Trajectories of plant communities in Massachusetts, U.S.A. cranberry farms discontinued from agriculture

Christopher Neill (cneill@woodwellclimate.org)
Woodwell Climate Research Center
Anastasia Pulak
Woodwell Climate Research Center
Haley Miller
Woodwell Climate Research Center
Benjamin Hoekstra
Woodwell Climate Research Center
Sarah Klionsky
University of Connecticut

Research Article

Keywords:

Posted Date: September 7th, 2022

DOI: https://doi.org/10.21203/rs.3.rs-1995062/v1

Christopher Neill[1], Anastasia Pulak[1], H. Miller[1,2], B. Hoekstra[3,4] and S. Klionsky[5]

Trajectories of plant communities in Massachusetts, U.S.A. cranberry farms discontinued from agriculture

1. Woodwell Climate Research Center, Falmouth, MA, USA

2. Clemson University, Clemson, SC, USA

3. University of Massachusetts Cranberry Experiment Station, East Wareham, MA, USA

4. Current address: 6962 N. Sheridan Rd, Chicago, IL

5. University of Connecticut, Storrs, CT, USA

Corresponding Author: cneill@woodwellclimate.org

Abstract Retirement of cultivated croplands creates potential for ecosystem and wetland restoration, but vegetation and soil legacies of cropping influence the development of post-agriculture vegetation. In low-lying coastal watersheds of southeastern Massachusetts, cranberries (*Vaccinium macrocarpon* Aiton) are cultivated in commercial "bogs" largely on diked, leveled and sanded bog beds created from historic wetlands. Current low cranberry prices and expanding cranberry production elsewhere now increase the likelihood of cranberry farmland retirement. We quantified the trajectories of plant species richness and cover, and plant characteristics (life form, native or non-native, wetland or non-wetland) in a chronosequence of cranberry bog beds that spanned from cultivated bog beds to those retired from cropping and revegetated for 90 years with no post-cropping management. Species richness increased from active bog beds to 10-20 year-old bog beds and subsequently decreased. Post-retirement species richness was overwhelmingly dominated by native species. Shrub and tree richness and cover increased steadily over time. The richness of wetland, upland and facultative species all increased quickly after retirement and then declined in the oldest retired bog beds. The basal area and canopy cover of red maple (*Acer rubrum*) and pitch pine (*Pinus rigida*) increased over time. Vegetation followed a relatively predictable succession trajectory and the plant community after five to nine decades was predominantly forested and dominated by non-wetland plants. Encouragement of long-term persistence of greater diversity and cover of wetland plant species on retired cranberry farms will likely require active hydrological and soil modifications that decrease sand depth and raise water tables.

Introduction

Cessation of crop cultivation on agricultural lands initiates changes to the succession and composition of vegetation that develop over many decades. These changes are often initiated by shifts in farming practices caused by human migration, industrialization, expanded trade or increased opportunities for crop specialization. For example, expansion of rail and barge transportation from the Midwest to the Northeast U.S. in the middle of the 19th century contributed to the widespread abandonment of farmland and subsequent regrowth of forest (Whitney 1994). More recent contractions of farmland have resulted in expansion of forests in Europe, Central and South America, the Caribbean and other locations (Keenan et al. 2015; Chazdon et al. 2000; Grau et al. 2000). Future retirement of farmlands presents opportunities for restoration of historic or targeted plant communities.

In many locations, the unmanaged reestablishment and succession of vegetation results in plant communities that resemble those in the original vegetation (Foster 1992). In other cases, a history of agricultural use results in the establishment of vegetation that differs from pre-agricultural vegetation (Motzkin et al. 1996; Foster et al. 2003; Cramer et al. 2008). In some cases full recovery of species richness takes many decades or centuries (Dupouey et al. 2002; Rozendaal et al. 2019). Differences in trajectory are caused by changes to soils that create conditions unfavorable to original native plant species (Huennecke et al. 1990; Kulmatiski et al. 2006), changes to the water table and hydrology (Leppa et al. 2020), introduction of new and often non-native plants (Brown and Boutin 2009; Kuhman et al. 2011) or barriers to plant recruitment (Bellemare et al. 2002). In some cases, even subtle legacies, such as increases in soil pH, continue to influence plant communities after agricultural activity has ceased (Neill et al.

2007). Understanding the effects of agricultural legacies could help land managers enhance desired vegetation or restoration outcomes on former agricultural lands.

The native North American fruit, large cranberry (*Vaccinium macrocarpon* Aiton), is the most valuable agricultural food crop in Massachusetts. Cultivated cranberries are a native Ericaceous shrub that requires sandy soils, low soil pH, and relatively low rates of nitrogen (N) fertilization compared with other crops (CCCCGA 2021). Beginning in the late 1800s, growers developed commercial cranberry farms largely on former peat wetlands located near streams and ponds. Farmers use these water supplies to flood individually-diked, cultivated beds ("bogs") as part of the typical annual crop management cycle (Thomas 1990). Although the vegetation from which most individual commercial bogs were created is not known precisely, former wetlands likely were a combination of the Red Maple (*Acer rubrum*) swamps (Golet et al. 1983) and Atlantic White Cedar (*Chamaecyparis thyoides*) swamps (Laderman 1989) that are still common in the region. Creation of commercial bogs from wetlands typically involved leveling, establishing perimeter and interior ditches, installing structures to manage water flow, retaining underlying peat to impede drainage, and applying 2-5 cm of sand every 2-5 years to reduce pests and encourage growth of new fruit-bearing vines (Sandler 2010).

The total area of cranberry cultivation in Massachusetts has remained relatively stable at about 5,000-6,000 ha since 1960 and the total production rate of about 2 million barrels/yr has changed little since 1980 (USDA 2020). During the same time, the cultivated area of cranberries in Wisconsin (the other main U.S. cranberry-growing region) has increased from 2,000 to more than 8,000 ha, and production has increased from 700,000 to more than 5 million barrels/yr. A recent report on the Massachusetts cranberry industry concluded that its future will be enhanced by intensifying some of the currently-cultivated area by renovating existing beds with better

water control and planting high-yielding cranberry cultivars while simultaneously retiring less profitable or more environmentally-sensitive areas (MA DAR 2016). The report encouraged development of "green exit strategies" to provide farmers with mechanisms to retire portions of existing croplands. A recent analysis concluded that about 30% of the cultivated areas of cranberry farms have been modernized; 20% are prime candidates for retirement because they are environmentally sensitive, hard to manage, or unlikely to modernize; and approximately 50% are candidates for either modernization or retirement (Hoekstra et al. 2020).

Because cranberry farms originated as natural wetlands and occur in low-lying areas near streams and ponds, future retirements are potentially important opportunities to restore the approximately 20% of wetlands in Southeastern Massachusetts that formerly were converted to cranberry farms (Tiner and Zinni 1988). Restored wetlands can provide wildlife habitats, opportunities for recreation and other ecosystem services including carbon (C) storage in vegetation and soils and improved water quality (Mitsch et al. 2015). However, it is not clear that passive revegetation alone will result in recolonization by wetland vegetation and produce desired ecosystem functions. Observations of recently-retired farms suggest that drainage ditches and years of sanding create conditions that favor plant species such as pitch pine (*Pinus rigida*) that are widespread in surrounding well-drained uplands (Noyce 2007). Previous studies also indicate that soil organic matter stocks and indicators of biogeochemical cycling even in intentionally restored wetlands on former cranberry farms more closely resemble conditions in active bogs than those in comparable natural wetlands even after many years (Ballantine et al. 2017). There are also concerns that retired farms could become locations for colonization and spread of non-native or invasive species, although vegetation in retired cranberry farms in New

Jersey indicated that non-native species are not large components of post-retirement plant communities (Klee et al. 2019).

Understanding the trajectories of plant communities in retired cranberry bogs that are left to revegetate with little or no management intervention is important because farm retirements currently outpace the availability of personnel and funding for active restoration projects. Recently-developed restoration strategies aim to lessen the effects of agricultural legacies by filling bog ditches to restore wetland hydrology, removing sand layers to expose underlying peat, and relying on buried seed banks to restore native wetland plants (Living Observatory 2020). Understanding how plant communities are likely to develop in the absence of active restoration strategies can help stakeholders prioritize where investments in restoration will provide the greatest benefits.

We quantified plant communities in a chronosequence of 23 active and retired cranberry bogs that ranged in age from currently-farmed to bogs retired for 90 years. At each bog we quantified the presence and cover of each plant species; measured tree stem density, canopy cover and stem diameters; and determined soil texture, bulk density, and total C and N content. We classified plant species as native or non-native and assigned morphology and plant wetland indicator designations to evaluate broad plant communities and species-specific patterns over time.

Methods

Study sites

We identified four cranberry farms in active production and 13 former cranberry farms that had been retired for between three and 90 years at the time of sampling. All sites are located in Plymouth, Barnstable, Bristol, or Nantucket County in Southeastern Massachusetts (Fig. 1; Table

S1). We chose sites based on Massachusetts Department of Environmental Protection spatial data of active cranberry farms and the 2018 Massachusetts Department of Ecological Restoration GIS data layer on retired cranberry farms. Some sites contained multiple physically distinct bog beds of the same former farm that were retired in different years. For sites composed of more than one physically distinct bed, we did not sample multiple beds that were retired in the same year but in some cases we sampled multiple beds that were retired in different years. We sampled 23 beds across the 17 retired and active cranberry farms and treated each bed as a replicate for our analysis. All sites were adjacent to forested land. The retired bogs had similar initial soil conditions due to similar underlying soils and consistent sand application when they were actively farmed.

When possible, we determined the last year of commercial production from farm owners or managers and defined year one of retirement as the first year without crop production. For older retired farms for which information from owners was not available, we estimated the retirement age based on town records or aerial images. We assigned each bog bed to one of five age class bins: age class 0 (Active), age class 1 (1-9 years retired), age class 2 (10-20 years retired), age class 3 (21-49 years retired), and age class 4 (50 or more years retired).

Vegetation sampling

We sampled 21 bog beds from June to September of 2019. We sampled the Lower Bog bed of the Coonamessett River in 2017 and Windswept Bog in 2020. In each bog bed, we generated ten plots by selecting random coordinates within the bounds of the bed and designating each of these points as the southeast corner of a 3 x 3 m sampling plot. Upon locating the predetermined coordinates in the field with a hand-held GPS, we delineated each plot with a PVC frame.

In each plot, we identified all species present and assigned each a numerical value corresponding to the estimated percent cover of each species present: R=Rare (one small individual), 1=<1% cover, 2=1-2% cover, 3=3-5% cover, 4=6-15% cover, 5=16-25% cover, 6=26-50% cover, 7=51-75% cover, 8=76-100% cover. This method was identical to that used to assess other low-stature, species-rich vegetation in the same region (Lezberg et al. 2006, Wheeler et al. 2015). We also assigned percent cover categories for bare ground, standing water, leaf litter, and woody debris. We did not identify mosses to species but assigned one value for the total moss cover per plot. For all plants that we were unable to identify to species in the field, we took notes and collected specimens or detailed photographs. We compared specimens and photos to specimens in the Woods Hole Oceanographic Institution/Marine Biological Laboratory herbarium to identify samples to the finest possible taxonomic level following Haines (2011).

To assess trends in functional ecology, we assigned each species designations of native or non-native, life form (graminoid, forb, vine, shrub, tree), and wetland indicator status (OBL, FACW, FAC, FACU, UPL). We assigned native or non-native status based on Cullina et al. (2011) and categorized life history based on the USDA, NRCS PLANTS Database (USDA, NRCS 2021). We assigned wetland status based on the U. S. Army Corps of Engineers (2018) National Wetland Plant List (v3.4). For any species missing a functional designation, we assigned a category based on its habitat and the characteristics of species in the same genus. We also assigned functional designations to plants that we identified to genus but not species based on the designations of the species present in the given county, unless there was variety within the genus (e.g., species identified to genus in which the genus contained both native and non-native species). We included in our analyses plants that we identified to genus only if we were confident that they represented a unique species in the plot, and plants that shared similar

morphology to another species in the plot were not included to avoid over-estimating species richness.

We quantified percent canopy cover, tree stem density, and tree basal area at each plot. We determined percent canopy cover using a spherical crown densitometer (Forestry Suppliers Convex Model A) at the plot center and at each plot corner. We determined stem density and basal area by counting and measuring diameter at breast height (DBH) of all stems ≥ 2 cm DBH within a 4 m radius of the plot center. We used tree DBH and species-specific allometric equations to estimate tree biomass and aboveground C in trees as 50% of tree biomass.

Soil sampling

We collected soil cores at each plot to characterize the composition, moisture, and density of soils across the chronosequence. We collected soils for the Lower bed of the Coonamessett River in 2017, Farley Bog and Windswept Bog in 2020, and all other beds in 2018 one year before we conducted vegetation and tree surveys. We collected one 5-cm diameter soil core to 30 cm in each plot and separated it in the field into 0-5 cm, 5-10 cm, and 10-30 cm below the soil surface. We estimated the gravimetric moisture by oven drying after removing litter and aboveground vegetation. We used gravimetric moisture and the volume of each sample to determine bulk density. We estimated percent soil C and N at each depth by grinding and combusting soil subsamples on a Vario MAX cube analyzer (Ronkonkoma NY). Because soil volumes changed as soil organic matter accumulated in surface soils in retired bogs, we estimated changes in soil C and N stocks by calculating the additional soil depth required to obtain an equivalent soil mass compared with the mean soil mass to 30 cm in active bogs using the method that Davidson and Ackerman (1993) developed for assessing changes to soil stocks along soil chronosequences.

Data analysis

We characterized trends in plant vegetation for each age class using each bog bed as a replicate. We determined the total number of unique species across the ten plots in each bog bed and calculated the mean and standard error of species per bed for each age class. We calculated the mean and standard error of the number of species per bog bed for each category of native/non-native, life form, and wetland indicator. We also analyzed species richness by plot by calculating the mean number of species per plot for each bed and the mean and standard error among bog beds within each age class. To characterize species abundance, we estimated the percent cover of each species in a plot as the midpoint of the percent cover category assigned during vegetation surveying as in Wheeler et al. (2015). We used these midpoint values to calculate the mean percent cover of *V. macrocarpon* and each native/non-native, life form, and wetland category for each bed. We did not normalize percent cover values by the total plot cover and the percent cover values therefore represent the percent of the plot area covered by each vegetation category. Because vegetation canopies consist of multiple layers, the total percent cover in a plot can be greater than 100%. We determined the mean and standard error of percent cover for each category within each age class. For both species richness and cover analyses of wetland status, we grouped and categorized species with designations of OBL and FACW as wetland species and categorized species with designations of FACU and UPL as upland species. All data analysis was conducted in R version 4.0.3.

We calculated the mean percent tree canopy cover for each bog bed from the cover of each plot and used it to calculate the mean and standard error for each age class. For tree basal area and C stock, we used the sum of all trees in each bed to calculate the mean and standard error for each age class. We calculated the mean and standard error of soil C, N, density, and moisture at each depth interval for each age class.

We conducted non-metric multidimensional scaling (NMDS) ordination to visualize trends in the bed species composition of each age class (Kruskal 1964). For the analysis, we combined all the plots in each bed of each age class to construct a Bray-Curtis dissimilarity matrix for the percent cover of each species (Oksannen et al. 2020). We used the metaMDS function in the vegan package in R (R Core team 2020) with 100 randomized runs and three final axis iterations to determine a solution with a stress value <0.2. We depicted two axes to show shifts in species composition between beds and age classes. We also used NMDS ordination to visualize the plot-level cover of twelve notable species. The percent cover of each species in each plot was included in the Bray-Curtis dissimilarity matrix. We used the same metaMDS method as in the bed-level analysis. We highlighted abundant and focal species to provide examples of the change in species presence over time.

Results

Plant community

Total species richness per bed increased from a low of 11.8 ± 2.7 (mean plus or minus standard error) in active bog beds to 50.8 ± 5.0 in 10-20 year-old beds and then declined to 29.5 ± 6.0 in 50+ year-old beds (Fig. 2). Mean native species richness followed the same trend because native species comprised a large majority of total species. Non-native species richness per bog bed remained low across all age classes from a low of 0.5 ± 0.3 species in active bogs to 5.4 ± 2.4 species in 10-20 year-old beds (Fig. 2).

Mean forb species richness increased from 2.8 ± 1.1 species in active bogs to 21.0 ± 3.7 species in 10-20 year-old beds and then declined to 8.0 ± 1.8 species in 50+ year-old beds (Fig. 2). Mean graminoid species richness was also low in active beds, increased to 12.8 ± 1.3 species

in 10-20 year-old beds and then declined to 3.3 ± 2.0 species per bed in 50+ year-old beds. Overall richness of vine, shrub, and tree species was lower, and richness declined less in the oldest age classes (Fig. 2). Mean vine species richness increased from 3.0 ± 1.2 in active bog beds to 5.5 ± 0.7 in 1-9 year-old beds but declined little in subsequent age classes. Mean tree species richness was lowest (0.3 ± 0.3) in active beds and highest (5.3 ± 1.2) in 50+ year-old beds (Fig. 2). Shrub species richness was consistently greater than tree species richness and mean shrub richness increased from 3.3 ± 0.6 in active beds to 10.5 ± 1.7 in 50+ year-old beds (Fig. 2).

The mean richness of wetland species (OBL, FACW) increased from 5.5 ± 0.7 in active bog beds to 25.2 ± 3.7 in 10-20 year-old beds and decreased to 14.3 ± 3.7 in 50+ year-old beds (Fig. 2). Facultative and upland species richness followed the same trend. Mean facultative species richness increased from 4.3 ± 1.3 in active beds to 15.0 ± 2.0 in 10-20 year-old beds and then declined to 9.3 ± 2.0 in 50+ year-old beds. Mean upland species (UPL, FACU) richness increased from 2.0 ± 0.8 in active bog beds to 11.4 ± 4.1 in 10-20 year-old beds then decreased to 6.5 ± 1.9 in 50+ year-old beds (Fig. 2).

Mean vegetation cover per plot in active bog beds was composed largely of *V. macrocarpon* (81.6±5.6%) but that decreased sharply following retirement and continued to decrease to 0.7±0.6% in 50+ year-old beds (Fig. 3). Cover of native species (but not including *V. macrocarpon*) increased from 7.3±4.6% in active beds to 79.7±15.9% in 1-9 year-old beds and then to 105.9±7.5% in 50+ year-old beds (Fig. 3). Non-native cover remained low across all age classes with the highest non-native cover of 2.3±1.8% in 21-49 year-old beds (Fig. 3). Forb cover increased from 0.6±0.4% in active bog beds to 18.4±6.4% in 10-20 year-old beds then decreased to 8.8±3.6% in 50+ year-old beds. Graminoid cover increased from 0.4±0.2% in active

beds to 30.9±10.5% in 1-9 year-old beds and decreased to 0.6±0.3% in 50+ year-old beds (Fig. 3). Moss cover decreased from 3.6±3.3% in active bog beds to 3.1±2.7% in 1-9 year-old beds and was highest (12.3±4.2%) in 10-20 year-old beds. Vine cover increased from 3.6±3.3% in active bog beds to 38.1±14.5% in 10-20 year-old beds and decreased to 11.3±4.1% in 50+ year-old beds. Tree and shrub cover both increased continuously following bog retirement. Shrub cover (56.3±5.5%) and tree cover (32.8±8.6%) were highest in 50+ year-old beds (Fig. 3).

Wetland species cover increased from 3.1±2.3% in active bog beds to 30.8±8.0% in 21-49 year-old beds then decreased to 28.8±8.3% in 50+ year-old beds. Facultative species cover increased continuously following retirement from 3.6±2.0% in active bog beds to 66.5±5.6% in 50+ year-old beds. Upland species cover increased from 0.7±0.40% in active bog beds to 27.3±11.4% in 10-20 year-old beds then decreased to 14.5±5.5% in 50+ year-old beds (Fig. 3).

Mean total species richness per 3 x 3 m sampling plot increased from 3.7 ± 0.9 species in active bog beds to a maximum of 14.9 ± 1.3 species in 10-20 year beds. Patterns of mean species per plot of native and non-native species, plant life history categories and wetland indicator classes (Table S2) followed the trends in richness calculated per bog bed.

Tree canopy cover and tree basal area increased steadily following retirement. Mean percent canopy cover increased from 0 in active bog beds to 84.3% in 50+ year-old beds and mean basal area increased from 0 to 22.6 m^2/ha in 50+ year-old beds (Fig. 4). Red Maple (*Acer rubrum*) and Pitch Pine (*Pinus rigida*) accounted for the majority of the increase in basal area. Mean basal area was 11.0 m^2/ha for *A. rubrum* and 7.4 m^2/ha for *P. rigida* in 50+ year-old beds. Black Gum (*Nyssa sylvatica*), White Pine (*Pinus strobus*), and Gray Willow (*Salix cinerea*) increased in mean basal area over time but contributed less to total basal area (Fig. 4).

Species composition in active bog beds differed widely from retired beds of all ages (Fig. 5). Although composition overlapped among age classes, the NMDS ordination showed beds of each age class grouped together and composition shifted progressively over time (Fig. 5). Each age class had different species that were most common and abundant (Fig. 6). In active bog beds *V. macrocarpon* overwhelmingly dominated cover and cover of other species was low (Table S3). In 1-9 year-old beds, *V. macrocarpon* remained abundant but the herbaceous perennials poison ivy (*Toxicodendron radicans*), switchgrass (*Panicum virgatum*), northern dewberry (*Rubus flagellaris*), bristly dewberry (*Rubus hispidus*), wool-grass (*Scirpus cyperinus*), sedges (*Carex* spp.) and slender-leaved flat-topped goldenrod (*Euthamia caroliniana*) increased in cover (Table S4). In 10-20 year-old beds, *V. macrocarpon* remained the species with the highest cover, *T. radicans* increased, and *R. hispidus* and *R. flagellaris* were still present. *S. cyperinus* decreased but little bluestem (*Schizachyrium scoparium*), *P. rigida*, *A. rubrum* and moss cover increased (Table S5). In 21-49 year-old beds, *A. rubrum* became the species with the greatest cover, sweet pepperbush (*Clethra alnifolia*) increased, and some species widespread in wetlands, like swamp loosestrife (*Decodon verticillatus*) and high-bush blueberry (*Vaccinium corymbosum*), increased (Table S6). *T. radicans, P. rigida* and *R. hispidus* declined and *R. flagellaris* and *E. caroliniana* became much less abundant (Table S6). In the oldest 50+ year-old beds, cover of *C. alnifolia*, *A. rubrum* and *V. corymbosum* increased and cover of *T. radicans* and *P. rigida* declined. Cover of the native shrubs swamp azalea (*Rhododendron viscosum*), leatherleaf (*Chamaedaphne calyculata*), and winterberry (*Ilex verticillata*) and the native trees white pine (*Pinus strobus*), black tupelo (*Nyssa sylvatica*) and oaks (*Quercus* spp.) increased (Table S7).

Soils

Shallow soil percent C (0-5 cm) increased only slightly between 10-20 year-old beds and 21-49 year-old beds but then increased more substantially in 50+ year-old beds (Fig. 7). Soil C increased from 3% at 0-5 cm and 1% at 5-10 and 10-30 cm in active beds to 30.3% at 0-5 cm, 11.4% at 5-10 cm, and 2.8% at 10-30 cm deep after 50+ years (Fig. 7). Soil C stock fluctuated slightly between age classes but increased from 3.8±1.1 kg/m^2 in active beds to 16.3±2.6 kg/m^2 in 50+ year-old beds. Mean aboveground C stock in trees increased from 0 kg/m^2 in active and 1-9 year-old beds to 4.3 kg/m^2 in 50+ year-old beds. Soil N at 0-5 cm began to increase in 21-49 year-old beds and continued to increase to 1.25% in 50+ year-old beds. Soil N increased to 0.45% at 5-10 cm in 50+ year-old beds but remained very low at 10-30 cm. Soil N stock increased from 0.02±0.01 kg N/m^2 in active beds to 0.60±0.16 kg N/m^2 in 50+ year-old beds (Fig. 7).

Soil moisture was highest at 0-5 cm and generally increased with time following bog retirement (Fig. S2). Soil bulk density was lowest at 0-5 cm and higher but similar at 5-10 and 10-30 cm (Fig. S2). Bulk density remained relatively constant from 1-9 to 21-49 year-old beds but decreased in 50+ year-old beds (Fig. S2).

Discussion

Plant community

The trajectories of plant communities following retirement of cranberry bogs followed a consistent pattern over time. The abundance of cultivated *V. macrocarpon* declined quickly after retirement but cranberries remained present even in 21-49 year-old former bog beds. A large number of native graminoids and forb species rapidly colonized retired beds in the first two decades following retirement but graminoids and forb richness and cover declined in bogs retired for more than 20 years. Though tree and shrub richness and cover were lower than that of

graminoids and forbs, tree and shrub richness and cover increased slowly over time. Increases in tree canopy cover that occurred 20 or more years after retirement coincided with the onset of decline in graminoid and forb richness and cover. The structure of vegetation on bog beds retired for five or more decades consisted of nearly closed-canopy forests with abundant *A. rubrum* and *P. rigida* in the overstory and a variety of shrubs that occur in or around wetlands but that are not typically restricted to wetlands, including *C. alnifolia*, *V. corymbosum* and *R. viscosum,* in the understory. This trajectory, and especially the predominance of *A. rubrum* and *C. alnifolia* in older bog beds, was very similar to that observed in a chronosequence of five 3-80 year-old retired cranberry bog beds from New Jersey (Klee et al. 2019).

Following cranberry bog retirement, the initial increase in species richness and cover of herbaceous perennials, subsequent gradual decline in herbaceous species, and increase in tree and shrub species richness and cover after several decades, closely resembled the patterns reported in studies of secondary succession after abandonment of croplands in the eastern and central U.S. (Bard 1952; Bazzaz 1968; Pickett 1982; Cramer et al. 2008). The presence of the most common trees and shrubs in the youngest retired bogs indicated that this pattern resulted from the relatively rapid post-retirement recruitment of both herbaceous and woody species and then subsequent growth of woody species rather than the later recruitment of woody species. This was similar to patterns in many old fields (Bard 1952; Buell et al. 1971; Pickett 1982).

Plant species richness over time in retired cranberry bogs began to decline after two decades. This decline contrasted with the pattern in many old fields in which total plant species richness remains high for decades, even after the establishment of dense tree cover and shift of plant species richness from herbaceous to woody species (Pickett 1982; Monk 1983). Both the high diversity of native plant species that occur in open grass and shrublands on sandy soils in

the Massachusetts cranberry-growing region (Dunwiddie et al. 1996) and the low tree species richness in the region's upland forests (Motzkin et al. 2002) may contribute to this sequential rise and fall of plant species richness over time in retired bogs.

Several other features of the vegetation trajectories in retired bogs also differed from those in old fields. First, the flush of recruitment of herbaceous annuals or biennials such as Ragweed (*Ambrosia artemisiifolia*), Queen-Anne's Lace (*Daucus carota*), Northern Evening Primrose (*Oenothera parviflora*), or Sheep Sorrell (*Rumex acetosella*) that is typical very early in old-field succession, did not occur. Instead, almost all the herbaceous species that recruited early following bog retirement were perennial species that then remained present for many years. Thick existing year-round cover of *V. macrocarpon*, high litter cover, and absence of exposed bare soil likely contributed to the very low presence of these typical, short-lived, early-successional species. The low pH of soils and dense plant cover in cultivated cranberry bogs also potentially discourages these species from colonizing bog beds and contributing to the soil seed banks that typically drive early plant recruitment in old fields (Marks and Mohler 1985).

These same conditions also likely contributed to the overwhelming predominance of native species in the post-cropland floras of cranberry bogs compared with the diverse assemblage and high abundance of non-native species that typically occur quickly in the first one and two years in old fields on formerly cultivated lands (Bazzaz 1968; Pickett 1982; Gill and Marks 1991). While the number of non-native species in old fields declines over time (Pickett 1982), in retired bogs this collection of weedy and widespread non-native and native early-colonizing species did not occur. Low soil pH that closely resembles conditions in native soils may also contribute to the high relative proportion of native species that recruit in retired bog beds. Neill et al. (2007) and Von Holle et al. (2007) showed that forests in southeastern

Massachusetts that had a legacy of higher pH from applications as long as 50 years after liming contained many more non-native plant species than formerly cleared sites with unaltered native soil pH.

The recruitment of many native plant species into retired cranberry bogs likely derives from germination of seeds in buried soil seed banks. These seed banks may be particularly important for wetland-obligate or wetland-associated species such as *S. cyperinus*, *L. terrestris*, and *D. verticillatus* that became important components of the post-retirement flora. Many wetland plants have long-lived seeds that remain buried in soils for many decades before germinating following drawdown or disturbance (van der Valk and Davis 1978; Welling et al. 1988). Pond shores in the Massachusetts cranberry growing region also have rich buried seed banks (Neill et al. 2009). Ditches in active cranberry bogs may also be locations that allow native wetland plants to persist and many plants regarded as weeds by commercial cranberry growers are native wetland plants (Sandler et al. 2015). Some species that we encountered, such as the facultative shrub *C. alnifolia,* may have recruited from buried seeds because this species was found to germinate from regional pond shore seed banks (Neill et al. 2009). However, the presence and composition of seed banks in former cranberry bogs and the role of seed banks in shaping vegetation of post-retirement bogs remain largely unknown.

The colonization by woody plants after bog retirement followed a general pattern of early recruitment but relatively slow expansion of the trees *P. rigida* and *A. rubrum* following bog retirement, then a subsequent decline of *P. rigida* relative to *A. rubrum* and an increase in shrubs, particularly *C. alnifolia*. Both trees are abundant components of regional forests (Motzkin et al. 2002) and *C. alnifolia* is abundant along pond shores and wetland edges (Laderman 1989). *P. rigida* seeds germinate predominantly on exposed, sandy mineral soils (Bramble and Goddard

1942, Ledig and Little 1979) that typically occur following fires (Jordan et al. 2003) or abandonment of land from cultivation (Motzkin et al. 1996). Although soil exposure is low on newly-retired bog beds (Fig. S3) primarily because of high remaining *V. macrocarpon* cover, soil conditions favor *P. rigida* germination likely because of the high soil sand content created by regular sand applications during cranberry cropping. Because *P. rigida* occurs predominantly on well-drained soils, a slowing of the rate of increase in *P. rigida* basal area about 20 years after retirement is potentially associated with concurrent increases in soil moisture (Fig. S2). In contrast with *P. rigida*, *A. rubrum* is widespread on moist soils and can comprise more than 90% of tree cover in forested swamps (Golet et al. 1989). *A. rubrum* germinates readily in old fields (Rankin and Pickett 1989), but unlike *P. rigida*, it also germinates in forest understories (Golet et al. 1989). The increasing predominance of *A. rubrum* in older retired bog beds was consistent with these habitat preferences and seed germination characteristics. Native shrubs, including *C. alnifolia*, *V. corymbosum* and *C. calyculata,* were an important component of the flora of older retired bog beds. Moss facilitates germination of all of these species (Cullina 2002), so the increase of these species over time may be related to coincident gradual increase of moss cover. The presence of moss also increases the success of seedling establishment of White Pine (*Pinus strobus*) (Smith 1951), an upland tree that was a lesser component of basal area but also increased with time since retirement.

Although *P. rigida, A. rubrum, and P. strobus* are typically found in upland forests adjacent to former cranberry farms, the woody vegetation that developed over time on retired bog beds differed substantially from regional, well-drained, upland forests by the conspicuously low presence of oaks species (Black Oak, *Quercus velutina*; White Oak, *Q. alba*; Scarlet Oak, *Q. coccinea*) that dominate regional tree cover (Motzkin et al. 2002; Eberhardt et al. 2003). Nor did

the post-retirement vegetation resemble *C. thyoides* swamps, and we did not record *C. thyoides* at any site. The woody vegetation of bog beds more than five decades post-retirement most typically consisted of a relatively atypical mixture of *P. rigida*, *A. rubrum* and facultative or wetland-associated shrubs. These beds were also somewhat moister than typical regional uplands and are potentially becoming moister over time.

Although non-native species comprised less than 11% of species richness and less than 3% of plant cover across all active and retired bog ages, two species of non-native woody plants, Gray Willow (*Salix cinerea*) and Glossy False Buckthorn (*Frangula alnus*) may be of particular management concern because of their recent and rapid expansion. *S. cinerea* is a European willow that has become widely naturalized in wetlands including retired cranberry bogs in eastern New England (Rawinski 2005, Supplemental Information) and may replace native willows (Zinovjev and Kadis 2008). *F. alnus* is a shrub native to Eurasia and North Africa that has spread into forest understories and wetlands in northeastern North America (Kearlsey 1999, Frappier et al. 2003, McDonald et al. 2008). Control of both species is difficult, *S. cinerea* because of its extensive roots and clonal habit (Griffiths et al. 2018, LHPRISM 2021) and *F. alnus* because its fruits are widely consumed and spread by birds (Catling and Porebski 1994).

Soil and vegetation C stocks

Soil percent C and N and soil C and N stocks increased substantially only in the oldest 50+ year-old bog beds. This increase coincided with the large increase in the tree canopy that occurred between 21-49 year and 50+ year-old bog beds and likely reflected an increase in the depth of the soil Oa and Oe horizons that typically accumulate under forests of the region (Neill et al. 2007). Increases in C and N stocks were smaller than increases in soil percent C and N because there was a concurrent decrease in soil bulk density and hence surface soil mass in C and N-rich

surface soil layers. Soil percent C was similar to that observed in other active and actively restored former cranberry bogs (Bartolucci et al. 2021). The changes to soil percent C and N in 21-49 year-old retired bog beds were generally similar to the changes observed in 30-35 year-old and 50-55 year-old restored wetlands in central New York (Ballantine et al. 2009).

Rates of soil C accumulation for retired cranberry bogs of about 0.057 kg C/m^2/yr were somewhat higher than the broad global average soil accumulation rates for forests (0.034 kg C/m^2/yr) or grasslands (0.033 kg C/m^2/yr) on former agricultural lands (Post and Kwon 2000) and the 0.020 kg C/m^2/yr reported from 100 year-old aggrading mixed hardwood and Eastern Hemlock forests in central Massachusetts (Finzi et al. 2000). As a percentage of the soil C stock under agriculture, the increases we observed of roughly 70% after 70 years were much higher than the 6-9% increases reported in a review of soil C change on forest aggrading on former agricultural land (Nave et al. 2012). At the same time, the rates of soil C accumulation we measured were lower than a broad average of 0.118 g C/m^2/yr calculated for natural wetlands (Mitsch et al. 2013) but not atypical of the long time required to reestablish original rates of C sequestration in restored wetlands (Burden et al. 2019). Soil carbon accumulation rates intermediate between those in aggrading upland forests and natural wetlands is consistent with the vegetation composition of retired cranberry bog beds that was intermediate between upland forest and forested wetlands.

The rate of annual C accumulation in tree aboveground biomass that we measured of 0.06 kg C/m^2/yr was lower than rates for central Massachusetts hardwood forests of 0.28 kg C/m^2/yr measured by forest inventories (Eisen and Plotkin 2015), 0.200 kg C/m^2/yr for hardwood forest or 0.166 kg C/m*2*/yr for hemlock forest measured by eddy flux (Finzi et al. 2000). The rate we measured was more similar to the C accumulation rates of 0.053 kg C/m^2/yr and 0.089 kg

C/m^2/yr measured in New Hampshire and Pennsylvania hardwood forests (Hoover 2011). The coarse texture and low fertility of soils throughout the Massachusetts cranberry growing region (Upham 1969), regular sand applications to active bogs, and soil conditions wetter than typical upland forests, likely contributed to lower rates of annual aboveground C accumulation.

We found that soil moisture in retired bog beds increased with time since retirement. Although these values represented only one-time measurements during summer field visits, they suggested that surface soils became wetter over time. This trend was consistent with our observations of the slumping, deterioration and filling with organic material of the former bog bed drainage ditches in older retired bog beds. Deterioration and filling of ditches with organic matter likely has the effect of reducing bog bed drainage and raising local water tables (Living Observatory 2020) and groundwater inputs are important sources of water to both active and retired cranberry bogs (Hare et al. 2017; Neill et al. 2021). Increasing wetness over time spans longer than our oldest bed (90 years old), which suggests that while the typical vegetation we characterized largely resembled upland forest, longer-term vegetation trajectories could favor more species typical of wet forests over time. Because increasing soil inundation likely is associated with both slower tree growth and greater total accumulation of soil organic matter (including facilitation by moss cover), increasing soil moisture over time may increase the relative proportion of C stored in soils versus aboveground tree biomass. It is likely that soil moisture in retired bogs will be influenced strongly by local topography, and ground and surface water configurations.

Implications for wetland restoration management

Our findings have several potential implications for the management of the cranberry bogs that are likely to be retired in the future. We found that legacies of cranberry cultivation, including

sand deposition and the presence of drainage ditches promoted passive revegetation trajectories that resulted in young forests dominated by tree species characteristic of surrounding upland forests. Although many species of wetland obligate plants colonize retired cranberry bog beds, many of these species disappear in older retired bog beds, the cover of the remaining wetland obligate species decreases, and wetland species are replaced by more widespread facultative plant species. Although the vegetation that results 50+ years after cranberry bog retirement retains some wetland obligate plants and some wetland characteristics, the flora is strongly dominated by common and widespread non-wetland species.

Economic pressures on Massachusetts cranberry growers and the potential for wetland restoration has created interest in developing new methods for promoting natural wetland hydrology and the establishment of wetland-obligate vegetation in retired cranberry farmland. These active restoration methods include filling former bog ditches to raise groundwater levels and removing sand to lower bog bed elevations. Preliminary evaluations indicate that these methods result in higher water table elevations, moister soils and the colonization of a diverse array of herbaceous plant species (Living Observatory 2020). While the equivalent long-term trajectories of plant communities following more active restoration have not yet been evaluated, our results indicate that such interventions will be necessary to promote and sustain the development of future plant communities with larger proportions of wetland species on former cranberry farms.

Acknowledgments

This project was supported by grants from the Massachusetts Division of Ecological Restoration's Cranberry Program, the Fund for Climate Solutions of the Woodwell Climate Research Center, a summer research fellowship grant to Benjamin Hoekstra from Grinnell

College, the Agricultural Research Service of the U.S. Department of Agriculture at the University of Massachusetts Cranberry Station, and the USDA National Institute of Food and Agriculture Hatch project (CONS 01024). We think Andy Xu, Nathaniel Fay, and Lily Thompson for help with fieldwork. Pamela Polloni, Michael Whittemore, and the late Donald Schall graciously assisted with some plant surveys and plant identification. We thank the following for permission to conduct field sampling: Buzzards Bay Coalition, Jon Chorey, A. D. Colburn and Gary Anderson of the Falmouth Rod and Gun Club, Gilmore Cranberry Company, Harwich Conservation Trust, A. D. Makepeace Company, Mass Audubon, Mass Wildlife, Nantucket Conservation Foundation, Onset Fire District, Town of Falmouth MA, Town of Mashpee MA, Town of Plymouth MA and the UMass Cranberry Station. We thank Casey Kennedy for helping to coordinate sampling of active cranberry bogs and Paul Lefebvre for drafting the site map. An independent project by Genevieve Noyce in the Marine Biological Laboratory's Semester in Environmental Science Program provided the original inspiration for our chronosequence design. The authors also thank Linda Deegan, Glorianna Davenport and Alex Hackman for insights into the ecological trajectories of retired and restored cranberry farms.

Declarations

Ethical Approval

Not applicable. No animal or human subjects were involved.

Competing interests

The authors have no relevant financial or non-financial interests to disclose.

Authors' contributions

CN designed the study. AP and CN analyzed the data and wrote the manuscript. HM, BH and AP made the field measurements. SK contributed the multivariate statistical analysis and analysis of community change. All authors read and edited the manuscript.

Funding

This project was supported by grants from the Massachusetts Division of Ecological Restoration's Cranberry Program, the Fund for Climate Solutions of the Woodwell Climate Research Center, a summer research fellowship grant to Benjamin Hoekstra from Grinnell College, the Agricultural Research Service of the U.S. Department of Agriculture at the University of Massachusetts Cranberry Station, and the USDA National Institute of Food and Agriculture Hatch project (CONS 01024).

Availability of data and materials

The datasets generated and analyzed for this study are currently available from the corresponding author on request. Datasets associated with an accepted version of this manuscript will be permanently deposited in the Woods Hole Oceanographic/Marine Biological Laboratory data repository.

References

Bard GE (1952) Secondary succession on the Piedmont of New Jersey. Ecol Monogr 22:195-215

Bartolucci NN, Anderson TR, Ballantine KR (2021) Restoration of retired agriculture land to wetland mitigates greenhouse gas emissions. Rest Ecol 29: e13314

Ballantine KA, Anderson DR, Pierce EA, Groffman PM (2017) Restoration of denitrification in agricultural wetlands. Ecol Engin 106:570-577

Bazzaz FA (1968) Succession on abandoned fields in the Shawnee Hills, southern Illinois. Ecol 49:924-936

Bellemere J, Motzkin G, Foster DR (2002) Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. J Biogeogr 29:1401-1420

Bramble WC, Goddard MK (1942) Effect of animal coaction and seedbed condition on regeneration of pitch pine in the Barrens of central Pennsylvania. Ecol 23:330-335

Brown CD, Boutin C (2009) Linking past land use, recent disturbance, and dispersal mechanism to forest composition. Biol Cons 14:1647-1656

Buell MF. Buell HF, Small JA (1971) Invasion of trees in secondary succession on the New Jersey Piedmont. Bull Torrey Bot Club 98:67-74

Burden A, Barbutt A, Evans CD (2019) Effect of restoration on saltmarsh carbon accumulation in Eastern England. Biol Lett 15: 20180773.

Catling P, Porebski ZI (1994) The history of invasion and current status of glossy buckthorn, *Rhamnus frangula*, in southern Ontario. Can Field Nat 108:305-310

CCCCGA (Cape Cod Cranberry Growers Association) (2021) How cranberries grow. https://www.cranberries.org/how-cranberries-grow#:~:text=These%20factors%20include%20acid%20peat,originally%20created%20by%20glacial%20deposits

Chazdon RL, Lindenmayer D. Guarigusta RR, Crouzeilles R, Benayas RMR, Chavero LL (2000) Fostering natural forest regeneration on former agricultural land through economic and policy interventions. Env Res Lett 15:043002

Cramer VA, Hobbs RJ, Standish RJ (2008) What's new about old fields? Land abandonment and ecosystem assembly. Trends Ecol Evol 23:104-112

Cullina MD, Connolly, Sorrie B, Somers P (2011) The vascular plants of Massachusetts: a county checklist. Massachusetts Division of Fisheries and Wildlife, Westborough, MA

Cullina W (2002). Native trees, shrubs and vines: a guide to using, Growing and propagating North American woody plants. Houghton Mifflin, NY

Davidson, EA, Ackerman IL (1993) Changes in soil carbon inventories following cultivation of previously untilled soils. Biogeochem 20:161-193

Dunwiddie PW, Zaremba RE, Harper KA (1996) A classification of coastal heathlands and sandplain grasslands in Massachusetts. Rhodora 98:117-145

Dupouey JL, Dambrine, E, Laffite JD, Moraes C (2002) Irreversible impact of past land use on forest soils and biodiversity. Ecol 83:2978-2984

Eberhardt RW, Foster, DR, Motzkin G, Hall, B. (2002) Conservation of Changing Landscapes: Vegetation and land-use history of Cape Cod National Seashore. Ecol Appl 13:68-84.

Eisen K, Barker Plotkin A (2015) Forty years of forest measurements support steadily increasing aboveground biomass in a maturing, *Quercus*-dominant northeastern forest. J. Torrey Bot Soc 142:97-112.

Finzi, AC, Giasson M –A, Barker Plotkin AA, Aber JD, Boose ER, Davidson EA, Dietze MC, Ellison AM, Frey SD, Goldman E, Keenan TF, Melillo JM, Munger JW, Nadeloffer KJ, Ollinger SV, Orwig DA, Pdeterson N, Richardson AD, Savage K, Tang J, Thompson JR, Williams GA, Wofsy SC, Zhou Z, Foster DR (2020) Carbon budget of the Harvard Forest Long-Term Ecological Research site: pattern, process, and response to global change. Ecol Monogr 90(4), e01423

Foster DR (1992) Land-use history (1730-1990) and vegetation dynamics in central New England, USA. J Ecol 80:753-772

Foster DR, Swanson F, Aber J, Burke I, Brokaw N, Tilman D, Knapp A (2003) The importance of land-use legacies to ecology and conservation. BioSci 53:77-88

Frappier B, Eckert RT, Lee TD (2003) Potential impacts of the invasive exotic shrub *Rhamnus frangula* L. (Glossy buckthorn) on forests of southern New Hampshire. Northeast Nat 10:277-296

Gill DS, Marks PL (1991) Tree and shrub seedling colonization of old fields in Central New York. Ecol Monogr 61:193-205.

Golet FC, Calhoun AJK, DeGagon WR, Lowrey DJ, Gold AJ (1993). E*cology of red maple swamps in the glaciated Northeast: a community profile*. US Fish Wildlife Serv, Nat Wetlands Res Ctr. Biol Report 12

Grau R, Aide TM, Zommerman JK, Thomlinson JR, Helmer E, Zou X (2003) The ecological consequences of socioeconomic and land-use changes in postagriculture Puerto Rico. BioSci 53:1159-1168.

Griffiths JH, Armstrong R, Innes R, Terry J (2018) Can aerial herbicide application control Gray Willow (*Salix cinerea* L) and stimulate native plant recovery? Ecol Manage Restor 19:49-57

Haines A (2011) Flora Nova Angliae: a manual for the identification of native and naturalized higher vascular plants of New England. Yale University Press, New Haven

Hare DK, Boutt DF, Clement WP, Hatch CE, Davenport G, Hackman A (2017) Hydrogeological controls on patterns of groundwater discharge in peatlands. Hydrol Earth Syst Sci 21:6031-6048

Hoekstra B, Kennedy C, Neill C (2020) Trends in the Massachusetts cranberry industry create opportunities for restoration of formerly-cultivated riparian wetlands. Restor Ecol 28:185-195

Hoover CM (2011) Assessing seven decades of carbon accumulation in two U.S. northern hardwood forests. Forests 2:730-740

Huennecke LF, Hamburg SP, Koide R, Mooney HA, Vitousek PM (1990) Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. Ecol 71:478-491

Jordan MJ, Patterson WA III, Windisch AG (2003) Conceptual ecological models for the Long Island pitch pine barrens: implications for managing rare plant communities. For Ecol Manage 185:151-168

Kearlsey JB (1999) Inventory and vegetation classification of floodplain forest communities in Massachusetts. Rhodora 101:105-135

Keenan RJ, Reams GA, Achard F, de Freitas JV, Grainger A, Lindquist R(2015) Dynamics of global forest area: results form the FAO Global Forest Resources Assessment 2015. For Ecol Manage 352:9-20

Klee R, Zimmerman KI, Daneshgar PP (2019 Community succession after cranberry bog abandonment in the New Jersey Pinelands. Wetlands 39:777-888

Kulmatiski A, Beard KH, Stark JM (2006) Soil history as a primary control on plant invasion in abandoned agricultural fields. J Appl Ecol 43:868-876

Khuman TR, Pearson SM, Turner MG (2011) Agricultural land-use history increases non-native plant invasion in a southern Appalachian forest a century after abandonment. Can J For Res 41:920-929

Kruskal JB (1964) Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychomet 29:1-27.

Laderman A (1989) The ecology of Atlantic white cedar wetlands: a community profile. US Fish

Wildl Serv, Biol Rep 85(7.21)

Ledig FT, Little S (1979) Pitch pine (*Pinus rigida* Mill.): ecology, physiology and genetics. In: Forman RTT (ed) *Pine barrens: ecosystem and landscapes*. Academic Press, NY, pp 347-371

Leppa K, Korkiakoski M, Nieminen M, Laiho R, Hotanen J, Kieloaho A, Korpela L, Laurila T, Lohila A, Minkkinen K, Makipaa R, Ojanen P, Pearson M, Penttila T, Tuovinen J, Launiainen S (2020) Vegetation controls of water and energy balance of a drained peatland forest: responses to alternative harvesting practices. Agric For Meteor 295:1-17

Lezberg A., Buresch K, Neill C, Chase T (2006) Mechanical land clearing to promote establishment of coastal sandplain grassland and shrubland communities. Rest Ecol 14:220-232

LHPRISM (Lower Hudson Partnership for Regional Invasive Species Management) (2021) *Salix atrocinerea*. https://www.lhprism.org/species/salix-atrocinerea#:~:text=As%20with%20any%20other%20invasive,be%20hand%20pulled%20or%20sprayed

Living Observatory (2020) Learning from the Restoration of wetlands on cranberry farmland: preliminary benefits assessment. Living Observatory, Plymouth, MA

MA DAR (Massachusetts Department of Agricultural Resources (2016). The Massachusetts cranberry revitalization task force: final report. Massachusetts Department of Agricultural Resources, Boston

Marks PL, Mohler CL (1985) Succession after elimination of buried seed from a recently-plowed field. Bull Torrey Bot Club 112:376-382

McDonald RI, Motzkin G, Foster DR (2008) Assessing the influence of historical factors, contemporary processes and environmental conditions on the distribution of invasive species. J Torrey Bot Soc 135:260-271

Mitsch WJ, Bernal B, Nahlik AM, Mander U, Zhang L, Anderson CJ, Jørgensen SE, Brix H (2013) Wetlands, carbon, and climate change. Land Ecol 28:583-597

Mitsch WJ, Bernal B, Hernandez ME (2015) Ecosystem services of wetlands. International J Biodiv Sci Eco Serv Manage 121:1-4

Monk CD (1983) Relationshp of life forms and diversity in old-field succession. Bull Torrey Bot Club 110:449-453

Motzkin G, Foster DR, Allen A, Harrod J, Boone R (1996) Controlling site to evaluate history: Vegetation patterns of a New England sand plain. Ecol Monogr 66:345-365

Motzkin G, Eberhardt R, Hall B, Foster DR, Harrod D, MacDonald D (2002) Variation across Cape Cod, Massachusetts: environmental and historical determinants. J Biogeogr 29:1439-1454

Nave IE, Swanston CW, Mishra U, Nadelhoffer KJ (2013) Afforestation effects on soil carbon storage in the United States: a synthesis. Soil Sci Soc Am J 77:1035-1047

Neill C, Von Holle B, Kleese K, Ivy KR, Collins AR, Treat C, Dean M. (2007) Historical influences on the vegetation and soils of the Martha's Vineyard, Massachusetts coastal sandplain: implications for conservation and restoration. Biol Cons 136:17-32

Neill C, Scott L, Kennedy C, Jakuba J, McHorney R (2018) Nutrient balances in Southeastern Massachusetts cranberry bogs. Final report to the Buzzards Bay National Estuary Project, Massachusetts Office of Coastal Zone Management, April 18.

Neill C, Bezerra MO, McHorney R, O'Dea CB (2009) Distribution, species composition and management implications of seed banks in southern New England coastal plain ponds. Biol Cons 142:1350-1361

Noyce G (2007) Biogeochemistry and vegetation in a cranberry bog chronosequence. Semester in Environmental Science, Marine Biological Laboratory, Woods Hole, MA

Oksanen JF, Blanchet G, Friendly M, Kindt R, Legendre P. McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2020 vegan: community ecology package. R package version 2.5-7. https://CRAN.R-project.org/package=vegan

Pickett STA (1982) Population patterns through twenty years of oldfield succession. Vegetatio 59:45-59

Post WM, Kwon KC (2000) Soil carbon sequestration and land use change: processes and potential. Global Change Biol 6:317-327

R Core Team (2020). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Rankin WT, Pickett STA (1989) Time of establishment of red maple (*Acer rubrum*) in early oldfield succession. J Torrey Bot Club 1216:182-186

Rawinski T (2005) European gray willow (*Salix cinerea*): a message from Tom Rawinski. US Forest Serv Invasive Plants Newsbriefs 14.

Rozendaal DMA and 84 others (2019) Biodiversity recovery of Neotropical secondary forests. Sci Adv 5:eaau3114

Sandler H (2010) Best management practices for Massachusetts cranberry production. U Mass Cranberry Sta. East Wareham, MA. https://ag.umass.edu/cranberry/publications-resources/best-management-practices

Sandler H, Dalbec L, Ghantous K (2015) Identification guide for weeds in cranberry bogs. U Mass Cranberry Sta, East Wareham, MA

Smith DM (1951) The influence of seedbed conditions on the regeneration of eastern white Pine. Bulletin 545. Conn Agric Expt Sta, New Haven

Thomas JD ed (1990) Cranberry harvest: a history of cranberry growing in Massachusetts. Spinner, New Bedford

Tiner RW, Zinni W (1988) Recent wetlands trends in southeastern Massachusetts. US Fish Wildl Serv Nat Wetlands Inventory Proj, Newton Corner, MA

Upham CW (1969) Soil survey of Plymouth County, Massachusetts. US Dept Agric, Soil Cons Serv, US Gov Printing Office, Washington DC

US Army Corps of Engineers (2018) National wetland plant list, version 3.4. U. S. Corps of Engineers, Engineer Research and Development Center, Cold Regions Res Engin Lab, Hanover, NH

USDA (2020) United States Department of Agriculture National Agricultural Statistics Service. https://www.nass.usda.gov/Statistics_by_State/Massachusetts/index.php.

USDA, NRCS (2021) The PLANTS database national plant data team, Greensboro NC http://plants.usda.gov.

van der Valk AG, Davis CB (1978) The role of seed banks in the vegetation dynamics of prairie marshes. Ecol 59:322-335

Von Holle B, Motzkin G (2007) Historical land use and environmental determinants of nonative plant distribution in coastal southern New England. Biol Cons136:33-43.

Welling CH, Pederson Rl, Van der Valk AG (1988) Recruitment from the seed bank and the development of zonation of emergent vegetation during a drawdown in a prairie wetland. J Ecol 76:483-496

Wheeler MC, Neill C, Loucks E, Wieler A, Von Holle B, Pelikan M, Chase T (2015) Vegetation removal and seed addition contribute to coastal sandplain grassland establishment on former agricultural fields. Restor Ecol 23:539–547

Whitney GG (1994) From coastal wilderness to fruited plain: a history of eEnvironmental change in temperate North America from 1500 to the present. Cambridge U Press, Cambridge.

Zonovjev A, Kadis I (2008) European rusty willow *S. atrocineria* in eastern Massachusetts. Salicicoloa (http://172.104.19.75/articles/atrocinerea/)

Figure Legends

Fig. 1. Map of the locations of active and retired cranberry bog beds in Southeastern Massachusetts and active and retired bog beds sampled in this study.

Fig. 2. Total native and non-native plant species richness (A), plant species richness by life history group (B), and plant species richness by plant wetland indicator class (C) across a chronosequence of active and retired bog beds. The mean value for each age class is plotted at the midpoint year of the age class. Error bars represent the standard error of the mean.

Fig. 3. Cover of cranberries, native and non-native species (A), plant life history groups (B, C) and plant wetland indicator class (D) across a chronosequence of active and retired bog beds. The mean value for each age class is plotted at the midpoint year of the age class. Error bars represent the standard error of the mean.

Fig. 4. Changes in total tree basal area and canopy cover (A) and basal area of the five most dominant tree species (B) across a chronosequence of active and retired bog beds. The mean value for each age class is plotted at the midpoint year of the age class. Error bars represent the standard error of the mean.

Fig. 5. Non-metric multidimensional scaling analysis of vegetation across a chronosequence of active and retired bog beds.

Fig. 6. Non-metric multidimensional scaling analysis of vegetation of common components of retired bog bed vegetation that changed across a chronosequence of active and retired bog beds.

Fig. 7. Soil percent carbon (A), soil percent nitrogen (B), total soil carbon and nitrogen stock (C) and total aboveground C stock in tree biomass (D) across a chronosequence of active and retired bog beds. The mean value for each age class is plotted at the midpoint year of the age class. Error bars represent the standard error of the mean.

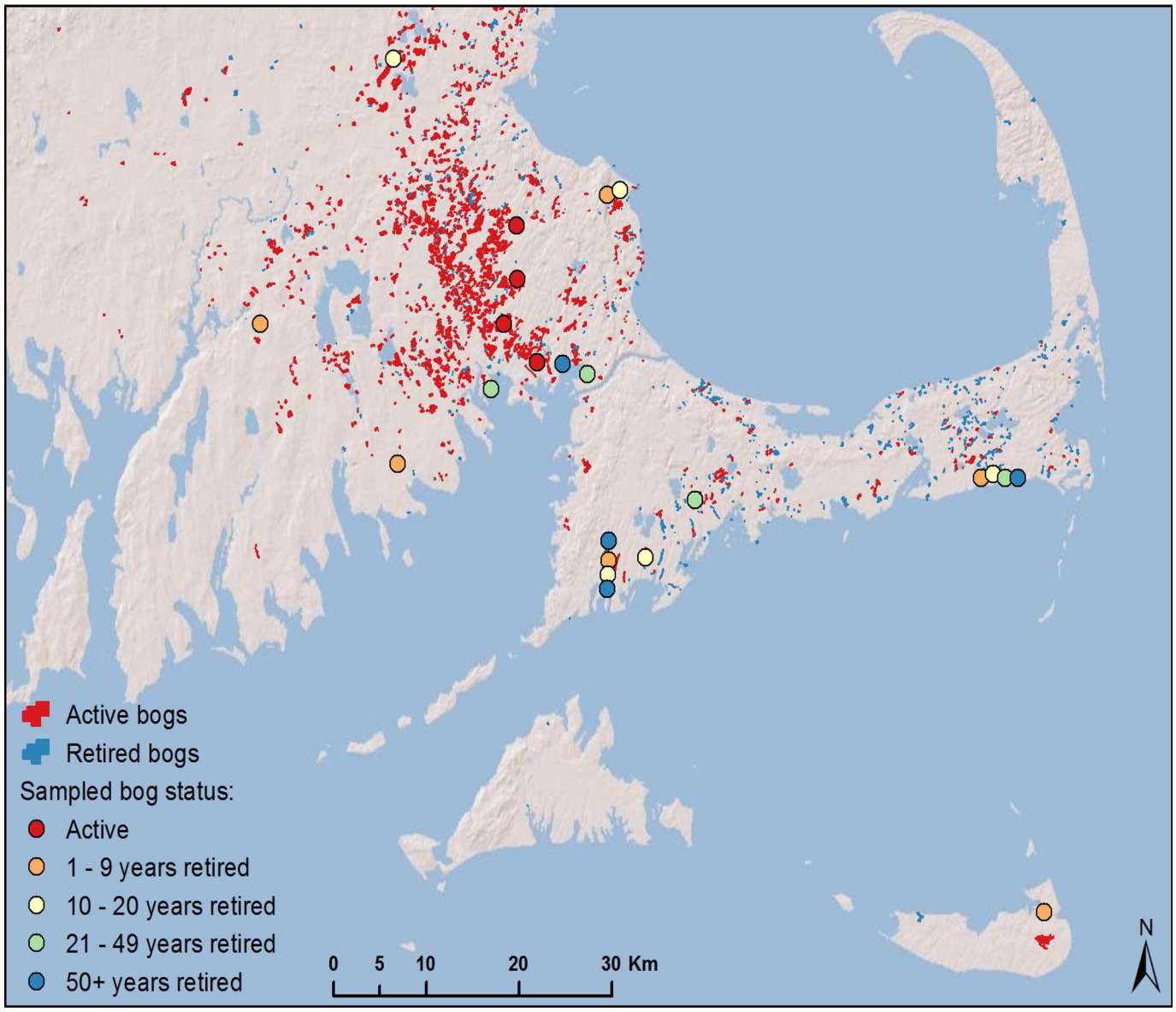
Active bogs
Retired bogs
Sampled bog status:
Active
1 - 9 years retired
10 - 20 years retired
21 - 49 years retired
50+ years retired
0 5 10 20 30 Km
N

Figure 1

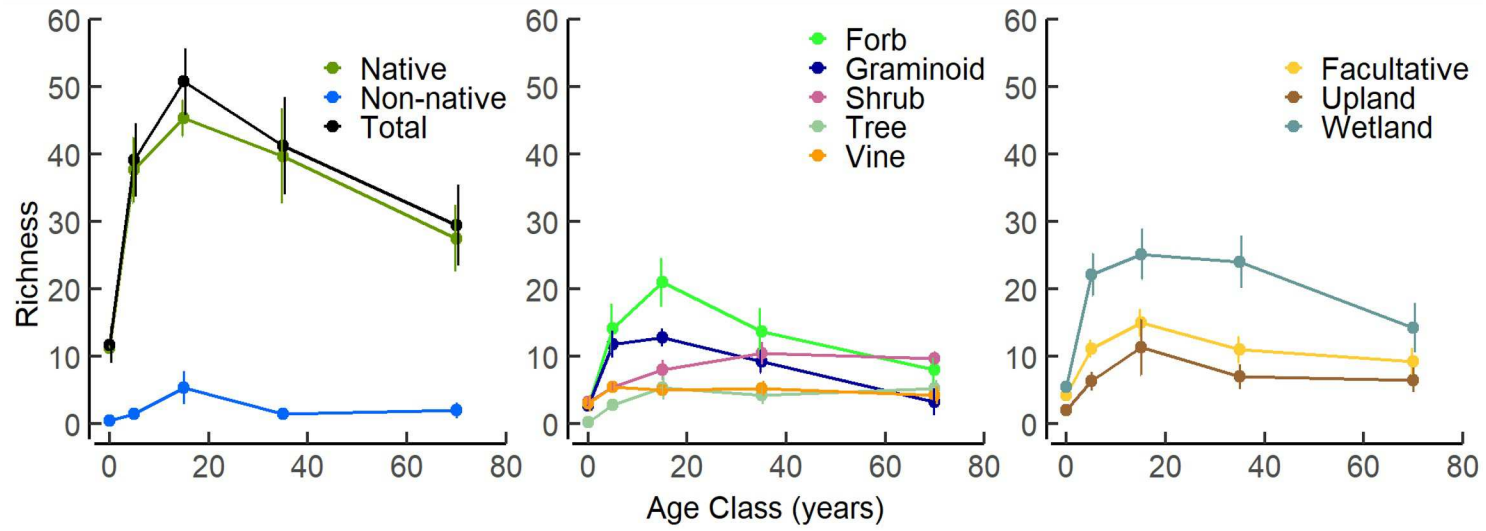
Richness
Native
Non-native
Total
Forb
Graminoid
Shrub
Tree
Vine
Facultative
Upland
Wetland
Age Class (years)

Figure 2

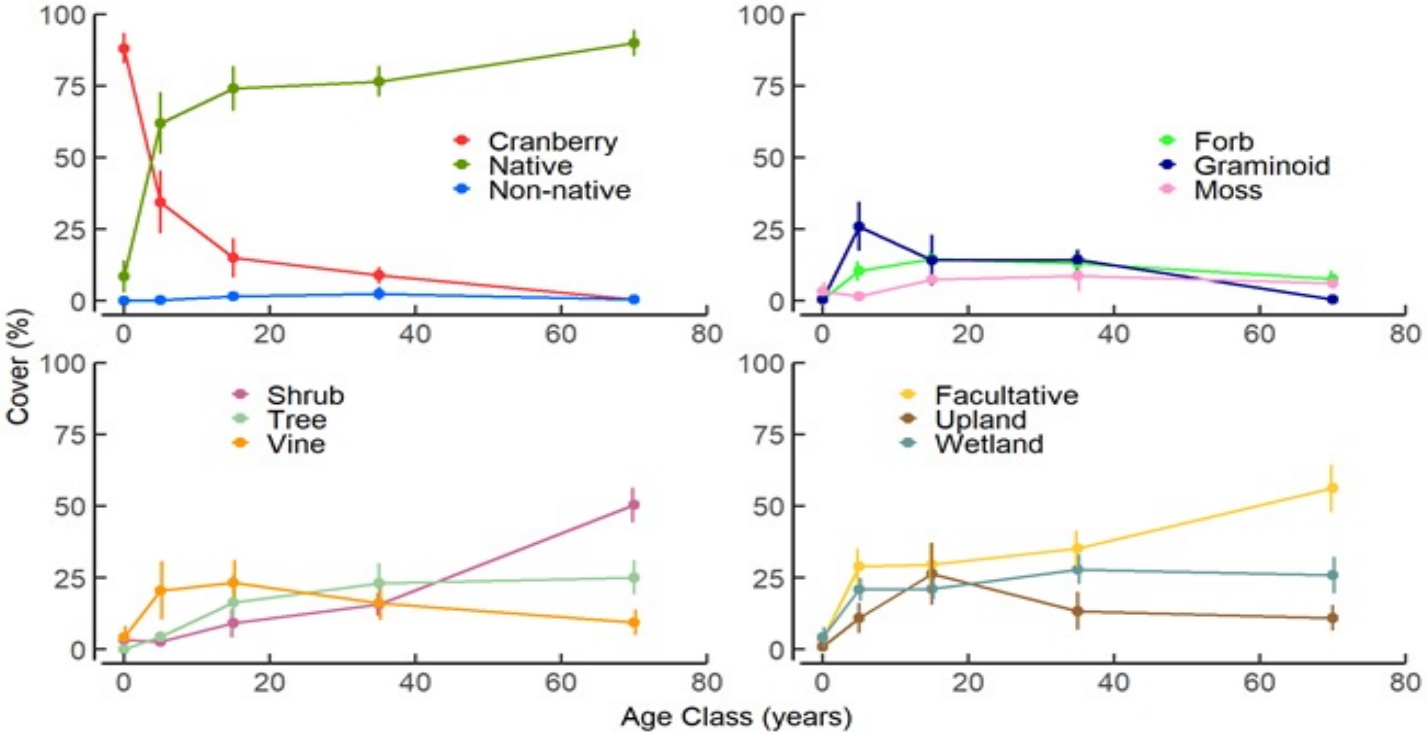
Cover (%)
Age Class (years)
Cranberry
Native
Non-native
Forb
Graminoid
Moss
Shrub
Tree
Vine
Facultative
Upland
Wetland

Figure 3

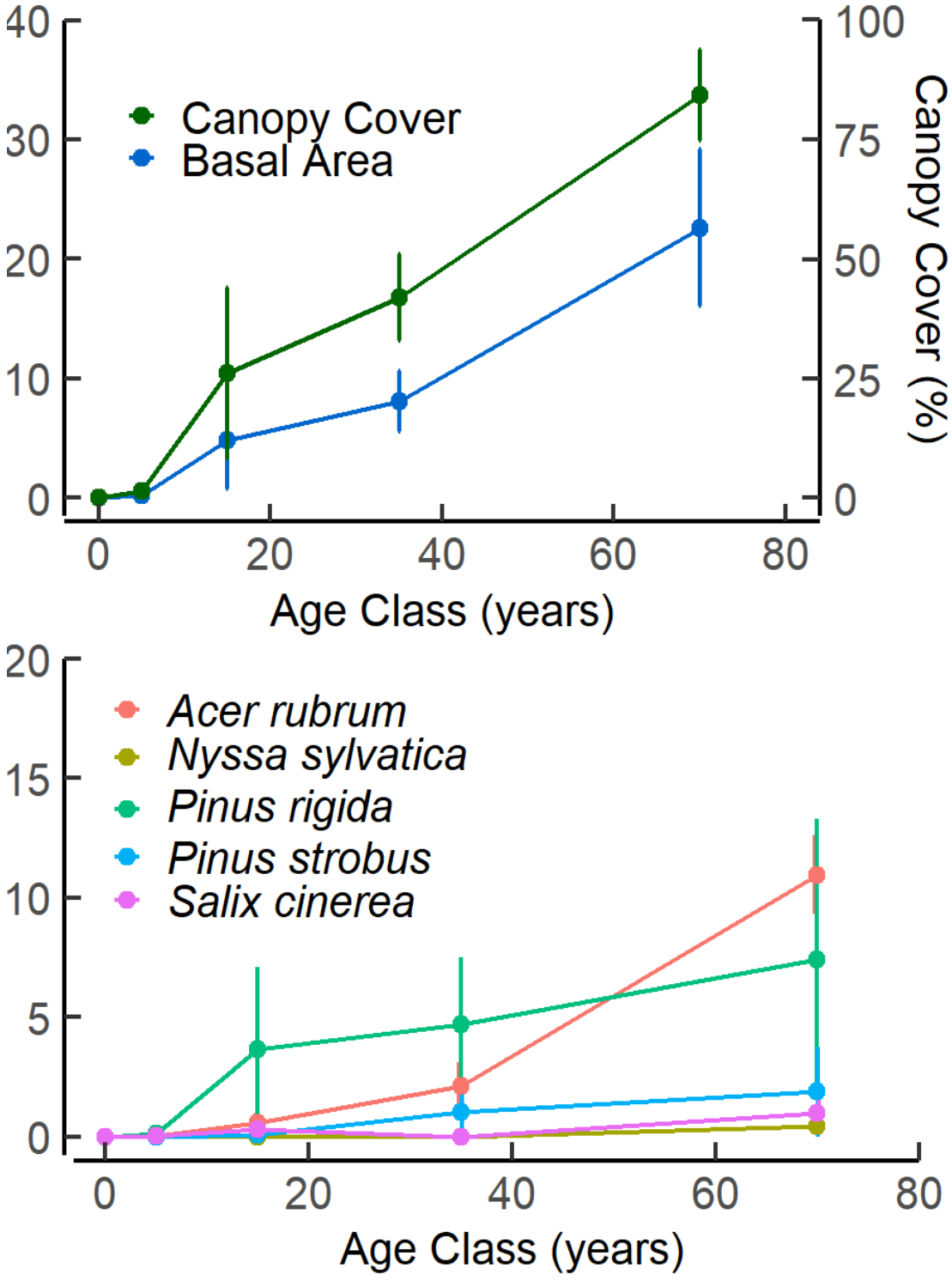
40
30
20
10
0
100
75
50
25
0
Canopy Cover
Basal Area
Canopy Cover (%)
0
20
40
60
80
Age Class (years)
20
15
10
5
0
Acer rubrum
Nyssa sylvatica
Pinus rigida
Pinus strobus
Salix cinerea
0
20
40
60
80
Age Class (years)

Figure 4

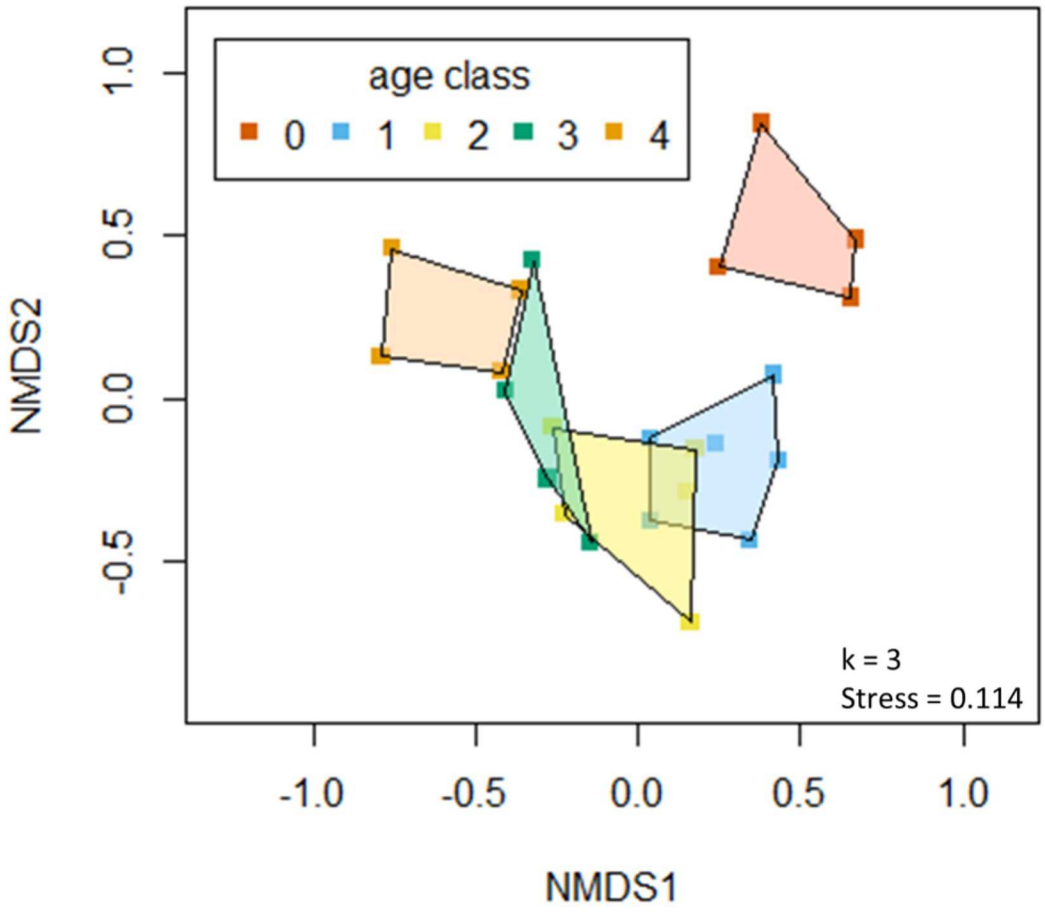

Figure 5

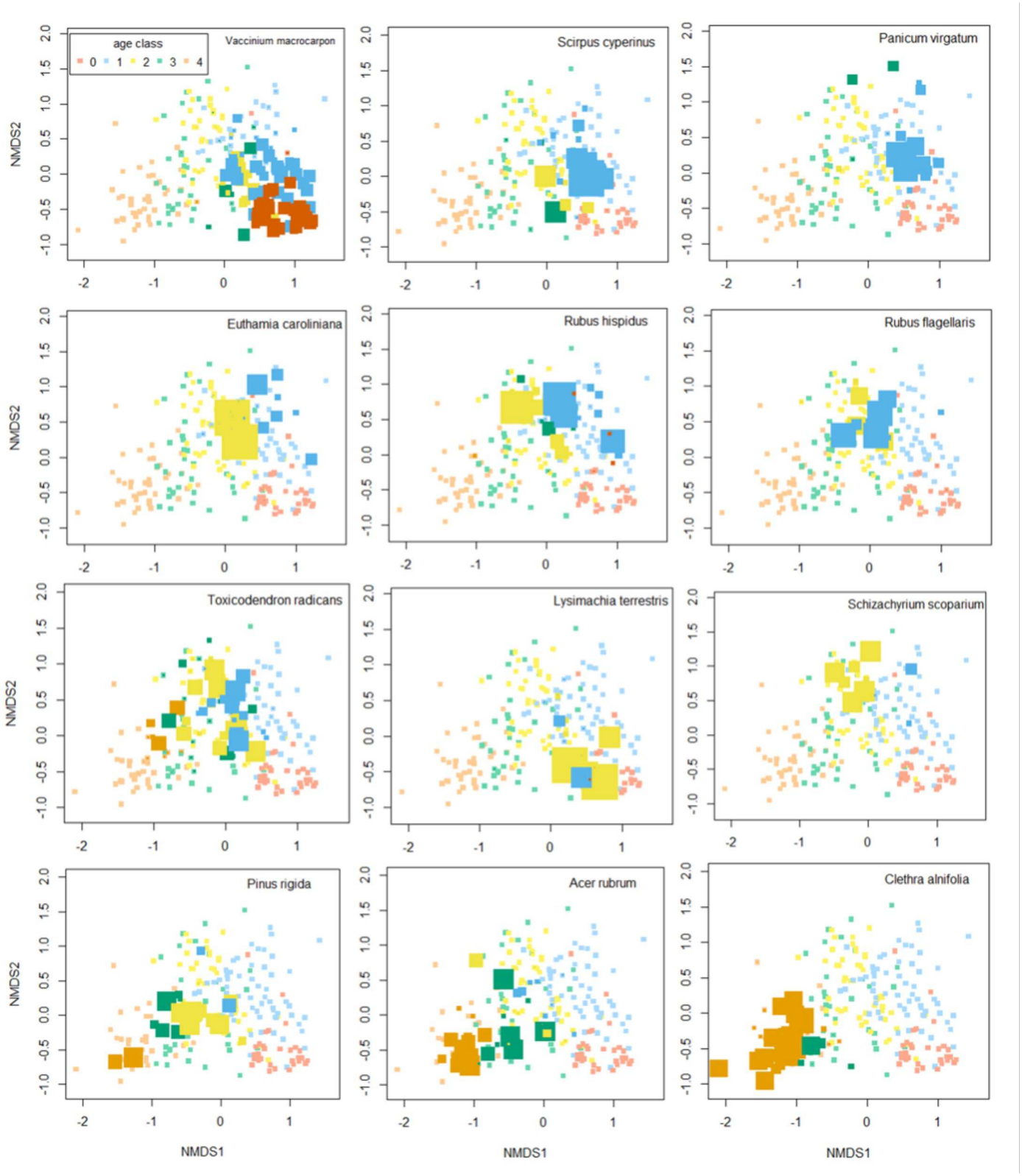
age class
0 1 2 3 4
Vaccinium macrocarpon
Scirpus cyperinus
Panicum virgatum
Euthamia caroliniana
Rubus hispidus
Rubus flagellaris
Toxicodendron radicans
Lysimachia terrestris
Schizachyrium scoparium
Pinus rigida
Acer rubrum
Clethra alnifolia
NMDS1
NMDS2

Figure 6

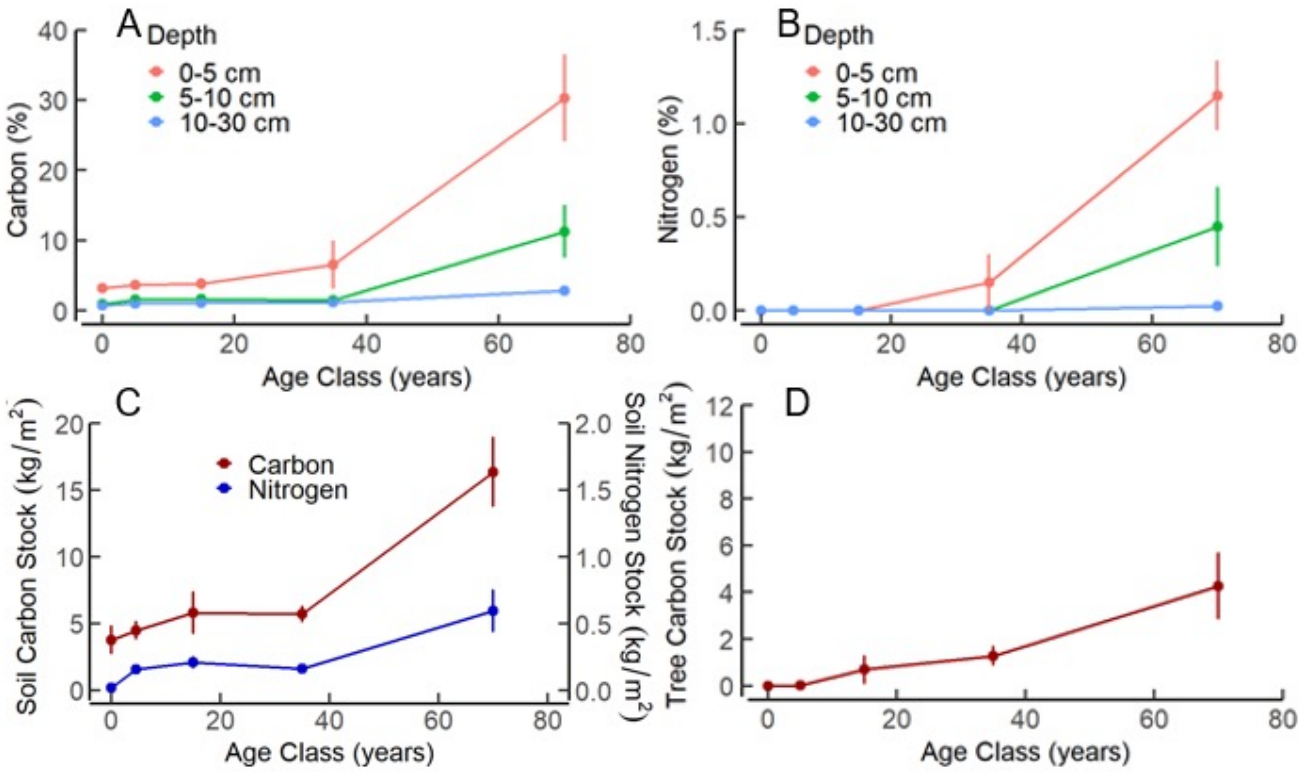
A
Depth
0-5 cm
5-10 cm
10-30 cm
Carbon (%)
Age Class (years)
B
Depth
0-5 cm
5-10 cm
10-30 cm
Nitrogen (%)
Age Class (years)
C
Carbon
Nitrogen
Soil Carbon Stock (kg/m²)
Soil Nitrogen Stock (kg/m²)
Age Class (years)
D
Tree Carbon Stock (kg/m²)
Age Class (years)

Figure 7

Table S1. Location and retirement information for sites and bog beds sampled.

Site	Bog bed	Retirement year	Age class	Longitude	Latitude
Frog Foot Bog	Frog Foot	Active	0	-70.7122	41.8005
State Bog	State	Active	0	-70.6683	41.7672
Rocky Pond	Rocky Pond North	Active	0	-70.6982	41.8862
White Springs Bog	White Springs	Active	0	-70.6962	41.8398
Windswept Bog	Windswept	2018	1	-70.0047	41.2954
Cold Brook Preserve	Southwest	2015	1	-70.0679	41.6730
Mill Brook Bogs	Mill Brook	2014	1	-71.0277	41.7953
Tidmarsh	Tidmarsh West	2014	1	-70.5767	41.9146
Coonamessett River	Reservoir	2013	1	-70.5721	41.5909
Mattapoisett Bogs	Mattapoisett	2011	1	-70.8470	41.6758
Childs River	Farley Bog	2010	2	-70.5247	41.5989
Coonamessett River	Lower	2006	2	-70.5729	41.5833
Burrage Pond	Burrage Pond	2002	2	-70.8624	42.0293
Tidmarsh	Farmstand Bog	2001	2	-70.5713	41.9170
Cold Brook Preserve	Northwest	2001	2	-70.0647	41.6754
Marks Cove	Marks Cove	1996	3	-70.7279	41.7434
Cold Brook Preserve	Southeast	1992	3	-70.0618	41.6727
Santuit Pond Land Banl	Santuit	1991	3	-70.4615	41.6502
Barrows Bogs	Barrows Bogs	1987	3	-70.6029	41.7583
Andrews River	Andrews River	1968	4	-70.0549	41.6739

Coonamessett River	Hatchville	1958	4	-70.5727	41.6132
Red Brook River	Red Brook West	1937	4	-70.6352	41.7663
Coonamessett River	Old Lower	1930	4	-70.5730	41.5814

Table S2. Mean plot richness for each vegetation category by age class.

Vegetation	Age Class 0	Age Class 1	Age Class 2	Age Class 3	Age Class 4
Native	3.42 ± 0.78	11.83 ± 1.37	13.68 ± 0.77	11.18 ± 1.12	8.60 ± 0.79
Non-native	0.20 ± 0.17	0.20 ± 0.09	0.90 ± 0.53	0.32 ± 0.11	0.30 ± 0.17
Forb	0.73 ± 0.50	4.13 ± 0.98	5.56 ± 0.86	2.98 ± 0.69	2.10 ± 0.55
Graminoid	0.65 ± 0.25	3.38 ± 0.67	2.80 ± 0.64	2.15 ± 0.25	0.58 ± 0.37
Shrub	0.40 ± 0.12	1.13 ± 0.26	1.84 ± 0.59	2.42 ± 0.03	3.15 ± 0.16
Tree	0.05 ± 0.05	0.77 ± 0.11	1.62 ± 0.70	1.35 ± 0.31	1.55 ± 0.31
Vine	0.85 ± 0.53	1.83 ± 0.52	2.22 ± 0.39	2.25 ± 0.55	1.48 ± 0.27
Facultative	1.02 ± 0.40	3.95 ± 0.41	4.52 ± 0.73	3.70 ± 0.48	3.65 ± 0.54
Upland	0.45 ± 0.18	1.47 ± 0.30	2.92 ± 1.06	1.30 ± 0.28	1.75 ± 0.51
Wetland	2.15 ± 0.39	6.75 ± 1.00	7.36 ± 0.90	6.42 ± 0.76	3.60 ± 0.88

Table S3. Fifteen most abundant plant species by cover in active cranberry bog beds (Age Class 0).

Species	Mean cover (%)
Vaccinium macrocarpon	88.04
Moss	3.29
Rubus hispidus	1.73
Spiraea alba	1.53
Smilax species	1.07
Kalmia angustifolia	1.01
Rubus flagellaris	0.69
Smilax rotundifolia	0.52
Vaccinium corymbosum	0.36
Aronia melanocarpa	0.33
Lysimachia terrestris	0.24
Scirpus cyperinus	0.19
Euthamia caroliniana	0.18
Dichanthelium acuminatum	0.17
Toxicodendron radicans	0.11

Table S4. Fifteen most abundant plant species by cover in 1-9 year-old beds (Age Class 1).

Species	Mean cover (%)
Vaccinium macrocarpon	34.42
Panicum virgatum	7.85
Toxicodendron radicans	7.76
Rubus flagellaris	5.74
Rubus hispidus	5.02
Scirpus cyperinus	4.13
Carex species	3.23
Euthamia caroliniana	3.05
Dichanthelium clandestinum	2.88
Acer rubrum	2.58
Moss	1.60
Agrostis species	1.57
Solidago rugosa	1.34
Erechtites hieraciifolius	1.18
Cyperus dentatus	1.16

Table S5. Fifteen most abundant plant species by cover in 10-20 year-old beds (Age Class 2).

Species	Mean cover (%)
Vaccinium macrocarpon	15.02
Toxicodendron radicans	12.82
Pinus rigida	10.34
Schizachyrium scoparium	8.18
Moss	7.50
Rubus hispidus	4.54
Rubus flagellaris	4.25
Acer rubrum	3.13
Lysimachia terrestris	2.97
Solidago rugosa	2.90
Morella caroliniensis	2.88
Vaccinium corymbosum	2.03
Euthamia caroliniana	1.79
Smilax rotundifolia	1.36
Scirpus cyperinus	1.28

Table S6. Fifteen most abundant plant species by cover in 21-49 year-old beds (Age Class 3).

Species	Mean cover (%)
Toxicodendron radicans	9.90
Acer rubrum	9.23
Vaccinium macrocarpon	8.91
Moss	8.70
Pinus rigida	6.81
Clethra alnifolia	4.48
Decodon verticillatus	3.70
Pinus strobus	3.53
Vaccinium corymbosum	3.34
Grass species	3.27
Rubus hispidus	3.13
Carex species	2.53
Panicum virgatum	2.41
Thelypteris palustris	2.38
Frangula alnus	2.06

Table S7. Fifteen most abundant plant species by cover in 50+ year-old beds (Age Class 4).

Species	Mean cover (%)
Clethra alnifolia	30.14
Acer rubrum	13.84
Vaccinium corymbosum	6.25
Moss	6.22
Rhododendron viscosum	6.06
Toxicodendron radicans	5.01
Chamaedaphne calyculata	3.10
Pinus rigida	3.02
Nyssa sylvatica	2.25
Quercus species	1.95
Pinus strobus	1.84
Smilax rotundifolia	1.79
Sparganium americanum	1.74
Impatiens capensis	1.64
Ilex verticillata	1.61

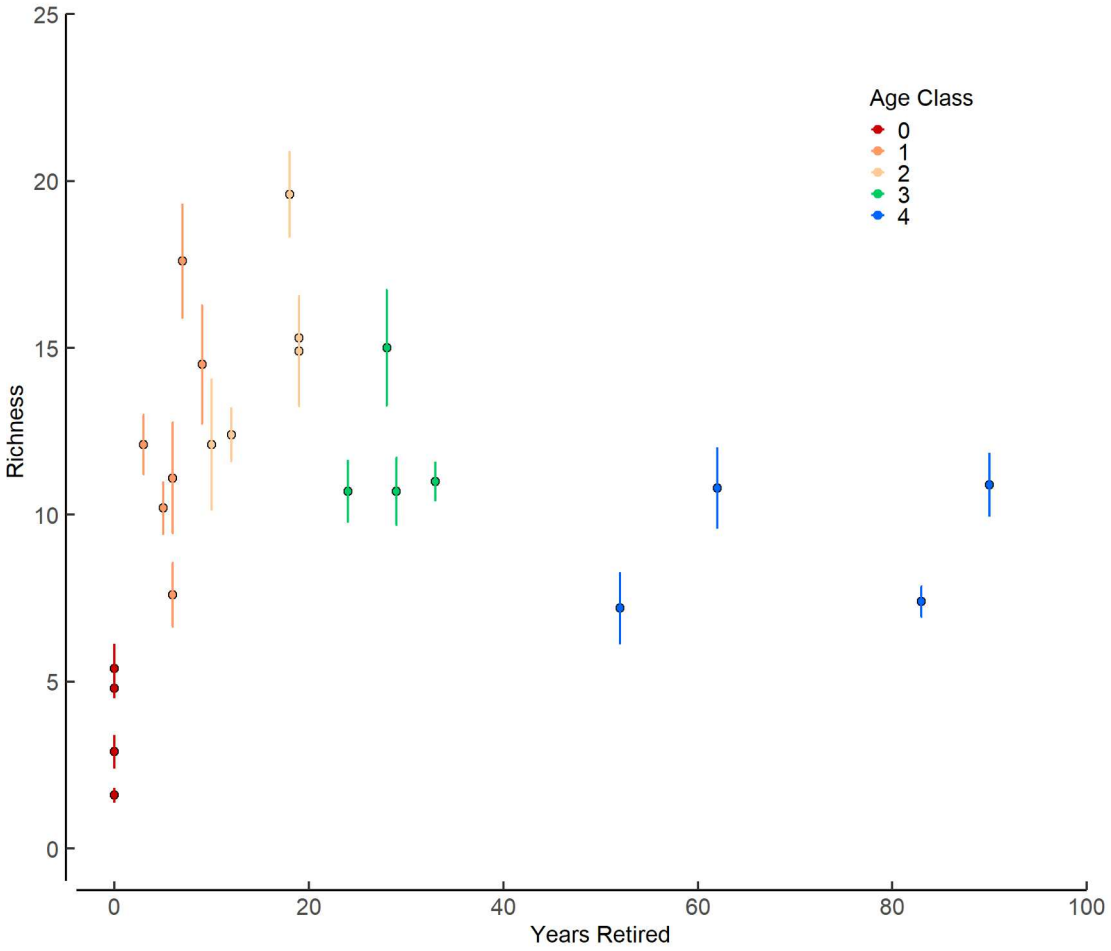
Age Class
0
1
2
3
4
Richness
25
20
15
10
5
0
0
20
40
60
80
100
Years Retired

Fig. S1