Distribution, Species Composition and Management Implications of Seed Banks in Southern New England Coastal Plain Ponds

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ABSTRACT

Buried seeds that germinate during periods of low water or water level drawdown can play important roles in shaping plant community composition, community dynamics and species richness in ecosystems with fluctuating water levels. Northeastern US coastal plain ponds have fluctuating water levels and contain a characteristic shoreline flora that contains many rare plants. The objectives of this study were to: (1) test whether geographically distant ponds in Cape Cod and Martha's Vineyard had distinct seed banks, (2) determine if hydrologic status as permanent and ephemeral ponds led to differences in seed banks, and (3) examine seed diversity and seed abundance across gradients of shoreline elevations and sediment characteristics. Viable seeds of 45 plant species were identified from 9 ponds. Native species dominated pond-shore seed banks and made up 89 to 100% of all species. There was high overlap in seed bank composition across hydrological classes and geographic regions. One hydrological class captured 73-76% of total species and one geographical region captured 69-78% of the total species recovered from the entire suite of seed bank samples. Seeds were relatively evenly distributed along the shorelines of ephemeral ponds but seed diversity and abundance were lower at low elevations in permanent ponds. Results suggest that strategies to protect pond shorelines to capture maximum diversity of coastal plain pond plants contained in pond sediment seed banks should be implemented across pond hydrologic classes and across a wide geographic area. Shoreline seed distributions indicate that ground-water withdrawals or climate changes that lower pond water levels in permanent ponds will reduce the diversity and abundance of plants recovered from seed banks by shifting water levels to a shoreline zone of high sediment organic matter where seed densities are lower. This effect will be much less in ephemeral ponds where seed diversity and abundance on pond bottoms was high.

Keywords: freshwater wetland; pond shore; seed germination

1. Introduction

The production of buried seeds capable of surviving in sediments over multiple years is an important life-history strategy for plants that occupy ponds, marshes and other wetlands where water levels exhibit significant seasonal or inter-annual fluctuations (van der Valk and Davis, 1978, van der Valk, 1981; Welling et al., 1988; Leck and Simpson, 1987; Wilson and Keddy, 1988; Kantrud et al., 1989). Buried seeds, which generally germinate during periods of low water or water level drawdown, play an important role in shaping plant community composition, community dynamics and species richness in these ecosystems (Spence, 1982; Keddy and Reznicek, 1986; Welling et al., 1998; Schneider, 1994). Buried seeds can also be significant sources of weedy and non-native species (Alexander and D'Antonio, 2003; Leck, 2003). Because the composition and distribution of buried seeds varies with sediment characteristics, shoreline position, and the frequency of flooding and drawdown, an understanding of these controls on seed banks composition and diversity is important for understanding the water level regimes or management strategies that conserve wetland plant dynamics and diversity or that promote specific plant species or vegetation mosaics (Pederson and van der Valk, 1984; van der Valk, 1988).

Coastal plain ponds of the coastal plain of northeastern United States and southeastern Atlantic Canada are ecosystems in which fluctuations of ground-water levels lead to large changes in pond water levels and to changes in the area of exposed pond shoreline (Letty, 1984; Keddy and Wisheu, 1989; Sorrie, 1994; McHorney and Neill, 2007). Coastal plain ponds were formed primarily as kettleholes during glacial retreat (Oldale, 1974; Mulligan and Uchupi, 2003). Annual fluctuations in precipitation and evapotranspiration drive seasonal and multi-year water level fluctuations (Sorrie, 1994; Zaremba and Lamont, 1993; Walter and Whelan, 2005; McHorney and Neill, 2007).

Germination from buried seeds along exposed shorelines and near-shore shallowly flooded zones is the primary mechanism for plant recruitment in coastal plain ponds (Sorrie, 1994; Schneider, 1994). Prolonged inundation during years or multiple years with high water levels generally eliminate adult plants of most shoreline grasses and forbs and prevent encroachment of woody shrubs and trees into lower-elevation portions of pond shorelines (Sorrie, 1994; Craine and Orians, 2004; McHorney and Neill, 2007). Plants that occupy coastal plain pond shorelines generally tolerate the acid and low-nutrient conditions that prevail in these ecosystems because of the ponds' geologic origin in areas of coarse and acidic soils formed predominantly on acidic glacial outwash (Oldale, 1974; Fletcher, 1993; Sorrie, 1994; Wisheu and Keddy, 1989).

The shorelines of southern New England coastal plain ponds contain a diversity of plant species and a high number of species that are regionally or globally uncommon or rare. These include Plymouth gentian (*Sabatia kennedyana*), Wright's panic-grass (*Dichanthelium wrightianum*), thread-leaved sundew (*Drosera filiformis*), two-flowered rush (*Juncus biflorus*), Maryland meadow beauty (*Rhexia mariana*) and at least 15 other species that appear on the Natural Heritage and Endangered Species lists in northeastern US states (Sinnott, 1912; Sorrie, 1994; Swain and Kearsley, 2001). Throughout their range, coastal plain ponds are hotspots for biodiversity and high priorities for conservation (Wisheu and Keddy, 1989; Barbour et al., 1998; Zaremba and Lamont, 1993; Primack and Woolsey, 1998). Because the highest density of coastal plain ponds occurs in regions of the states of Massachusetts, Rhode Island and New York that have a high suburban populations (Stone, 1998; Breunig, 2003), human activities now threaten the long-term persistence of coastal plain pond plants. Principal threats are alteration of water levels or water level dynamics by groundwater pumping for water supplies (McHorney and Neill, 2007), direct disturbance or trampling caused by recreational activities (Barbour et al., 1998) and nutrient enrichment of the regional groundwater (Valiela et al., 1992).

The floristic characterizations and inventories of coastal plain ponds indicate that adult plants of many shoreline species are absent when shorelines are flooded but recruit during water level drawdowns (Sinnott, 1912; Zaremba and Lamont, 1993; Lundgren, 1989). Schneider (1994) identified 32 species of plants that germinated from the sediments of two coastal plain ponds from Long Island, NY. Information on how seed bank distribution and composition vary among environmental gradients, such as shoreline elevation, hydrologic regime, geographic location and nutrient status, are potentially important for devising strategies and setting priorities for protecting coastal plain ponds, pond shoreline habitats and pond shoreline plant diversity. It is also important for understanding how diverse shoreline plant communities respond to changes in water level regimes caused by land use pressures and climate change.

Our objectives in this study were: (1) to quantify sediment seed bank species composition and abundance across a range of coastal plain pond locations on Cape Cod and the island of Martha's Vineyard, Massachusetts; (2) to compare seed bank composition in ponds with different hydrological regimes that ranged from permanent ponds to ephemeral ponds, (3) to compare seed bank composition across gradients of shoreline elevations to understand the effect of water level regime on seed distribution, and (4) to evaluate relationships between seed bank composition and abundance and shoreline sediment nutrient and organic matter content. We used field-collected sediments exposed to controlled humidity, temperature and light regimes in growth chambers and the identification of germinating seeds to quantify buried seed composition and density. We use the results to recommend approaches to regional conservation management for these geographically dispersed, species-rich shoreline plant communities.

2. Methods

2.1 Study sites and field collections

We sampled nine ponds in two coastal Massachusetts locations, Hyannis, MA on Cape Cod and the island of Martha's Vineyard, MA (Fig. 1). We sampled three permanent (Israel, Lamson, Mary Dunn) and two ephemeral ponds (Little Israel, Sinnott) in Hyannis and two permanent ponds (Duarte, Old House) and two ephemeral ponds (Google, Rainwater) on Martha's Vineyard. Permanent ponds retained surface water in all or nearly all years. Ephemeral ponds lost surface water in many years. Because water level records existed only for Mary Dunn, Israel and Lamson Ponds (McHorney and Neill, 2007), we classified the other ponds based on observations of land owners and managers during very dry years.

We determined seed bank composition by collection of sediment from the field and incubation under controlled moisture and temperature conditions designed to maximize seed germination (Pederson and Van der Valk, 1984; Leck and Simpson, 1987). Sediment samples were collected between August 18-20, 2005 from Martha's Vineyard and August 29-31 from Hyannis.

To facilitate sampling pond shorelines at random, we chose point along the pond shorelines and then established 8 transects around each pond shoreline at pre-determined regular distances (5-10 m depending on overall pond size). Along each transect, we collected sediments from either 4 elevations (in all Martha's Vineyard ponds and Hyannis ephemeral ponds) or 5 elevations (in Hyannis permanent ponds). The elevations were selected to include the entire elevation range of the shoreline zone that could be exposed by water level fluctuations within each pond. Each transect was laid out to extend from the high elevation “shrub” zone to either the permanently-flooded zone of highly organic pond-bottom sediments in permanent ponds or to the center of the pond basin in ephemeral ponds. Permanent ponds had steeper shorelines than ephemeral ponds. Transect elevations spanned 0.53 to 1.40 m in permanent ponds and 0.26 to 0.35 m in ephemeral ponds.

Sediments for growth chamber incubations were collected to a depth of 5 cm from quadrats of known area. On the dry shoreline or in shallow water (<50 cm), sediment was collected from within a PVC plastic ring of 113.4 cm^2. In deeper water, sediment was collected with an Eckmann dredge of 225 cm^2. Sediment samples were stored in plastic bags, and placed in a refrigerator at 10°C until placement into pots in the growth chambers.

2.2 Seed bank experiment

Seed bank composition was estimated from the number and species of seedlings that germinated from samples of the field-collected pond sediment placed in pots in Conviron® PGW36 growth chambers. A known mass of pond sediment from each bag was transferred to 15.2-cm diameter plastic pots that contained a mixture of 50% (by volume) sterile building sand and 50% sterile potting mix. Sediments were added to pots to a depth of 5 cm on top of the sand-potting soil mixture. Field-collected bags were weighed wet before and after transfer of sediment to the pots to determine the proportion of each bag (and therefore the area of pond bottom) represented by the potted sample.

Pots were placed in the growth chambers on September 2, 2005. Chambers were set for day-night and long-term average daytime and nighttime temperatures for Hyannis, MA in June. Day lengths and temperatures in the growth chambers were changed every 30 d to simulate mean conditions from July to October during the remainder of the 4-month experiment. Pots were allowed to drain freely and were watered to saturation 3 times per week. From 14 to 18 November all seedlings in the pots were counted and identified to species or the lowest taxonomic category possible.

Plants were classified into coastal plain pond-shore graminoids and forbs, widespread ruderal graminoids and forbs, woody shrubs and trees or submersed aquatics based on their life history characteristic and their restriction to coastal plain pond shores. Species were classified as native or introduced based on their historic presence in Barnstable County (Cape Cod) and Dukes County (Martha's Vineyard) based on Sorrie and Somers (1999). Species listed on the official State of Massachusetts List of Endangered, Threatened and Special Concern Species (MA NHESP, 2008) were also noted.

2.3 Sediment analysis

The organic matter content of each field-collected sediment sample was determined by ashing 10 g of fresh sediment in a muffle furnace at 450 ^{o}C for 5 h. Extractable inorganic nitrogen (N) was determined by extraction with 1N KCl. Ammonium in the extracts was measured colorometrically in the extracts by phenol-hypochlorite (Solorzano, 1969) and nitrate was measured on a Lachat autoanalyzer (Method 31-107-04-1-C). Acid extractable phosphate (Melich I phosphorus) was measured by extraction with HCl and H_2SO_4 (Kuo, 1996). Phosphate in the extracts was measured colorimetrically (Murphy and Riley, 1962). A subsample of wet sediment was dried at 60 ^{o}C to constant weight to allow calculation of organic matter and extractable nutrient content on a dry weight basis.

2.4 Data analysis

We used analysis of variance in SAS (Proc GLM, SAS version 9.03) to test for differences in the diversity and abundance of plant diversity and soil characteristics, using location (Hyannis or

Martha’s Vineyard), hydrological class (permanent or ephemeral) and elevation zone as class variables. We used Bonferroni adjusted t-tests for multiple means comparisons and used log or log+1 transformed data where transformation was necessary to meet the assumptions of a normal distribution. Means are reported ± standard error. We used the regression (SAS Proc REG) to test the relationship between sediment characteristics (extractable ammonium, nitrate, total inorganic N, phosphate, organic matter) and species richness and species abundance per sample.

We used the occurrence of species in the individual sediment samples to estimate total species richness of the plant community (including species not present in any sample) based on species accumulation curves. We used the incidence-based coverage estimator (ICE) (Chazdon et al., 1998) in EstimateS 8.0 (Colwell, 2006) to estimate the total species richness for individual ponds, permanent and ephemeral ponds and ponds in Martha’s Vineyard and Hyannis. We also used Estimates 8.0 to calculate the number of shared species and Chao's Abundance-based Sørensen index of similarity among samples from different ponds and between permanent and ephemeral ponds and ponds in Hyannis and Martha’s Vineyard. Chao’s abundance-based Sorensen index takes into account the contribution to the true value of this probability made by species actually present at both sites, but not detected in one or both samples. This approach has been shown to reduce the negative bias of traditional similarity indices, especially with incomplete sampling of rich communities (Chao et al., 2005; Colwell, 2006).

We also performed non-metric multiple dimensional scaling (NMS) with varimax rotation (Mather, 1976) to examine the overall similarity of the seed bank composition among ponds and to examine whether pond communities were more strongly related to hydrologic class (permanent or ephemeral), location (Hyannis or Martha’s Vineyard), or pond-shore zone (shrub, upper, lower, middle, or pond bottom). NMS does not make assumptions about underlying species response models and is therefore an effective ordination method for ecological community data (McCune and Mefford, 1999). Species occurring in less than 5% of pots were deleted prior to NMS ordination and standard step-down procedures were used to find the number of axes sufficient to reduce stress. We performed an NMS ordination of 50 runs with a stability criterion of 0.00001 and a maximum of 200 iterations on a Bray-Curtis dissimilarity matrix of species abundances in PC-ORD 5.0 (McCune and Mefford, 1999).

We performed indicator species analyses (Dufrene and Legendre, 1997) to examine the relationships of each species to hydrologic class, location, and pond-shore zone in PC-ORD 5.0. Indicator values quantify the exclusiveness and faithfulness of species to a particular group or class and are used to represent the power of a species to indicate environmental conditions. Indicator values range from 0 (no indication) to 100 (perfect indication). Indicator values were tested for statistical significance using a Monte Carlo test with 1000 randomizations.

3. Results

3.1 Seedling diversity and community composition

We identified 8089 individuals from 45 plant species from sediments in the nine ponds (Table 1). The total number of species per pond ranged from 13 in Sinnott Pond to 21 in Little Israel and Duarte Ponds (Table 2). Coastal plain pond-shore species made up 43 to 80% of species and widespread ruderal species made up 19 to 50% (Table 2). Woody species and submersed aquatic species occurred at low frequencies and each made up 10% or less of species in each pond. Native species dominated pond seed banks and made up 89 to 100% of species in all ponds. Only four introduced species were found. Four individuals of mouseear cress (*Arabidopsis thaliana*) occurred in one sample from Duarte Pond, four individuals of curly dock (*Rumex crispus*) occurred in two samples in Google Pond, two individuals of common purselane

(*Portulaca oleracea*) occurred in one sample from Google Pond, and one individual of germander speedwell (*Veronica chamaedrys*) occurred in one sample from Little Israel Pond. Non native species made up 0.1% of all individuals identified.

Three species listed as “special concern” on the Massachusetts List of Endangered, Threatened and Special Concern Species were encountered. Wright’s panic-grass (*Dichanthelium wrightianum*), Philadelphia panic-grass (*Panicum philadelphicum*) and Plymouth gentian (*Sabatia kennedyana)* occurred in the Hyannis ponds. Only *P. philadelphicum* (from 3 samples in Little Israel Pond) and *S. kennedyana* (from 1 sample each in Mary Dunn and Israel Ponds) occurred in more than one sample.

Permanent and ephemeral ponds had very similar numbers of total species encountered (34 species in permanent ponds, 33 species in ephemeral ponds) and few differences in the total number of species in different life history groups, native or introduced species, or MA-listed species (Table 2).

There were also no differences in the number of total species or life history groups between Hyannis and Martha’s Vineyard ponds (Table 2), but the Hyannis ponds had a greater number of MA-listed species (3 listed species, 0.6 ± 0.4 listed species pond^{-1}) compared with no listed species in the Martha’s Vineyard ponds.

Estimated species richness in the sediment seed banks of all ponds was 60 species (Table 2). Permanent ponds had slightly greater estimated species richness than ephemeral ponds (42 v. 38 species) (Table 2). Martha’s Vineyard ponds had higher estimated species richness than Hyannis ponds (44 v. 37 species) (Table 2). Little Israel, Mary Dunn and Duarte Ponds had the highest estimated species richness (Table 2). Little Israel and Mary Dunn Ponds had the highest number of rare species and the greatest likelihood of additional unsampled species in the sediment seed bank. No single pond captured as much as half of the total species richness estimated for all ponds. Species composition of ephemeral and permanent and Hyannis and Martha's Vineyard ponds was generally similar. Permanent and ephemeral ponds shared 22 species and had a Chao's Sorensen Index of 0.797. Ponds from Hyannis and Martha's Vineyard shared 21 species and had a Chao's Sorensen Index of 0.767.

Individual ponds varied greatly in the number of shared species and in their similarity (Table 3). For example, Mary Dunn Pond shared 12 to 13 species with Israel, Lamson and Little Israel Ponds in the same Hyannis Ponds complex, but also shared 13 species with Old House Pond and 14 species with Duarte Pond on Martha's Vineyard. Google Pond was the least similar to other ponds.

The NMS indicated that there was wide overlap in seed bank composition among ponds within permanent and ephemeral hydrologic classes and ponds from Hyannis and Martha's Vineyard. Ephemeral ponds had slightly higher scores and permanent ponds had somewhat lower scores on Axis 2 (Fig. 2A). Hyannis ponds had generally higher scores and Martha's Vineyard ponds had generally lower scores on Axis 1 (Fig. 2B). Distinct compositional patterns among zones of the pond-shore were not visible in the NMS ordination (Fig. 2C). Samples from the same ponds produced similar patterns in species composition and were located close together in ordination space compared with samples from ponds in different hydrologic classes or geographic regions (Fig. 2D).

The three calculated NMS axes were independent of one another, and cumulatively explained 51.3% of the total variation in seed bank composition. Axis 1 explained 12.4% of variation, and was most highly weighted by the abundance of needle spikerush (*Eleocharis acicularis*), Canada toadflax (*Linaria canadensis*) and bog white violet (*Viola lanceolata*). Axis 2 explained 18.1%

of variation, and was most highly weighted by the abundance of marsh cudweed (*Gnaphalium uliginosum*), lesser Canadian St. Johnswort (*Hypericum canadense*), woodland rush (*Juncus subcaudatus*), marsh seedbox (*Ludwigia palustris*), fall panic-grass (*Panicum dichotomiflorum*). Axis 3 explained 20.8% of variation, and was most high weighted by the abundance of bentgrass (*Agrostis hyemalis var. hyemalis*) and brownfruit rush (*Juncus pelocarpus*).

NMS conducted on the composite species composition of each pond showed that permanent and ephemeral ponds formed two distinct groups but with a wide range of composition within groups (Fig. 3). Ephemeral ponds all had low scores on Axis 1 and permanent ponds all had low scores on Axis 2. Axis 1 scores were most influenced by sweet pepperbush (*Clethra alnifolia*), dwarf St. Johnswort (*Hypericum mutilum*), clasping water horehound (*Lycopus amplectens*), low water milfoil (*Myriophyllum humile*) and *J. pelocarpus*. Axis 2 scores were most highly weighted by *A. hyemalis* var *hyemalis*, devil's beggartick (*Bidens frondosa), G. uliginosum, J. subcaudatus,* marshpepper knotweed (*Polygonum hydropiper*), marsh smartweed (*Polygonum hydropiperoides*), little hogweed (*Portulaca oleracea*) and curly dock (*Rumex cripsus).* Google Pond was the most different from the other ponds because it contained high abundance of *A. hyemalis* var. *hyemalis, G. uliginosum and J. subcaudatus*.

Indicator species analysis demonstrated that the relative abundance and frequency of individual species in particular groups indicated particular hydrologic class, geographic location and pond-shore zone. For location, 12 species were indicators of Martha's Vineyard, while four species were indicators of Hyannis (Table 4). For hydrologic class, 11 species were indicators of ephemeral ponds while six species were indicators of permanent ponds (Table 4). Fewer species were indicators of pond-shore zone, with only three species indicating the shrub zone, one species indicating the lower zone, one species indicating the middle zone, and two species indicating the pond bottom (Table 4). *J. pelocarpus* had the highest significant indicator value, indicating permanent hydrology with high levels of exclusivity and fidelity.

3.2 Effects of elevation and sediment characteristics

The total number of species encountered in permanent ponds declined with decreasing shoreline elevation from a high of 28 species in the shrub zone to 18 in the pond bottom (Fig. 4A). This pattern was caused predominantly by a greater number of ruderal species in the shrub zone of the permanent ponds (Fig. 4B). The total number of species encountered in ephemeral ponds varied from 22 to 23 and changed little with depth (Fig. 4A). More total species were encountered at mid, lower and pond-bottom depths in ephemeral ponds (Fig. 4A). The number of coastal plain pond-shore species in permanent ponds changed little with depth (Fig. 4B). The number of coastal plain pond-shore species in ephemeral ponds generally increased with decreasing elevation (Fig. 4B) and was similar to the number in permanent ponds at mid, low and pond-bottom elevations. Permanent ponds had the highest number of ruderal species in the shrub zone (Fig. 4B). Ephemeral ponds had more ruderal species along the middle pond-shore elevations (Fig. 4B).

The mean number of species per sediment sample declined with decreasing elevation in permanent ponds but was generally similar across elevation zones in ephemeral ponds (Fig. 4C). The number of species per sample reflected the pattern of total number of species. Ephemeral pond bottoms had a higher number of species per sample than permanent pond bottoms. Permanent and ephemeral ponds differed little in the mean number of coastal plain pond-shore species per sample, but ephemeral ponds generally had more ruderal species.

The mean total number of individuals per m^2 of pond-shore in permanent ponds ranged from 3080 to 7370 but showed no clear pattern with elevation zone (Fig 5A). The total number of individuals per m^2 of pond-shore in ephemeral ponds ranged from 2050 to 8850 in and generally increased at lower pond-shore elevations (Fig. 5A). Coastal plain pond-shore species dominated the total number of individuals in both permanent and ephemeral ponds (Fig. 5B). The mean number of individuals of ruderal species was greater in ephemeral ponds (1000 to 2490 m^{-2}) than in permanent ponds (270 to 870 m^{-2}). In permanent ponds, the number of coastal plain pond-shore species varied with elevation while in ephemeral ponds the number of coastal plain pond-shore species increased at lower shoreline elevations (Fig. 5B). In both permanent and ephemeral ponds, the highest mean number of ruderal individuals occurred in the pond bottom (Fig. 5B).

Organic matter in both permanent and ephemeral ponds was high in the upper elevation shrub zone, low in the mid-shoreline and increased again at the lowest elevation (Fig. 6A). Sediment percent organic matter in the upper shoreline of permanent ponds was very low (Fig. 6A). Sediment extractable ammonium in permanent ponds was uniformly low in shoreline elevations but higher in the permanently-flooded pond bottom (Fig. 6B). Extractable ammonium in ephemeral ponds was higher in the uppermost shoreline elevations (Fig. 6B). Extractable nitrate was very low, much lower than extractable ammonium, and uniformly low in both permanent and ephemeral ponds except for high values in ephemeral pond-bottoms (Fig. 6C). Extractable phosphate was generally low but greater in ephemeral ponds in all but the lower-mid shoreline (Fig. 6D). Mean sediment percent organic matter and mean extractable ammonium, nitrate and phosphate were significantly higher in ephemeral ponds than in permanent ponds (Table 5).

Total species number per sample was also significantly related to sediment total extractable inorganic N ($F=25.3$, $p<0.0001$), extractable ammonium ($F=25.4$, $p<0.0001$) and percent organic matter ($F=27.0$, $p<0.0001$). Species number was not related to extractable nitrate or phosphate. The total number of individuals per sample was also related to sediment total extractable N

(F=13.9, p<0.0002) and to extractable ammonium (F=13.9, p<0.0001), extractable nitrate (F=81.1, p<0.0001) and percent organic matter (F=8.4, p<0.0001). Overall, however, sediment characteristics explained less than 10% of the variation in number of species or number of individuals.

4. Discussion

4.1 Seed bank and sediment composition

Sediments from coastal plain pond shorelines contained diverse and abundant viable seeds. The abundance of pond-shore species (species that are largely restricted to coastal plain pond shores in their distribution) was greater than the abundance of more widespread ruderal species that occur over much wider portions of the coastal plain landscape. In addition, the number of species and abundance of seeds in seed banks were overwhelmingly dominated by native species. This confirms the vital role that buried seeds play in the maintenance of native species-rich coastal plain pond-shore plant communities (Sorrie, 1994; Schneider, 1994). Pond shorelines retained a very high preponderance of native species even though they experience high physical disturbance and ponds are located within a landscape that is now highly fragmented by residential development. Schneider (1994) also found very low occurrence of non-native species in Long Island, NY coastal plain ponds in a similar suburbanizing region. The very low occurrence of non-native species precluded any analysis of controls on their presence.

The low occurrence and abundance of viable seeds of shrubs was unexpected given the abundance of shrubs upgradient of pond shorelines. Shrub recruitment to coastal plain pond-shores may occur by vegetative reproduction from the upland pond-shore edge or by occasional rain of short-lived seeds of tree or shrub species (Craine and Orians, 2004). It is also possible that the moist soil conditions provided in the growth chambers were inappropriate for most shrub species. However, we feel this was unlikely because most native shrubs of the pond-shore zone have relatively generalized germination requirements (Cullina, 2002).

The presence of *Myriophyllum humile* as the only submersed aquatic species that occurred in any numbers in the seed bank suggested that vegetative reproduction may be the dominant mode of response of submersed aquatic species to fluctuating water levels or that moist but not flooded conditions provided in the growth chamber were not suitable for germination of submersed aquatic species. Schneider (1994) lists only one species, eastern purple bladderwort (*Utricularia purpurea*) that germinated only in standing water. Because we did not test seed germination under different environmental conditions, our results are almost undoubtedly an underestimate of the total abundance of viable seeds.

The differences in overall community composition and species richness between permanent and ephemeral ponds and between Hyannis and Martha’s Vineyard ponds were relatively small. Ephemeral ponds had higher overall abundance of ruderal species, presumably caused by more frequent drawdown of the entire pond. Ephemeral ponds also did not exhibit the drop in species richness at the lowest pond-shore elevation zone that occurred in permanent ponds. While the permanently-flooded pond-bottom zone in permanent ponds never provided conditions favorable for seed germination of species requiring moist but not flooded conditions, the occasional drying of the entire pond-bottom of ephemeral ponds would allow seed germination and regular replenishment of the seed bank of ephemeral ponds with these species. Seed bank composition was more similar within permanent ponds and within ephemeral ponds than it was within Hyannis or Martha’s Vineyard ponds. This suggests that hydrologic conditions were a greater determinant of seed bank (and likely overall plant community) composition than geographic proximity.

Lower nutrient levels in permanent ponds were most likely related to the generally sandy substrates that typically characterize the shrub and mid shoreline zones of permanent ponds. This is typical of the highest quality pond-shores in regions where coastal plain ponds occur (Wisheu and Keddy, 1989). Higher extractable nitrate in ephemeral ponds was likely associated with high rates of nitrification that can occur during late-summer drawdowns in seasonally flooded soils (Neill 1995). We found no evidence that sediment organic matter or nutrient content were important controls of species richness or abundance. Higher nitrogen and organic matter content of pond-bottom sediments were associated with lower species richness and abundance, but pattern was undoubtedly also influenced by the permanent flooding of permanent pond bottoms.

Several species that were present as adult plants in the shoreline flora of the Hyannis ponds were notable for their absence from the seed bank. These included bluejoint (*Calamagrostis canadensis*), purple false foxglove (*Agalinis purpurea*), drumheads (*Polygala cruciata*) and sundews (*Drosera filiformis*, *D. intermedia*). In addition, a number of rare species present as adult plants in Hyannis ponds were not captured in the seed bank samples. While the composition of the seed bank provides information on the potential vegetation that will develop after the disturbance of water level drawdown, a better understanding of the seed longevity and germination requirements of many species is required to be able to predict the composition of the standing shoreline vegetation from seed bank samples. Because of their limited spatial distribution, the rarest species are difficult to capture with sampling of small areas of pond sediments typically done for seed bank samples. Estimated species richness based on incidence-based cover estimators provide reasonable indications of in which ponds seeds of these species are most likely to occur.

We did not stratify seeds before planting samples directly into experimental pots. This may have resulted in an underestimation of the number germinable seeds if seeds produced in the year of collection had not yet overwintered. This bias is likely to be small because: (1) most coastal plain pond-shore species flower and set seed after the August collection date and few seeds produced during the current growing season would have been missed, and (2) seeds remain viable for many years and seeds produced during the current growing season make up a small fraction of total viable seeds. The flowering dates and duration of seed viability in seed banks have not been determined for the vast majority of species found on coastal plain pond shorelines. We conducted our germination trials using moist but not flooded soils. This likely captured the vast majority of species that germinate on exposed substrates or in either flooded or nonflooded conditions (Schneider, 1994). Our potting medium was a mixture of sand and organic rich potting soil. In a test of the effect of growth medium on seed germination in similar coastal plain ponds, decreasing organic matter content increased the density of olive spike-sedge (*Eleocharis olivacea*) and quagmire yellow-eyed grass (*Xyris smalliana*) but had little overall effects on seed germination (Schneider, 1994).

4.2 Conservation implications of seed banks

Our results have several implications for conservation and management of coastal plain pond shoreline plant communities. First, ephemeral and permanent ponds had roughly equal value as reservoirs of seeds of the typical coastal plain pond-shore plant species that comprise what is regarded for management purposes (Swain and Kearsley, 2001) as a shoreline plant community of high regional conservation concern. Second, geographic proximity did not clearly correspond to floristic similarity. For example, while adjacent permanent ponds Lamson and Israel had similar floras, geographically distant Mary Dunn and Old House Ponds were also similar. Third, one hydrological class captured 73-76% of total species and one geographical region captured 69-78% of the total species recovered from the entire suite of seed bank samples. These results suggest that conservation efforts designed to protect pond shorelines to maximize the diversity of coastal plain pond plants contained in pond sediment seed banks should be implemented across pond hydrologic classes and across a wide geographic area. Because ephemeral ponds do not contain all shoreline habitats particularly during dry years when the entire pond is dry and often low in diversity of adult plants, ephemeral ponds (such as Little Israel Pond) can be overlooked as reservoirs of high seed diversity. Past strategies to protect clusters of ponds have been effective because members of pond clusters tend to contain large and small ponds with a range of hydrologic regimes. Our findings also suggest that protection of even single ponds that are relatively distant from other clusters of coastal plain ponds (such as Google Pond) has value for increasing the richness of plants contained in pond-shore seed banks at the regional scale.

Because water level fluctuations play a dominant role in shaping the coastal plain pond-shore plant community, alterations to the pattern of ground-water level fluctuation or levels will ultimately influence plant community composition and richness. Pumping of ground-water for municipal use can lower water levels and reduce the occurrence of the high water levels needed to prevent shrub encroachment to the pond-shore (Craine and Orians, 2004; McHorney and Neill, 2007). Climate change in the northeastern US is projected to cause higher annual precipitation but higher precipitation variability and greater incidence of short-term drought (NECIA 2006). Our results indicate that changes to water level regimes will not result in expansion of non-native species from sediment seed banks because few non-native seeds were present. In ephemeral ponds, our results suggest that changes to the zone of water level fluctuation will have little immediate effect on species composition or richness because seeds are relatively evenly distributed along pond shorelines. However, because the entire pond area of shallow ephemeral ponds now functions as shoreline habitat, changes that shift water level fluctuations to lower on the ponds shoreline would quickly reduce the area of pond-shore habitat or eliminate it completely if water levels dropped below the level of the pond bottom.

In permanent ponds, changes that shift water level fluctuations to lower on the pond shoreline would cause an immediate reduction in seed germination during drawdown years because seed density and diversity were lower in the highly organic sediments that dominate the current permanently-flooded pond-bottom zone. The longer-term implications of such shifts in shoreline zones are not clear. It seems unlikely that climate changes will be severe enough to eliminate many permanent ponds completely. Because the sediments of coastal plain pond-shores within the dominant zone of water level fluctuation tend to be sandy and low in organic matter, it is likely that this zone would re-develop over time at a lower elevation. It is unclear whether this change would occur over time scales that would prevent species losses caused by a reduction in suitable shoreline habitat.

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Figure Captions

Fig. 1 Location of coastal plain ponds in Hyannis (A) and Martha's Vineyard (B). Permanent ponds (P) have surface water in all years. Ephemeral ponds (E) have surface water in many years but dry completely approximately every 3 to 10 years.

Fig. 2. Non-metric multiple dimensional scaling of seed bank composition in nine coastal plain ponds. Samples were classified according to (A) hydrology. (B) location, (C) shoreline zone, or (D) pond. Symbols are: S=Sinnott Pond, MD=Mary Dunn Pond, I=Israel Pond, L=Lamson Pond, LI=Little Israel Pond, G=Google Pond, OH=Old House Pond, R=Rainwater Pond, D=Duarte Pond.

Fig. 3. Non-metric multiple dimensional scaling of seed bank composition based on the composite composition of each pond.

Fig. 4. Distribution of total species encountered along a gradient of shoreline elevation. (A) is the total number of all species sampled at each elevation in permanent and ephemeral ponds. (B) is the total number of coastal plain pond-shore and ruderal species sampled at each elevation in permanent (filled symbol) and ephemeral (open symbol) ponds, (C) is the mean number of species encountered per sample in each shoreline zone, (D) is the mean number of coastal plain pond-shore and ruderal species encountered per sample in permanent (filled symbol) and ephemeral (open symbol) ponds. Errors are ± standard error.

Fig. 5. Mean number of individuals of (A) all species m^{-2} and (B) mean number of pond-shore and ruderal species m^{-2} in permanent and ephemeral coastal plain ponds. Filled symbols are permanent ponds, open symbols are ephemeral ponds. Errors are ± standard error.

Fig. 6. Distribution of (A) organic matter, (B) extractable ammonium, (C) extractable nitrate and (D) extractable phosphate along a gradient of shoreline elevation in coastal plain ponds.

Filled symbols are permanent ponds, open symbols are ephemeral ponds. Errors are ± standard error.

Table 1 - The percent frequency of occurrence of species recovered from the seed banks of permanent and ephemeral coastal plain ponds. Species were classified as pond-shore obligates (P), widespread ruderals (R), woody (W), or submersed aquatic (S) based on their life history characteristics and whether they are largely restricted to coastal plain pond-shores. Introduced species are noted with an (*). Species status on MA Endangered Species List, Watch List (WL) or Special Concern (SC) is noted. Species rank is overall rank in abundance and frequency. Number in parenthesis below each pond is number of samples collected.

				Permanent					Ephemeral			
Species	Life history class	Species rank Abund	Freq	Israel (40)	Lamson (40)	Mary Dunn (40)	Duarte (32)	Old House (32)	Little Israel (32)	Sinnott (32)	Google (32)	Rain-water (32)
Agrostis hyemalis var. *hyemalis*	R	4	3	28	18	23	41	13	94	41	47	9
Agrostis stolonifera	P	35	35						3			
Arabidopsis thaliana *	R	31	35				3					
Bidens frondosa	R	27	32								6	
Clethra alnifolia	W	31	29	3			6					
Coreopsis rosea	P	13	9	45	5	8		41	3			19
Cyperus dentatus	P	12	6	35	13	20	19	16	25	13		53

Dichanthelium wrightianum (SC)	P	35	35						3			
Eleocharis acicularis	P	6	17	3		30		44				
Eleocharis obtuse	P	25	27									13
Eupatorium rotundifolium	R	35	35					3				
Euthamia graminifolia	R	14	10	10			6	19	16	13	3	63
Fimbristylis autumnalis	P	21	22					50				
Gnaphalium uliginosum	R	7	15				3				97	
Gratiola aurea	P	9	5		13	45	28	22	34	9	9	59
Hemicarpha micrantha	P	41	35					3				
Hypericum canadense	P	3	1	83	65	18	84	81	56	50	22	53
Hypericum mutilum	P	18	11	15	5	20	44	6		9	3	16
Juncus canadensis	P	17	22	3	5	3		6	9	25		
Juncus pelocarpus	P	1	2	90	70	28	91	41	3	9		9
Juncus subcaudatus	P	5	13					9			81	16
Linaria canadensis	R	10	7			23	38	31	3		63	

Lindernia dubia var. anagallidea	P	14	12	10	5	8	31		3		41	6
Ludwigia palustris	P	2	18								78	
Lycopus amplectens	P	30	27			3	9					
Myriophyllum humile	S	18	16			23	13	44				3
Oenothera biennis	R	41	35				3					
Panicum dichotomiflorum	R	11	8		3	5	22	3	16		53	53
Panicum philadelphicum (SC)	P	27	29						9			
Panicum verrucosum	P	16	14	10	8	3	9	6	28	9		16
Polygonum hydropiper	P	29	26			3	6		3		6	
Polygonum hydropiperoides	P	41	35								3	
*Portulaca oleracea **	R	35	35								3	
Potentilla canadensis	R	35	35				6					
Proserpinaca palustris	S	24	24						28			
Rhexia virginica	P	23	20	10	18					13		25

Rhynchospora capitellata	P	20	21		5				19	31		
Rumex crispus *	R	31	29								9	
Sabatia kennedyana (SC)	P	35	32	3		3						
Scleria reticularis	P	34	32		5							
Spiraea tomentosa	W	22	19				31		13		31	
Stachys hyssopifolia	P	41	35			3						
Triadenum virginicum	P	26	25	8						16		
Veronica chamaedrys *	R	41	35						3			
Viola lanceolata	R	8	4	55	15	13	19		75	53	19	44

Table 2 - Summary of the total number of species and total number of coastal plain pond-shore species, widespread ruderal species, woody shrubs and trees, native species, introduced species and MA State listed species recorded from seed banks of permanent and ephemeral southeastern MA coastal plain ponds. Estimated species richness was calculated by the incidence-based cover estimator (ICE) for individual ponds or permanent and ephemeral ponds. Errors are ± standard error.

Hydrologic class	Pond	Observed species richness	Estimated species richness	Coastal plain pond-shore	Widespread ruderal	Woody shrub/tree	Submersed aquatic	Native	Introduced	MA listed
All ponds		45	60	26	15	2	2	41	4	3
Permanent	Israel	16	19	12	3	1	0	16	0	1
	Lamson	15	15	12	3	0	0	15	0	0
	Mary Dunn	19	24	14	4	0	1	19	0	1
	Duarte	21	24	9	9	2	1	20	1	0
	Old House	18	20	12	5	0	1	18	0	0
	Total	34	42	21	10	2	1	33	1	3
	Mean no. pond^{-1}	17.8 ± 1.1	20.4 ± 1.7	11.8 ± 0.8	4.8 ± 1.1	0.6 ± 0.4	0.6 ± 0.2	17.6 ± 0.9	0.2 ± 0.2	0.4 ± 0.2
Ephemeral	Little Israel	21	30	12	7	1	1	20	1	2

	Sinnott	13	13	10	3	0	0	13	0	0
	Google	18	22	8	9	1	0	16	2	0
	Rainwater	16	16	11	4	0	1	16	0	0
	Total	33	38	19	11	1	2	30	3	2
	Mean no. pond^{--1}	17.0 ± 1.7	20.3 ± 3.8	10.3 ± 0.9	5.8 ± 1.4	0.5 ± 0.3	0.5 ± 0.3	16.3 ± 1.4	0.8 ± 0.5	0.2 ± 0.2
Hyannis	*Total*	31	37	20	7	2	2	30	1	3
	Mean no. pond^{-1}	16.8 ± 1.4		12.0 ± 0.6	4.0 ± 0.8	0.4 ± 0.2	0.4 ± 0.2	16.6 ± 1.3	0.2 ± 0.2	0.6 ± 0.4
Martha's Vineyard	*Total*	35	44	19	13	2	1	32	3	0
	Mean no. pond^{-1}	18.3 ± 1.0		10.0 ± 0.9	6.8 ± 1.3	0.8 ± 0.5	0.8 ± 0.3	17.5 ± 0.8	0.8 ± 0.5	0 ± 0

Table 3 - Shared number of species and Chao’s abundance-based Sorensen similarity index (shaded) among all ponds.

	Sinnott	Mary Dunn	Israel	Lamson	Little Israel	Google	Old House	Rainwater	Duarte
Sinnott		8	10	10	9	7	9	10	8
Mary Dunn	0.572		12	12	13	9	13	12	14
Israel	0.711	0.799		11	10	6	10	11	10
Lamson	0.677	0.736	0.967		12	7	10	12	10
Little Israel	0.898	0.770	0.887	0.961		10	11	11	13
Google	0.317	0.215	0.112	0.176	0.273		8	9	12
Old House	0.408	0.926	0.887	0.501	0.581	0.335		12	11
Rainwater	0.748	0.765	0.112	0.930	0.892	0.398	0.582		12
Duarte	0.223	0.858	0.787	0.951	0.947	0.250	0.633	0.922	

Table 4 - Indicator values (IV) for hydrologic class (ephemeral or permanent), location (Hyannis or Martha’s Vineyard) and shoreline zone. Indicator values range from 0 (no indication) to 100 (perfect indication).

	Location			Hydrologic class			Shoreline zone		
Species	Group	IV	p <	Group	IV	p <	Group	IV	p <
Agrostis hyemalis	Hyannis	27.6	0.006	Ephemeral	40.5	0.001	Shrub	19.4	0.017
Coreopsis rosea	---	---	---	Permanent	16.0	0.001	Middle	14.2	0.008
Cyperus dentatus	---	---	---	---	---	---	---	---	---
Eleocharis acicularis	Vineyard	9.7	0.030	Permanent	15.3	0.001	---	---	---
Euthamia graminifolia	Vineyard	18.5	0.001	Ephemeral	21.2	0.001	---	---	---
Fimbristylis autumnalis	Vineyard	12.8	0.001	Permanent	9.0	0.002	Lower	7.2	0.047
Gnaphalium uliginosum	Vineyard	23.2	0.001	Ephemeral	22.9	0.001	---	---	---
Gratiola aurea	Vineyard	22.2	0.008	Ephemeral	22.6	0.011	---	---	---
Hypericum canadense	---	---	---	Permanent	41.1	0.001	---	---	---
Hypericum mutilum	---	---	---	---	---	---	---	---	---
Juncus canadensis	Hyannis	7.6	0.010	Ephemeral	7.5	0.014	---	---	---

Juncus pelocarpus	---	---	---	Permanent	62.2	0.001	---	---	---
Juncus subcaudatus	Vineyard	27.2	0.001	Ephemeral	24.7	0.001	---	---	---
Linaria canadensis	Vineyard	29.8	0.001	---	---	---	Shrub	22.1	0.001
Lindernia dubia	Vineyard	16.7	0.001	---	---	---	---	---	---
Ludwigia palustris	Vineyard	20.0	0.001	Ephemeral	20.5	0.001	---	---	---
Myriophyllum humile	Vineyard	10.4	0.011	Permanent	14.9	0.001	---	---	---
Panicum dichotomiflorum	Vineyard	28.9	0.001	Ephemeral	27.3	0.001	Underwater	28.9	0.001
Panicum verrucosum	---	---	---	Ephemeral	11.5	0.014	---	---	---
Rhexia virginica	---	---	---	---	---	---	---	---	---
Rhynchospora capitellata	Hyannis	10.3	0.002	Ephemeral	12.7	0.001	Underwater	11.6	0.004
Spiraea tomentosa	Vineyard	14.7	0.001	---	---	---	Shrub	10.8	0.016
Viola lanceolata	Hyannis	30.6	0.001	Ephemeral	39.6	0.001	---	---	---

Table 5 - Mean sediment characteristics in permanent and ephemeral ponds. Errors are ± standard error.

	Permanent (n=184)	Ephemeral (n=128)	F	p<
Organic matter (%)	12.1 ± 1.5	34.7 ± 2.7	64.14	0.0001
Extractable ammonium (µg N/g dry soil)	14.4 ± 2.1	25.8 ± 3.5	8.72	0.0034
Extractable nitrate (µg N/g dry soil)	0.03 ± 0.01	0.27 ± 0.08	12.24	0.0005
Extractable phosphate (µg P/g dry soil)	0.30 ± 0.07	0.90 ± 0.14	17.80	0.0001