida* is detrimental to the existence of indigenous species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Litter</th>
<th>Shade</th>
<th>Shade + litter</th>
<th>Block</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F-ratio</td>
<td>P</td>
<td>F-ratio</td>
<td>F-ratio</td>
</tr>
<tr>
<td>Coreopsis rosea</td>
<td>5.375</td>
<td>0.028</td>
<td>2.773</td>
<td>0.107</td>
</tr>
<tr>
<td>Drosera intermedia</td>
<td>15.703</td>
<td>0.0005</td>
<td>5.741</td>
<td>0.024</td>
</tr>
<tr>
<td>Euthamia tenuifolia</td>
<td>0.255</td>
<td>0.618</td>
<td>2.025</td>
<td>0.166</td>
</tr>
<tr>
<td>Panicum spp.</td>
<td>44.551</td>
<td>&lt;0.0005</td>
<td>6.643</td>
<td>0.016</td>
</tr>
<tr>
<td>Rynchospora capitellata</td>
<td>8.681</td>
<td>0.007</td>
<td>3.533</td>
<td>0.071</td>
</tr>
<tr>
<td>Sphagnum spp.</td>
<td>15.564</td>
<td>0.0005</td>
<td>0.182</td>
<td>0.673</td>
</tr>
<tr>
<td>Viola lanceolata</td>
<td>9.285</td>
<td>0.005</td>
<td>7.553</td>
<td>0.011</td>
</tr>
<tr>
<td>Unoccupied</td>
<td>42.667</td>
<td>&lt;0.0005</td>
<td>18.257</td>
<td>0.0002</td>
</tr>
</tbody>
</table>

Results of two-way ANCOVAs, with Block as covariate (N= 8). Effects significant at P < 0.05 are in bold.
The first explanation relies on the fact that plant species vary in their sensitivity to environmental conditions such as anoxia or hypoxia in the soil resulting from waterlogging (Drew, 1997). Length and depth of flooding could therefore directly exclude some species from lower elevations to create the observed zones within the plant community (Bell, 1980; Spence, 1982; Rheinhardt and Faser, 2001). Moisture gradients up and down a pond shore may also affect which species’ seeds and propagules will survive and germinate (van der Valk, 1981; Lenssen et al., 1999). Thus, species distributions could also be influenced by their regeneration niche (Grubb, 1977) in relation to flooding and related abiotic conditions.

Fig. 4. Mean frequency of eight most common taxa and categories under four treatments (with one standard error, \( N = 8 \) per treatment).
Alternatively, it is possible that flood-mediated competition is the key factor in structuring the herbaceous community. Periodic flooding may keep out woody species thereby opening the area to a variety of less competitive ones (Keddy, 1983). Grace and Wetzel (1981) found that of two species of *Typha* (Typhaceae), the one usually restricted to lower (wetter) locations grew at least equally well on drier sites when the competing species was removed. For the species that normally dominated the drier sites, the abiotic factor (excess water) limited its range; for the less competitive species, the biotic factor (the presence of the other species) was limiting. The relative importance of competition in a system such as coastal plain pond shores may be determined by the frequency of disturbance (Keddy, 1989). With frequent flooding, flood tolerance is the key to determining species distributions; with reduced disturbance, competition plays a bigger role.

Our data from naturally occurring pine stands on Cape Cod pond shores show that pitch pines are negatively correlated with herbaceous cover. However, it is impossible to establish cause and effect in this system for two reasons. First, areas supporting *Pinus rigida* saplings were in both cases slightly higher in elevation than areas free of the trees. Higher elevation means a greater distance to the water table and a longer time since last flooding, both of which are factors in determining the distribution of plants along the pondshore elevation gradient (Keddy, 1984; Schneider, 1994; Wilcox, 1995). Thus, we could not distinguish between changes caused by the presence of pitch pines and pre-existing conditions that might simultaneously encourage pines and inhibit herbaceous species. Second, natural observations alone could not identify the mechanisms by which pitch pines excluded or inhibited other plants.

Our simulation of litter and shade demonstrates that the introduction of these factors by living *P. rigida* saplings can change the plant community in just one growing season, even in the zone where pondshore species normally thrive. Pine litter had a significant effect on all but one of the taxa, while shade had a smaller effect on each of them and was significant in three of seven cases. Both litter and shade caused significant decreases in overall species richness and total plant coverage. In a natural situation, when pitch pines are growing for several years they undoubtedly multiply the effects recorded in this experiment, as indicated by the virtually total exclusion of herbaceous plants from the understory of the pine stand at Campground Pond. We suggest that an earlier start date (before May 1) or a multi-year study would have produced even stronger effects.

### 4.3. Conclusions

Disturbance, in this case periodic flooding, is a major factor structuring some habitats that are rich in rare species (Hill and Keddy, 1992). Areas more frequently inundated support a different group of plant species than those that are drier and flood less frequently. The resulting concentric rings of vegetation types around these ponds is a striking feature noted by many observers (Graham and Henry, 1933).

This study demonstrates that the litter and shade from large, rapidly growing pitch pine saplings can have significant impacts on the environment regardless of recent hydrologic regime at that particular site. When reduced flooding facilitates pitch pine invasions, our results indicate that the presence of these trees on the pond shore are a direct threat to pondshore endemics. As pine invasion proceeds to alter areas of the pond shore, indigenous species will be squeezed into less area. This process may locally extirpate some rare taxa if they happen to be confined to the same area that the pines invade. Therefore, there is a practical interest in determining what factors encourage or prevent the invasion of pitch pines. It would be helpful to conservationists to know how much flooding is necessary to keep a pond shore free of these upland species.

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