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ORIGINAL PAPER

Vegetative composition and community structure associated with beaver ponds in Canaan valley, West Virginia, USA

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Abstract Beavers (*Castor canadensis*) can cause dramatic changes in vegetative composition and diversity. Although alterations by beaver have been studied extensively, little attention has been paid to the effects beaver impoundments have on rare plants. Effective conservation of riparian and wetland rare plant species must consider the responses of vegetation to changes in hydrology that can occur when beaver populations are present. The goal of this research was to establish the occurrence of locally rare plant species, examine community composition, and analyze vegetative community structure of vegetation associated with beaver ponds in Canaan Valley, West Virginia, USA. Species richness and diversity were similar between plots located inside beaver ponds and adjacent to beaver ponds ($P > 0.05$). Although no significant difference in rare plant species was detected among pond ages, the oldest ponds (>56 years) had twice as many rare species as the youngest ponds (≤6 years). The youngest ponds had higher overall mean species richness (S) than ponds 7–56 years old ($P < 0.05$), but S returned to similar levels in the oldest ponds. Of the 15 rare species observed, most were classified as obligate (9) or facultative wetland (4) species. The youngest ponds contained the fewest number of rare species. Multiple response permutation procedure (MRPP) analyses of community structure detected no relation between community composition and either pond age or size. However, both MRPP and non-metric multi-dimensional scaling showed proximity to pond was important in herbaceous community structure. Wetlands in beaver ponds also were shown to be distinct from adjacent wetland areas. Conservation of existing beaver populations is necessary so that the entire spectrum of pond ages is available for the maintenance of rare plant species and communities.

Keywords Canaan valley · *Castor canadensis* · Pond · Rare plant species · Vegetation

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Introduction

Beavers (*Castor canadensis* Kuhl) influence streams and wetlands across much of North America. The dam-building activities of these semi-aquatic mammals alter forest succession by flooding areas (Barnes and Dibble 1988; Naiman et al. 1988), leading to changes in sediment retention, invertebrate communities, vegetative composition, and stream morphology (Naiman et al. 1986; Wright et al. 2002). Herbivory by beavers also can have a dramatic effect on successional trends along streams (Barnes and Dibble 1988).

Beaver use of ponds are typically less than 10 years (Wright et al. 2002); however, beaver-induced communities, such as fens and wet meadows, may be enduring stages of succession instead of temporary patches (Naiman et al. 1988). This observation may be applicable to Canaan Valley, WV, USA, where some beaver impoundments have persisted for at least 56 years based on photographic history. In Canaan Valley, beaver pond development occurs on two different landscapes. On the low-gradient valley floor, larger ponds are frequently located near the lower reaches of lower-order, slow-moving, meandering streams where habitat and food are abundant. These areas are sites for lodges and winter food caches, and are often surrounded by a network of smaller, transient satellite ponds that connect the main pond and increasingly distant food sources. In this landscape, ponds and dams tend to be larger and are occupied for longer periods of time; some are extremely resilient, outlasting beaver abandonment by decades. Along higher-order, smaller streams that extend from the edge of the valley floor up-slope, beaver ponds occur in a stair-step pattern up the drainage. These ponds tend to be smaller and deeper, with shorter but taller dams, and fewer satellite ponds present. After pond abandonment, these dams tend to deteriorate rather rapidly because of higher stream velocity. As ponds dry, a succession of sedges (*Carex* spp.), rushes (*Juncus* spp.), and grasses (*Calamagrostis* spp.) occur, sometimes lasting for decades until suitable food sources are reestablished. Thus, the current sub-climax community could be long-term if beaver flooding and herbivory suppress the growth of the local climax plant communities. Long-term changes in vegetation communities and succession have been documented after beaver inhabitance (Neff 1957; Naiman et al. 1986; Barnes and Dibble 1988; Wright et al. 2002).

The ecological effects of beavers may be beneficial or disruptive to wetland plant communities. Beavers increase wetland area by creating new wetlands from upland or riparian areas (Wright et al. 2002). Beaver have the ability to modify and create new habitats, with the potential to positively and negatively influence ecosystems (Jones et al. 1997). Plant species richness increases (Wright et al. 2002) and changes in species composition occur (Mitchell and Niering 1993) following beaver dam construction. Although beaver herbivory alone may not completely change community structure (Donkor and Fryxell 1999), beaver flooding in bogs of the northeastern United States caused dramatic shifts in habitat types and diversity, creating new fens and supporting more hydric species (Mitchell and Niering 1993). Flooded ponds also accumulated seed banks, which lead to germination and establishment of new vegetation growth when changes in water levels occur (Le Page and Keddy 1998).

Beavers are again important in the northeastern United States and understanding their role in maintaining and altering floristic communities is essential (Mitchell and Niering 1993). At times beavers are managed to reduce interference with human activities or to influence typical succession patterns. At the landscape level beaver activity can increase species richness (Wright et al. 2002), but the impacts of beaver ponds on locally rare vegetation and community composition have not been well described. Yet it has important implications for resource managers as they try to maintain the balance between healthy beaver populations and rare plant conservation. Given the longevity of some impoundments, we hypothesize that older ponds are important habitats for rare plant species. We also hypothesize that larger beaver ponds may harbor more species because they contain a larger number of microsites for plant establishment and persistence. Our objectives were to (1) quantify plant species composition and richness in beaver ponds; (2) quantify the relations between pond age and size and rare plant species; and (3) quantify the relations between pond age and plant community structure.

Methods

Study site

This study took place in Canaan Valley, located in Tucker County, West Virginia, USA. Canaan Valley is a large (22.5 km long, 5 km wide) anticline valley at an elevation of up to 1,006 m. The precipitation during summer months (June–August) averages 36.5 cm and the average temperature is 17.7°C (Southeast regional climate Center 1996). During winter (December–March) the average temperature is −3.5°C (National Climate Data Center 2003), and the freeze-free period lasts an average of 90 days (Beverage 1967). The Blackwater River runs through much of the valley and beaver activity is centered in several of the smaller drainages of the river.

The vegetation of Canaan Valley is boreal with many northern species occurring at the southernmost bounds of their ranges in the valley, which leads to communities and species that while globally abundant, are locally rare (Fortney 1993). Wetland areas with beaver ponds are often dominated by herbaceous communities such as sedges (*Carex* spp.) and common rush (*Juncus effusus*) and by scrub-shrub communities, particularly meadowsweet (*Spiraea alba*). Although the valley may have been more forested in the past, the valley floor now contains one of the largest freshwater wetland complexes in the eastern United States. Over 50 rare plant species, including 36 rare wetland plant species, have been identified within the valley, as well as 35 rare plant communities. Much of the floristic diversity in the area may be attributed to the wetland habitats available.

Fortney and Rentch (2003) cite beaver activity as a possible influence in a >40% loss in developing coniferous forests. Although extirpated from West Virginia in the 1850s, beavers were re-introduced to the Canaan Valley area of West Virginia around 1936 (Swank 1949). Although some communities are slowly returning to the valley (Brooks 1957); Fortney and Rentch (2003) suggested beaver presence as one factor leading to the decreased abundance of several rare plant communities in the valley since 1975. Plant communities such as red spruce (*Picea rubens*) forests are still present in Canaan Valley, but the abundance has been greatly reduced due to extensive logging and most tree species are absent or sporadic around beaver ponds.

All surveys were conducted on beaver ponds located in Canaan Valley National Wildlife Refuge. The refuge was established in 1994. The 6,169-ha refuge contains much of the wetland areas in the central and northern portions of the valley. Wetland areas where most beaver activity occurs was acquired in early 2002, with beaver trapping being prohibited within refuge boundaries until the 2004–2005 season.

Vegetation sampling

Vegetation surveys were conducted in 2004 and 2005 on 38 randomly selected beaver ponds, stratified by size class in relative proportion to abundance: 6 large (>4,000 m^2), 11 medium (>1,000–4,000 m^2), and 21 small (>100–1,000 m^2). Sampling occurred from late June to early September 2004 and late June 2005 to maximize rare species and minimize unknown species (Rentch and Anderson 2006; Rentch et al. 2008). All ponds smaller than 100 m^2 were removed from sampling selection as surveyors would likely be unable to find those patches.

Three belt transects were used to sample vegetation at each pond. The three transect directions were selected from eight possible ordinal compass bearings. Bearings that crossed the main dam of the pond were excluded. Each transect ran along a randomly selected direction, beginning at the edge of the open water. Transects extended beyond the end of the influence of the pond to capture two additional herbaceous plots, which also were still in the wetland. We considered the influence of the pond to end when a distinct change in vegetative community composition resulted due to a clear increase in elevation. We used 1.0 × 1.0 m herbaceous plots every 5 m and 5.0 × 5.0 m shrub plots every 10 m along each transect; trees were absent from our transects. Within all herbaceous plots, a cover class was assigned for each observed vascular species, bryophytes, woody debris, bare ground, and open water. The following cover class scale was used to estimate cover: 1–5% = 1, 6–25% = 2, 26–50% = 3, 51–75% = 4, 76–95% = 5, 96–100% = 6 (Daubenmire 1968). In shrub plots, these cover classes were used to estimate cover of any shrub species present. Walk-around surveys also were used at each pond to capture any species not observed within transect plots (Balcombe et al. 2005a). These surveys were typically conducted within 5 m of the pond, with observers documenting all species that were not recorded along transects. Plant species were identified using Strausbaugh and Core (1977), and nomenclature was standardized according to Kartesz (1999).

Age classes were determined by digitizing all visible ponds from four sets of aerial photographs (1945, 1969, 1997, 2003) obtained from the US Department of Agriculture (1945, 1969), US Geological Survey (1997), and the West Virginia statewide addressing and mapping board (2003). The program ArcMap 9.1 was used to overlay all digitized pond polygons and compare the relative temporal occurrence and size of each pond (ESRI 2005). Broad age classes, based on available aerial photographs, were determined as follows: 1–6, >6–35, >35–56, and >56 years.

Statistical analyses

The program PC-Ord was used to calculate species richness (S′) and the Shannon–Weaver index of diversity (H′, Shannon and Weaver 1949) (dependent variables) for each quadrat. Location (inside vs. outside of beaver ponds) was our independent variable. Data were analyzed using an analysis of variance (ANOVA, PROC GLM) in the statistical software SAS (SAS Institute Inc 2003). Data were tested for normality and homogeneity of variances. Transect data only were used for all analyses except for species richness data. Species richness analyses used data from transects and walk-around surveys together.

Rare plant richness per pond was rank-transformed using SAS (PROC RANK) because data would not meet assumptions of a parametric test, then compared by age class using ANOVA (PROC GLM; SAS Institute Inc 2003). A two-way ANOVA was used to compare mean species richness (dependent variable) of herbaceous communities among age and size classes (independent variables). All interaction effects were tested for significance. An alpha level of 0.05 was considered significant for all tests. All data are presented as untransformed means.

Community structure analyses of ponds based on (1) location inside vs. outside the beaver pond, (2) age class, and (3) size class were performed using Multiple Response Permutation Procedures (MRPP) in PC-Ord (McCune and Mefford 1999). Multi-response permutation procedures test the hypothesis that no difference exists between species composition of selected areas. This is a non-parametric multivariate technique requiring *a priori* selection of test areas (location, age, and size). This procedure calculates a T-statistic, a P value, and an A-statistic. Separation between groups is described by the T-statistic. The likelihood of reaching the observed difference (T) is evaluated using the P value. The A-statistic estimates within-group homogeneity compared to what is expected by chance, with $A = 1$ in completely identical plots and $A = 0$ in those communities equal to chance expectation. The Sørenson (Bray–Curtis) dissimilarity index was used during these tests. The Sørenson index is considered suitable for ecological data, as it performs better in more heterogeneous datasets and is not as sensitive to outliers as other indices (McCune and Mefford 1999).

Nonmetric multidimensional scaling (NMS) was used to compare community composition and structure of portions of each study area that were within and adjacent to the area influenced by each pond. To reduce covariance of species in the original distance matrix, species that occurred in less than six ponds were removed, yielding a reduced matrix of 76 pond sampling sites (38 in and 38 out) and 51 species. Because input values were proportional data, we also used an arcsine square-root transformation to improve normality (McCune and Mefford 1999) and further reduce covariance (final species covariance = 194%). To ensure that the reduced data set retained the original community data structure, we performed a Mantel test of the original and reduced matrices using Sorenson city block distance measure and 1,000 randomized runs. This test yielded a $P = 0.001$, suggesting that we reject the null hypothesis that there was no relation between the two matrices.

Nonmetric multidimensional scaling was first conducted using 50 runs of real data and 400 iterations, along with 100 runs of randomized data for a Monte Carlo test of significance that similar results could have been achieved by chance along ($P < 0.001$). Following Monte Carlo testing, a three dimensional solution was chosen for the final ordination. We report final stress and instability of the ordination, and coefficients of determination (R^2) for ordination axes, calculated as the proportion of variation explained in the reduced matrix relative to the original matrix. We then used the inside/outside categorical variable in a secondary matrix to help interpret the ordination results. We report Pearson product-moment correlations between the primary matrix (species) and ordination axes for variables that had the strongest linear relation ($r \geq 0.3$).

We used weighted averages to analyze the herbaceous wetland communities inside and outside the influence of each pond based on moisture gradient (Atkinson et al. 2005; Balcombe et al. 2005a).

Averages were calculated using a combination of species coverage and wetland indicator status (WIS) values. The following WIS values were given to each species: 1 = obligate, 2 = facultative wetland, 3 = facultative, 4 = facultative upland, and 5 = upland (US Fish and Wildlife Service 1996). We then calculated weighted averages using the formula:

$$\text{Weighted average} = \frac{(y_1u_1 + y_2u_2 + \cdots + y_m u_m)}{100}$$

where y = relative cover estimates per species and u = the WIS value per species (Atkinson et al. 1993). We calculated % hydrophytic vegetation as obligate, facultative wetland, and facultative plants excluding facultative minus plants (USACoE Laboratory 1987). A paired t-test was used to compare mean weighted averages of vegetative communities and % hydrophytic vegetation inside and outside the influence of beaver ponds.

Results

We recorded 203 plant species during 38 pond surveys including 15 rare species (Table 1), of 36 rare wetland plant species known to occur in the valley (Bonner 2005). The most commonly occurring herbaceous species included *Rubus hispidus* and *Solidago uliginosa* and the most common woody species was *Spiraea alba* (Table 2). Walk around surveys captured 48 species that were not observed in herbaceous or shrub plots along transects (Bonner 2005).

There were no differences between mean S′ ($F_{1,699} = 0.49$, $P = 0.485$) and H′ ($F_{1,699} = 0.01$, $P = 0.955$) in areas influenced by beaver ponds compared to areas not influenced by ponds (Table 3). Among age and size classes, herbaceous communities associated with ponds were similar in S′ (age: $F_{3,29} = 0.09$, $P = 0.967$; size: $F_{2,29} = 1.14$, $P = 0.335$) and H′ (age: $F_{3,29} = 0.25$, $P = 0.863$; size:

Table 1 Rare plant species observed during transect and walk-around surveys of beaver ponds in Canaan Valley, West Virginia, USA, 2004–2005

Species name	Common name	Observations[a]	WIS[b]	Global[c]	State[d]
Abies balsamea	Balsam fir	2	Fac	G5	S3
Campanula aparinoides	Marsh bellflower	2	Obl	G5	S3
Carex atherodes	Awned sedge	1	Obl	G5	S1
Carex canescens	Hoary sedge	24	Obl	G5	S3
Carex comosa	Bearded sedge	1	Obl	G5	S2
Carex projecta	Necklace sedge	1	Facw	G5	S1
Drosera rotundifolia	Sun dew	3	Obl	G5	S3
Glyceria grandis	American mannagrass	5	Obl	G5	S2
Glyceria laxa	Northern mannagrass	1	NL	G5	S1
Juncus filiformis	Thread rush	1	Facw	G5	S2
Salix discolor	Glaucous willow	2	Facw	G5	S2
Scirpus atrocinctus	Black-girdle bulrush	19	Facw+	G5	S3
Scirpus microcarpus	Small-flowered bulrush	14	Obl	G5	S3
Vaccinium macrocarpon	Small cranberry	4	Obl	G4	S2
Veronica scutellata	Marsh speedwell	3	Obl	G5	S1

Nomenclature follows Kartesz (1999)

[a] Observations are the number of ponds at which each species was observed

[b] WIS indicates the wetland indicator status of each species (US Fish and Wildlife Service 1996)

Possible status, in order of decreasing wetland fidelity: *obl*, obligate; *facw,* facultative wetland; *fac,* facultative; *facu*, facultative upland; *upl,* upland. *NL* not listed

[c] Global indicates the status of each species across its range: *G1* critically impaired, *G2* imperiled, *G3* vulnerable, *G4* apparently secure, *G5* secure

[d] State shows the status of each species in West Virginia: *S1* critically impaired; *S2* imperiled, *S3* vulnerable, *S4* apparently secure, and *S5* secure

Table 2 Most commonly occurring plant species (frequency) around beaver ponds in Canaan Valley, West Virginia, USA based on the number of ponds at which each species occurred

Scientific name	Mean cover[a]	SD[b]	Maximum cover[c]	Ponds[d]
Rubus hispidus	17.816	11.981	47.22	36
Solidago uliginosa	7.662	7.637	25.83	31
Juncus effusus	2.710	2.970	13.18	31
Glyceria canadensis	2.341	3.825	16.55	30
Triadenum virginicum	1.394	2.016	7.50	29
Hypericum ellipticum	0.979	1.925	10.50	29
Carex scoparia	0.919	1.326	5.63	26
Solidago rugosa	2.858	3.757	15.23	25
Gallium tinctorium	1.407	2.572	14.07	25
Juncus subcaudatus	1.188	1.865	8.41	25
Spiraea alba	14.322	22.698	97.50	24
Carex canescens	1.428	2.842	13.64	24
Danthonia compressa	2.845	3.765	13.09	23
Carex echinata	2.032	3.152	16.09	22
Sparganium erectum	1.606	2.889	11.50	22
Pteridium aquilinum	1.066	2.233	10.45	21
Polygonum satittatum	0.282	0.457	1.81	21
Carex folliculata	1.522	2.577	9.20	20

Nomenclature follows Kartesz (1999)

[a] Mean is average cover for each species

[b] S D is the standard deviation of cover percentage for each species

[c] Maximum cover is the greatest cover percentage of each species for one pond

[d] Ponds is the number of ponds at which each species was observed

$F_{2,29} = 0.12,\ P = 0.890$). The frequency of rare plant occurrence also showed no significant differences among pond age classes ($F_{3,34} = 1.38$, $P = 0.266$). Additionally, our results show no significant difference in total herbaceous and shrub S′ among size classes ($F_{2,35} = 0.63,\ P = 0.539$) but show age classes having a significant effect on S′ at the pond level ($F_{3,34} = 3.28,\ P = 0.033$). Post-hoc analysis shows that the youngest ponds have the highest species richness and that they differ significantly from the two middle age-classes of ponds (Table 3). Average percent cover was higher in areas not influenced by ponds ($t_{37} = -4.09,\ P < 0.001$), but was similar among age classes ($F_{3,34} = 2.69$, $P = 0.062$). Although percent hydrophyte cover also was similar among age classes ($F_{3,34} = 0.66$, $P = 0.584$), it was greater in areas influenced by ponds ($t_{37} = 5.67,\ P < 0.001$). Overall, results indicate that while all areas are diverse, shorter-lived ponds provide habitat for a wide range of species.

Weighted averages were calculated for 38 ponds using cover estimates of 150 herbaceous species. Mean averages for communities inside ($\bar{x} = 1.0$, $SE = 0.07$) and outside ($\bar{x} = 2.1$, $SE = 0.15$) the influence of beaver ponds were both below 3.0, indicating all communities support predominantly hydrophytic vegetation (Kindscher et al. 1998). Results showed significantly lower values ($t_{37} = -6.64$, $P < 0.001$) for herbaceous communities associated with beaver ponds (Table 3). This indicates more obligate wetland communities when influenced by beaver impoundments.

Multi-response permutation procedures were run using total vegetative occurrence and using rank-transformed shrub and herbaceous cover (Table 4). An analysis of herbaceous communities based on proximity to beaver ponds showed an influence of location on the vegetative community composition ($P < 0.001$). Our MRPP results of vegetation occurrence shows no significant influence of size ($P = 0.095$) or age ($P = 0.503$) on herbaceous community structure around beaver ponds. Similar results were found for shrub community composition based on age ($P = 0.357$) and size ($P = 0.840$) classes.

Our 3-axis ordination had a final stress of 13.3 and a final instability of 0.0001 after 85 iterations. Community data sets often have final stress values between 10 and 20, and values less than 20 indicate more or less reliable solutions (McCune et al. 2002). The ordination was significantly different from the Monte Carlo

Table 3 Multiple analyses of vegetation data from Canaan Valley, West Virginia, USA, 2004–2005

Index	Plot location		Pond Age (Years)			
	Inside x̄ (SE)	Outside x̄ (SE)	>56 x̄ (SE)	>36–56 x̄ (SE)	>6–36 x̄ (SE)	≤6 x̄ (SE)
Total percent cover	73.138a (1.603)	97.672b (2.966)	80.521a (7.866)	88.682a (8.827)	65.686a (5.095)	57.563a (13.559)
Species richness/plot	5.683a (0.130)	5.522a (0.169)	5.088a (0.238)	5.459ab (0.276)	6.035a (0.194)	5.591ab (0.426)
Diversity/plot	1.171a (0.025)	1.168a (0.033)	1.044b (0.049)	1.116ab (0.055)	1.249a (0.037)	1.146ab (0.083)
Total species richness/ pond[a]	–	–	41.833ab (4.020)	35.00b (2.070)	33.368b (2.930)	49.60a (5.163)
Rare plant species richness[a]	–	–	3.167a (0.703)	2.000a (0.463)	2.158a (0.336)	1.400a (0.510)
Weighted averages	1.020a (0.071)	2.053b (0.145)	1.106a (0.114)	1.343a (0.228)	0.915a (0.037)	0.798a (0.177)
% Hydrophytic[b]	97.581a (0.805)	86.743b (2.023)	98.606a (0.763)	95.411a (2.369)	97.963a (1.236)	98.369a (0.562)

Index represents the dependent variable being tested. Groups were tested between locations in relation to beaver ponds (plot location) and for differences among age (pond age). All numbers shown are untransformed data

The same lower case letter following means indicate no significant differences between plot location or among pond ages ($P > 0.05$)

[a] Data from walk around surveys are included. Plot location cannot be determined

[b] % hydrophytic includes obligate, facultative wetland, and facultative plants excluding facultative minus plants (USACoE Laboratory 1987)

simulation ($P < 0.01$), and the total variation explained by the three axis solution was 86%.

Figure 1 shows the spatial relations of plots and select species along axes 2 and 3. Axis 2 accounted for 22% of the variation of plots in species space. Percent cover of bryophytes was strongly correlated with this axis ($r = -0.79\%$), as were *Solidago uliginosa* (+0.50), and *Eleocharis obtusa* (−0.41). Vectors connecting pairs of inside-outside plots were primarily oriented along axis 3, consistent with the larger percent variation explained by this axis (49%). Communities that were classified as outside the area influenced by the pond occurred primarily in the upper portion of the ordination. Species that were strongly positively correlated with axis 3 included *Rubus hispidus* ($r = +0.80$), *Solidago rugosa* (0.60), *Danthonia compressa* (+0.55), *Euthamia graminifolia* (+0.53) and *Pteridium aquilinium* (+0.48), all with wetland indicator statuses ranging from facultative wetland to upland. Within pond-plots were arrayed along the bottom of the ordination. These plots were less tightly clustered, and were characterized by more emergent and obligate wetland species with negative correlations to axis 3 such as *Eleocharis obtusa* ($r = -0.49$), *Leersia oryzoides* (−0.44), *Carex canescens* (−0.40) and *Sparganium chlorocarpum* (−0.33) (Table 5). Percent cover of open water also was negatively correlated with this axis ($r = -0.51$). Plot placement in the ordination and axis 3 species correlations suggest that this axis represents a combination moisture/elevation gradient, with plots arranged from open water at the bottom of the ordination to drier, higher plots at the top of the ordination.

Discussion

The beaver ponds in Canaan Valley create high quality wetland habitats that differ in species composition from those areas immediately outside the beaver impoundments. As most community changes were distinct upon gradient changes, topography and the resulting hydrology may be important factors in this analysis of community composition. Basin morphology and resulting hydrology also were found to be important factors in large scale vegetative composition patterns in New Hampshire (Koning 2005). In our study, younger ponds (1–6 years) showed a higher species richness than ponds 7–56 years of age. Although we used four age groups in the analyses, the two middle groups did not differ, indicating that the higher species richness may be due to the ponds being new to the landscape. When flooding occurs,

Table 4 Results of the multiple response permutation procedure (MRPP)

	Distance[a]	Obs. delta[b]	Exp. delta[c]	A[d]	T[e]	P value[f]
Age-Herbaceous		0.501	0.5	−0.0029	0.097	0.503
>56 years	0.395					
>35–56 years	0.495					
>6–35 years	0.526					
≤6 years	0.547					
Size-Herbaceous		0.483	0.5	0.033	−1.368	0.095
Small	0.355					
Medium	0.481					
Large	0.559					
Age-Shrub		0.495	0.5	0.009	−0.261	0.357
>56 years	0.518					
>35–56 years	0.543					
>6–35 years	0.473					
≤6 years	0.469					
Size-Shrub		0.513	0.5	−0.0267	0.961	0.840
Small	0.473					
Medium	0.551					
Large	0.465					
Location-Herbaceous		0.398	.5	0.202	−23.266	<0.001
Inside	0.433					
Out	0.362					

Testing the null hypothesis of no significant difference in herbaceous or shrub community composition between sites based on size and age classes and location in relation to beaver ponds in Canaan Valley, West Virginia, USA

[a] Distance is the mean Sørenson distance between each combination of quadrats from each size or age class

[b] Observed delta is determined from sample data

[c] Expected delta is calculated from a null distribution

[d] A is the chance-corrected within-group agreement

[e] T is the MRPP test statistic

[f] P-value was significant at 0.05 for all tests

the established plant community is largely displaced and replaced by guilds of more water-tolerant species (Mitchell and Niering 1993). Many of these are rare plants that tolerate wetlands with shallow standing water such as *Carex atherodes*, *C. canescens*, and *Juncus filiformis* (Squires and van der Valk 1992). The high species richness associated with these youngest ponds may be attributed to a combination of new species growth along with species remaining from periods before inundation. This supposition is supported by a higher SE to mean ratio for the weighted averages. Balcombe et al. (2005a) cites the possibility of competitive exclusion occurring as wetlands age, which could explain the 7–56 year-old wetlands harboring fewer species. While S′ was significantly lower for two middle age groups, the oldest ponds show mean S′ that is equivalent to the high levels found in the youngest beaver ponds. This eventual increase in S′ may be due to stabilization of community structure (i.e., improved evenness) and a reduction in the coverage of aggressive colonizers after disturbance. In created wetlands, older ponds have higher levels of organic matter (Atkinson and Cairns 2001), which is necessary for wetland stabilization (Balcombe et al. 2005a).

Vegetative community structure is an important indicator of wetland function (Balcombe et al. 2005a), and may affect the community composition of other guilds, particularly invertebrates (Anderson and Smith 2000) and amphibians (Anderson et al.

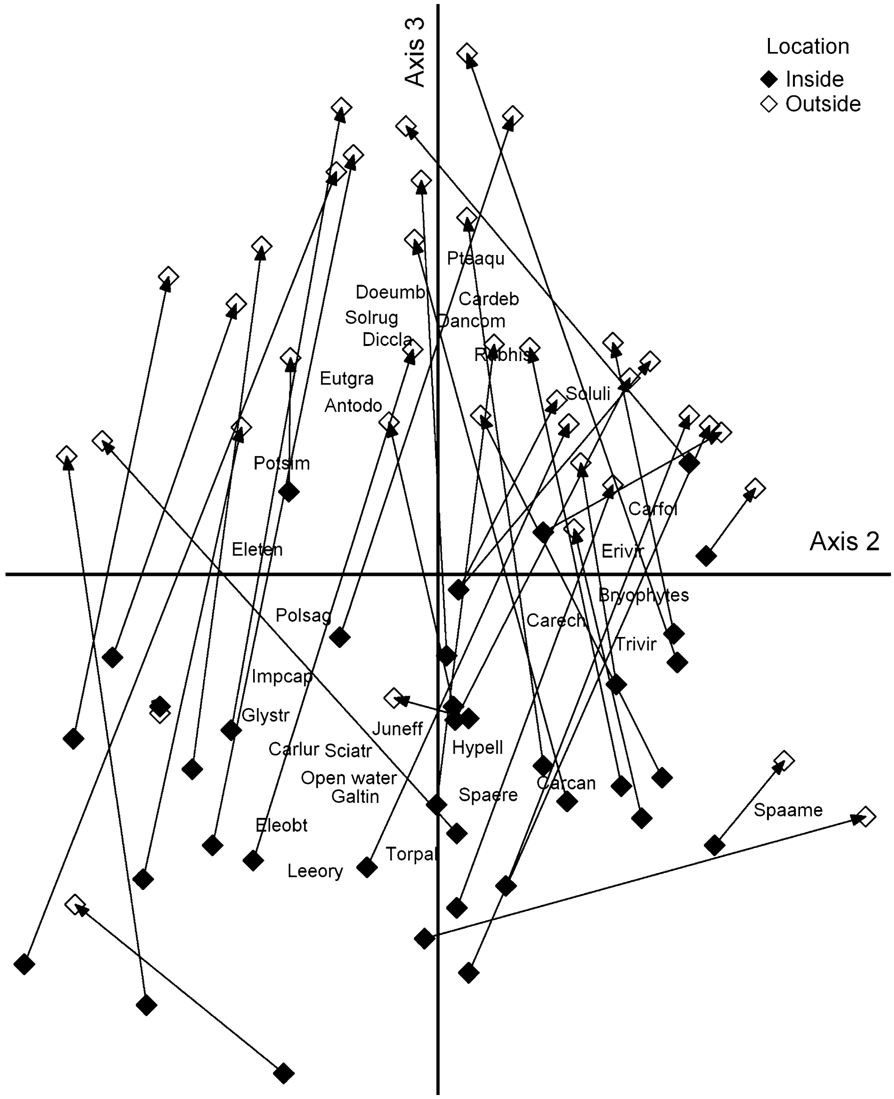

Fig. 1 Nonmetric multidimensional scaling ordination of plant species cover values for 36 beaver ponds in Canaan Valley, West Virginia, 2004–2005. *Solid diamonds* indicate communities inside the influence of the impoundment; *hollow diamonds* represent communities outside the influence of the pond. Six-letter abbreviations of species with Pearson product-moment correlations with correlation axes ≥ 0.30 are shown. Vectors connect pairs of inside–outside ponds

1999; Balcombe et al. 2005b). Proximity to impoundment was found to be a significant factor in determining herbaceous community composition. Our MRPP comparison of surveys inside and outside the influence of impounded water indicates a community shift occurs as distance from ponds increases. This is supported by NMS analysis of these communities and examination using weighted averages. The most explanatory axis (Axis 3) describes almost one half of the variation in pond vegetation ($R^2 = 0.49$). We believe this axis to be representative of a decreasing water level as distance from a pond increases. Species strongly positively correlated with Axis 3 include facultative upland species (i.e., *Pteridium acquilinium*), facultative (i.e., *Solidago rugosa*) and facultative wetland (i.e., *Rubus hispidus*) species. However, negative correlations were exclusive to obligate wetland species (i.e., *Leersia oryzoides, Carex canescens,* and *Sparganium chlorocarpum*), bryophytes, and open water. Moreover, weighted averages indicate that areas outside the pond's influence were more facultative wetland habitats than those communities influenced by beaver ponds. Habitat differences were apparent when individual species average cover values were compared between areas inside and outside the pond's influence. For example, average cover of *Carex canescens*, *Dulichium arundinaceum*, *Eleocharis obtusum*, and *Ludwigia palustris* were all ten times greater inside the pond's influence. In contrast,

Table 5 Correlations of herbaceous species and cover types associated with two primary axes in non-metric multi-dimensional scaling (NMS) ordination for beaver ponds in Canaan Valley, West Virginia, USA

Species name	Correlation[a]	Status[b]	Axis[c]
Bryophytes	−0.68		2
Solidago uliginosa	−0.556	obl	2
Open water	−0.553		3
Carex canescens	−0.398	obl	3
Bryophytes	−0.352		3
Carex folliculata	−0.321	obl	2
Leersia oryzoides	−0.318	obl	3
Gallium tinctorum	0.376	obl	2
Dichanthelium clandestinum	0.394	fac+	3
Pteridium aquilinum	0.429	facu	3
Leersia oryzoides	0.459	obl	2
Euthamia graminifolia	0.466	fac	3
Rock/Bare ground	0.498		2
Eleocharis obtusa	0.501	obl	2
Solidago rugosa	0.607	fac	3
Rubus hispidus	0.792	facw	3

Nomenclature follows Kartesz (1999)

Possible status, in order of decreasing wetland fidelity: *obl,* obligate; *facw,* facultative wetland; *fac*, facultative; *facu*, facultative upland and *upl*, upland

[a] Correlation is the r-value of each species or cover type. Most strongly correlated ($r > 0.30$) species are shown

[b] Wetland indicator status is shown for each species (US Fish and Wildlife Service 1996)

[c] Axis indicates the ordination axis to which the species or cover type is correlated

Doellingeria umbellata, *Solidago rugosa*, and *Pteridium acquilinum* were greater than ten times more abundant in habitat beyond the influence of the beaver pond. These shifts in species composition and wetland indicator status are probably due to more species being adapted to long-term saturation or inundation near beaver ponds. A difference in both structure and fidelity of wetland vegetation in areas influenced by beaver ponds indicates this habitat provides unique conditions for certain communities.

However, our MRPP analyses showed no significant influence of pond age or size on community composition. Although this does not preclude their having a role in community structure, this does indicate that any role would be small in comparison with other factors. Activity levels, as well as abandonment, were not used as qualifications for pond surveys. The potential differences in abandoned beaver ponds are great. Beaver foraging activity, or lack thereof, could affect nutrient flow in surrounding areas (Johnston and Naiman 1987); thereby affecting present vegetative composition. Some ponds, although still retaining water, could have been in an alternate successional stage due to recent abandonment, thus affecting our analysis of community structure. Vegetative communities are often dictated by soil nutrients, type, and moisture (Barbour et al. 1987, Olde Venterink et al. 2003; Drohan et al. 2006). These factors were not sampled during this study. However, they have the potential to influence species composition, growth, and persistence. Future studies of vegetation in beaver habitats may require the incorporation of these variables plus water depth and microtopography into sampling and analyses.

Although more than twice as many rare plant species occurred on the oldest ponds compared to the youngest ponds, there was no statistically significant difference in rare plant species richness. We believe the lack of significance can be contributed to the small number of locations where individual rare plants occurred, a problem inherent in sampling rare species (Steidl et al. 1997). We believe our sampling protocols were adequate to pick up rare species in beaver ponds due to the combination of plot sampling and walk-around visual surveys (Poon and Margules 2004). Older ponds were found to harbor some rare plant species not found elsewhere in our study area. One such species, *Carex atherodes*, is the southernmost population in its distribution and the only location known in West Virginia. Several rare plant species and communities occur at the periphery of their range in our study area. In a study of a perennial rare plant species *Lychnis viscaria*, peripheral populations experienced lower genetic diversity than central populations and genetic isolation was greater than expected by distance between populations (Lammi et al. 1999). These details may be significant for Canaan Valley, where many rare plant species and rare plant communities, but not necessarily individuals occur (see Fortney 1975). However, Lammi et al. (1999) also found that peripheral populations could maintain similar fitness levels as core populations. This finding may suggest that other rare plant populations, such as those found in Canaan Valley, are still viable and may be able to expand or persist with conservation efforts. Overall, it appears that a diversity of beaver pond ages is desirable to maximize floristic diversity in Canaan Valley.

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