

LOCAL VS. LANDSCAPE CONTROLS ON PLANT SPECIES RICHNESS IN BEAVER MEADOWS

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Abstract. There is considerable interest in determining whether the species richness of communities is determined by forces controlling dispersal into patches that operate at the landscape scale, or forces controlling persistence that act at the local scale. Understanding the relative importance of these two classes of factors in controlling within-patch species richness is particularly important when patches are created via ecosystem engineering. In such cases, factors affecting the population dynamics or behavior of a single species could indirectly affect species richness if richness is controlled primarily by landscape-level factors. We used a combination of experimental mesocosms and field observations to determine whether species richness in beaver wetlands in the Adirondack Mountains (New York) is more strongly controlled by the position of the wetland in the landscape or by within-wetland hydrology. Drainage rate had a significant effect on both richness and composition in mesocosms, with well-drained treatments having significantly higher richness than poorly drained treatments. Seed germinated from the seed bank in sediments collected from different ponds showed relatively small differences in richness or community composition in mesocosms, suggesting a comparatively small effect of dispersal limitation on species richness. Experimental results were mirrored in a survey of 14 meadows over two years, which indicated that variability in water table depth was consistently a significant predictor of species richness, while meadow area and isolation showed little relation to richness. The survey also suggested that the number of years since beaver had abandoned a site was a significant predictor of the number of species found in beaver meadows. The results indicate that species richness in beaver meadows is strongly controlled by local factors, but that the population dynamics of beaver could also potentially affect species richness by altering the age distribution of meadows across the landscape.

Key words: Adirondack Mountains, New York (USA); beaver; beaver meadow; dispersal limitation; ecosystem engineer; heterogeneity; seed bank; species richness; wetlands.

INTRODUCTION

There has been considerable debate over whether the number of species found in a patch is more strongly controlled by forces acting at the landscape or local level. In a patchy landscape, the number of plant species found in any particular patch is the result of the interaction between dispersal and persistence. For a species to be present in a patch, it must first disperse from the regional species pool into the focal patch, then establish and persist. The species richness of a patch will be the sum of those species present in the regional species pool that successfully disperse into and persist in the patch (van der Valk 1981).

Dispersal into a patch is primarily controlled by factors relating to the patch's position in the landscape. Island biogeography theory predicts that island size and isolation from mainland source populations should ex-

ert the strongest controls on the species richness of an island (MacArthur and Wilson 1967). More recently, neutral models of biogeography have suggested that difference in species richness in patches should be primarily controlled by differences in dispersal (Bell 2001, Hubbell 2001). Numerous studies have shown that, indeed, less isolated and larger islands and habitat patches receive more colonists and contain more species than small, isolated islands (Simberloff and Wilson 1969, Simberloff 1976, Rydin and Borgegard 1988, Kohn and Walsh 1994).

Relative to the more global factors determining arrival at a patch, factors influencing plant establishment and persistence are largely local factors and operate within the patch. For a species to persist in a patch, individuals must be able to tolerate local abiotic and biotic conditions. When species differ in their capacity to establish under different abiotic conditions, patches with internal heterogeneity in such conditions are likely to have higher species richness than patches with little internal heterogeneity (Hutchinson 1959, Huston 1994, Wilson 2000). In addition to the constraints imposed by the abiotic environment, species can be excluded from a patch by the presence of competitively dominant

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species or herbivores (Parker and Root 1981), or the absence of mutualistic or facilitative species (Bertness and Hacker 1994). Plant species richness typically increases after a patch is created, but later declines due to dominance by competitively superior species (Billings 1938, Reiners et al. 1971, Sousa 1979). The rate with which competitive exclusion occurs may be a function of site productivity (Huston 1979).

Understanding the relative importance of local vs. landscape-level controls on species richness in patches becomes particularly relevant when patches are generated by organisms. If patches are created by ecosystem engineers (Jones et al. 1994), the density, reproductive rates, and behavior of the engineer have the potential to alter the number, persistence, and position within the landscape of the patches they create (Gurney and Lawton 1996). Altering patch dynamics (e.g., the distribution of patches across a landscape or the average time patches are active) can affect patch isolation, age distribution, and size, but is less likely to markedly affect within-patch heterogeneity. Thus, the role of ecosystem engineers in controlling species richness within engineered patches will depend on whether patch-level richness is more strongly affected by controls on dispersal or controls on establishment and persistence.

We examined the relative importance of landscape-level versus local control of species richness in beaver meadows. The Adirondack landscape is dotted with beaver meadows, which are wetlands that form at sites formerly dammed by beaver and subsequently abandoned. These habitats are an ideal system for examining the relative importance of local and landscape-level controls on plant species richness. Wetlands tend to have a patchy distribution across the landscape, and the composition of wetland plant communities can be strongly affected both by dispersal and the abiotic environment of the site (van der Valk 1981, Brose 2001). Dispersal of seeds by mechanisms such as hydrochory (Honnay et al. 2001) or zoochory (Mueller and van der Valk 2002) can lead to wetlands that differ in richness and composition depending on their location relative to other wetlands. Wetlands are often characterized by fluctuating water levels (Mitsch and Gosselink 1993), and colonization of newly exposed sediments, typically via a seed bank, can generate strong spatial patterns in wetland vegetation (Gaudet 1977, van der Valk and Davis 1978, Leck 1989). Wetland plants are also markedly influenced by subtle physical environmental gradients, particularly water level (Gemborys and Hodgkins 1971, Walker and Wehrhahn 1971, Keddy 1984). Thus, heterogeneity in the physical environment can control species richness in wetlands (Vivian-Smith 1997, Pollock et al. 1998, Brose 2001).

Beaver meadows are particularly useful wetland systems for studying the role of landscape-level and local processes in structuring wetland plant communities. All meadows are created by the same mechanism, i.e., flooding of the riparian zone by beaver followed by

draw down when the pond is abandoned, yet individual meadows are highly variable in richness and composition (McMaster and McMaster 2000). Individual meadows form distinct patches in the landscape with clearly defined edges (Johnston and Naiman 1987, Terwilliger and Pastor 1999), forming "islands" of wetland habitat that contain an herbaceous plant community that is markedly different from that of the adjacent, unmodified riparian zone (Wright et al. 2002) and upland forest (Wright 2002). Furthermore, since beaver meadows are the only large open wetlands in the central Adirondacks, they are the only habitat available for many wetland species. As such, meadows make a significant contribution to landscape-level diversity, increasing species richness of the riparian zone by 33% (Wright et al. 2002). Variability between meadows is potentially important in contributing to this large landscape-level effect.

Here we combine mesocosm experiments and field observations of beaver meadow richness to examine the relative importance of landscape-level and local controls on species richness in beaver meadows in the central Adirondacks. The study had two specific objectives. First, to determine the effect of seed bank source (from ponds with varying degrees of isolation from active meadows, reflecting constraints on dispersal) and drainage rate (reflecting constraints on establishment) on richness and composition of experimental beaver meadow communities. Second, to determine if results from this experiment could predict patterns found in a large scale study of beaver meadows that measured plant species richness and factors influencing both dispersal (size, isolation, and age of the site) and establishment (depth to water table and variability in water table depth).

METHODS

Site description

All research was conducted on the Huntington Wildlife Forest (HWF), a 6000-ha preserve located in the central Adirondack Mountains, New York (latitude 44°00' N, longitude 74°13' W). The topography is mountainous with elevations ranging from 457 to 823 m. The predominant vegetation consists of mixed northern hardwood and coniferous forest. HWF has a mean annual temperature of 4.4°C, and mean annual precipitation is 1010 mm.

The primary form of disturbance in the riparian zones of the Adirondacks is the damming of streams by beaver, resulting in the creation of ponds that can inundate areas ranging from 0.4 to 24 ha (Dickinson 1971). On the HWF, beaver remain active at a site for an average of 4 years (range 1–20 years; C. Demers, unpublished data). Once abandoned, dams disintegrate causing ponds to drain and exposing accumulated sediments. These sites then develop into wet meadows dominated by *Calamagrostis canadensis* and several



FIG. 1. Map of the Huntington Wildlife Forest (HWF) in the Adirondack Mountains, New York, showing sites of active beaver ponds where sediments were collected for the mesocosm experiment (stars) and the beaver meadows (open circles) that were surveyed for patterns of plant species richness. Naturally occurring lakes are gray, and the bold line represents the boundary of HWF.

species of *Carex*. Most sites show considerable spatial heterogeneity in how quickly they drain; areas near the upland edge generally dry quickly, while areas adjacent to the former dam can remain under standing water for several years (J. P. Wright, *personal observation*). Once formed, these meadows can persist for over 70 years, and rarely, if ever, revert back to the original, forested riparian zone (Remillard et al. 1987).

Seed bank and drainage experiment

To determine the importance of dispersal constraints in controlling species richness in early successional beaver meadows, we collected sediment from the bottom of six active beaver ponds located throughout HWF

(Fig. 1). Sediments were collected from throughout each pond in June 1999, and all sediments from a site were thoroughly mixed before distributing them across mesocosms designed to simulate conditions in a newly drained beaver pond. Mesocosms consisted of 0.785-m² plastic wading pools with holes drilled into the sides 10 cm from the bottom to facilitate drainage. To test the effect of drainage rate on species richness, half of the mesocosms (fast-drainage treatment) had an additional row of holes on the sides, 5 cm from the bottom, as well as an array of holes in the bottom of the wading pool. The slow-drainage treatment had only the higher holes on the sides and no drainage through the bottom of the mesocosm. There were four replicates of each

TABLE 1. Characteristics of beaver meadows selected for the survey of within-meadow patterns of plant species richness.

Meadow	Area (ha)	Distance to nearest meadow (m)	Years since abandonment	Mean water table depth (cm)	Water table depth (SD)	Rarefied species richness	
						2000	2001
Adjidaumo 1	1.04	504	3	-6.8	2.40	25.5	27.0
Adjidaumo 2	1.04	504	3	-2.1	6.82	31.9	29.6
Adjidaumo 3	1.05	596	5	-6.1	5.33	35.5	30.8
Boundary	1.12	303	17	-9.8	5.35	37.3	36.1
Little Sucker Brook	1.14	690	8	-45.5	19.03	44.3	40.6
Panther Brook	0.31	598	5	-35.1	21.86	48.5	44.3
Rianna	1.38	278	6	-23.0	12.47	43.1	38.2
Spruce Peninsula	0.33	246	3	-16.1	6.75	18.9	17.3
Truckah	0.50	134	6	-27.2	10.02	49.5	43.3
Willow	1.23	623	19	-12.4	6.75	41.9	35.4
Wolf 1	0.23	135	7	-23.2	10.12	47.5	38.0
Deer Pond	4.22	357	5	-2.8	4.85	N.D.	30.0
Upper Sucker Brook	0.31	157	14	-11.4	6.67	N.D.	34.5
Wolf 2	0.34	135	10	-0.7	7.58	N.D.	30.0

Notes: Mean water table depth represents the mean of measurements made early (late June) and late (late August) in the growing season of 2001. Richness estimates in both 2000 and 2001 are rarefied to reflect the number of species found in 30 samples in order to correct for differences in sampling intensity between meadows. Richness values for meadows that were not surveyed in 2000 are designated N.D.

site by drainage treatment combination, yielding a total of 48 experimental units.

Mesocosms were set into the ground to a depth of 10 cm to stabilize sediment temperatures and were arrayed in four blocks in a sandpit devoid of vegetation. The sandpit minimized seed rain from nearby plants, facilitated drainage, and provided the full-sun environment characteristic of newly exposed beaver pond sediments. Sediment was added to the mesocosms to a depth of 10 cm. Mesocosms were watered weekly with water from a nearby pond if there had been no significant precipitation during the previous week, with all treatments receiving ~4 L of water each time they were watered.

In August 1999 and 2000, one-quarter of each mesocosm was selected at random for harvesting. All individuals were harvested, collecting both above- and belowground biomass, sorted by species, and dried to constant mass at 60°C before weighing. After the 2000 harvest, soil samples were collected to determine soil moisture, organic matter content (OM), and total inorganic nitrogen concentrations (TIN). A 20-g subsample of each soil sample was dried to constant mass at 60°C to determine soil moisture content. Organic matter content of soil was calculated from subsamples based on percent mass loss of dried soils after ashing at 450°C until soils reached a constant mass. An additional subsample was used to determine TIN. Inorganic nitrogen was extracted from ~20 g of soil using 2 mol/L KCl (Robertson et al. 1999). Following extraction, KCl solutions were frozen until they were analyzed for nitrate and ammonium concentrations using an Alpkem autoanalyzer at the Institute of Ecosystem Studies analytical lab, Millbrook, New York. Nitrate and ammonium concentrations were summed to calculate TIN, and are reported on a milligrams of TIN per grams of dry soil basis.

To compare soil moisture conditions observed in mesocosms with those found in the field, we collected soil from throughout a typical beaver meadow (Rianna; Table 1) in June 2000. Soil samples were collected adjacent to the 50 vegetation plots set up for the meadow survey. Soil moisture content of two 20-g subsamples from each plot was measured by drying to constant mass at 60°C.

Meadow survey

In July 2000, 11 meadows were surveyed to determine the relative importance of landscape-level (area, isolation) vs. local (mean water table depth, variation in water table depth, age) variables in influencing species richness. In July 2001, these meadows were re-surveyed along with three additional meadows. Meadows spanned a range of area and times since abandonment, and were located throughout the HWF (Table 1, Fig. 1). At each site, a point on the bank of the stream was picked at random for the start of a sampling grid. Grids consisted of five 50-m transects running perpendicular to the primary direction of the stream, separated from each other by 10 m. Each transect contained ten 0.5 × 1.0 m plots, spaced at 5-m intervals, yielding 50 sample plots per site. At sites that were too small to accommodate the entire sampling grid ($n = 6$), plots that occurred in the adjacent forest were excluded from all analyses.

In each plot, all species of herbaceous vascular plants were identified (see the Appendix). The depth to water table at each plot was monitored using a 1-m slotted well constructed of 1.12-cm (0.5-inch) polyvinyl chloride (PVC) pipe (Sobczak and Findlay 2002). Water table depths were measured early in the growing season (late June) and late in the growing season (late August), and the average of these two measurements was used as an index of the relative moisture regime experienced

by plants within a plot. In sites dominated by tussock sedge (*Carex stricta*), depth to water table was calculated from the soil surface rather than the tops of the tussocks in order to standardize methods across sites. We also measured the elevation above mean stream elevation for each plot as an index of flooding frequency (Pollock et al. 1998). However, as elevation was strongly correlated with water table depth (Pearson correlation coefficient between-site means = 0.917; between-site standard deviations = 0.902), elevation measurements were not used in further analyses.

We created a GIS layer mapping all beaver-modified areas on the HWF in ArcView (ESRI 2000) from digitized, color infrared aerial photographs taken in April 1998. This map was used to determine the area of each site and the straight-line distance to the nearest meadow. Historical aerial photographs (taken at ~10-yr intervals from 1957 to the present) and annual surveys of beaver activity on HWF (performed every fall from 1951–1957 and 1979 to present; C. Demers, *unpublished data*) were used to determine the last time beaver were active at a site. Since beaver ponds typically drain within a year of abandonment, the year of the last recorded beaver activity was used as a surrogate for the age of a meadow.

Data analysis

Data on mesocosm richness from the experiment were analyzed with a mixed-model, randomized, complete-block ANOVA using GLM (SYSTAT 1997). Seed source (i.e., the pond in which sediments were collected) was treated as a random factor with six levels, while drainage was treated as a fixed factor with two levels. Because some species were classified to different levels of taxonomic resolution in different years, separate analyses were run for the first and second years of the experiment. To test for the possibility that a significant effect of seed source on richness could be due to differences in sediment chemistry rather than differences in seed bank composition, we performed randomized, complete-block ANOVAs with seed source and drainage as factors and TIN and OM as dependent variables using GLM (SYSTAT 1997). TIN concentrations were log transformed prior to analysis to meet assumptions of a normal distribution. We also performed linear regressions between richness and TIN, and richness and OM to examine the influence of these chemical factors on species richness.

We compared the species composition of the different mesocosms by performing a nonmetric multidimensional scaling ordination using the biomass of each species in each experimental unit (McCune and Meford 1999). To determine treatment effects on composition, we calculated the mean ordination values for each treatment along the two axes that showed the highest correlation between ordination distances and distances in the original n -dimensional space (Axes 2 and

3 in both years). We then calculated 95% confidence intervals about those means.

To determine the best predictors of species richness within the meadows selected in the field survey, we performed a multiple regression with the following predictor variables: mean water table depth of the site as determined by the wells, standard deviation of site water table depth, time since site abandonment, distance to nearest beaver meadow, and meadow area. We also included a quadratic term for time since abandonment in the model to test for the possibility of a decrease in richness in older meadows. Due to differences in meadow size of some of the sites, the sampling grid contained some cells that were not located within the meadow. To correct for differences in sampling intensity between sites, we calculated a rarefied estimate of species richness that was based on the number of plots in the smallest site (Colwell 1997). This estimate of richness was used as the dependent variable in the model. Both site age and area were log transformed to meet assumptions of a normal distribution of values. We used GLM to conduct the multiple regression analysis with a backward stepwise procedure to eliminate nonsignificant predictors ($P > 0.15$) from the model (SYSTAT 1997). Separate analyses were conducted on data from the 2000 and 2001 surveys.

To further test the importance of landscape-level controls on site composition, we compared compositional similarity of sites linked by potential dispersal corridors with unconnected sites. If the composition of sites is strongly controlled by dispersal, sites connected by dispersal corridors should share more species than unconnected sites. We used two separate techniques for classifying sites as connected to reflect two dominant modes of dispersal for wetland plants. In the “Stream migration” model, two sites were classified as connected if one site was downstream of the other, reflecting dispersal via hydrochory. In the “Drainage migration” model, two sites were classified as connected if the streams draining both sites emptied into the same large body of water, reflecting dispersal by animal vectors, which might move preferentially along stream corridors. The “Stream dispersal” model divided sites into seven separate clusters, and the “Drainage dispersal” model divided sites into three clusters (considering streams draining into eastern and western Rich Lake as separate drainages). We calculated Morista-Horn similarity indices (Colwell 1997)⁴ for all pairwise comparisons of sites based on the relative incidence of species at each site in 2001. Using this quantification of similarity among sites, we tested for difference in similarity within clusters and between clusters using GLM (SYSTAT 1997).

RESULTS

Effect of site and drainage treatments on mesocosm soils

By the end of the second year of the experiment, soils in the drained treatments were 27% drier than

TABLE 2. Comparison of soil moisture measurements in mesocosms and a natural beaver meadow.

Site	Minimum	Maximum	Mean	SD
Mesocosms	0.223	0.817	0.552	0.140
Natural meadow	0.259	0.877	0.662	0.137

Note: Values for minimum, maximum, and mean are in fraction water by mass.

those in the undrained treatments (mean fraction water by mass = 0.47 ± 0.02 and 0.64 ± 0.02 [mean ± 1 SE], respectively; $t_{24} = 5.68$, $P < 0.001$). The range of soil moisture conditions in experimental mesocosms closely matched the range seen in a natural meadow (Table 2). Drainage treatment had no effect on OM ($F_{1,33} = 1.19$, $P = 0.28$); however, sediments collected from the different sites did differ significantly in soil OM ranging from a mean of $20.3\% \pm 0.038$ (at site SPR) to $48.3\% \pm 0.038$ (at site SNA) ($F_{5,33} = 8.81$, $P < 0.001$). Although these differences could potentially lead to differences between sites in species richness that was independent of seed bank composition, a linear regression showed no relationship between soil organic matter and species richness ($P = 0.47$, $r^2 = 0.01$). The drainage treatment also showed no significant effect on TIN ($F_{1,33} = 2.78$, $P = 0.11$), but there was a significant sediment source effect on TIN ($F_{5,33} = 3.52$, $P = 0.01$). Furthermore, there was a weak, but statistically significant, negative relationship between TIN and species richness ($P = 0.02$, $r^2 = 0.12$; Fig. 2).

Effect of site and drainage treatments on mesocosm richness

After both one and two growing seasons, the species richness of mesocosms was affected by the drainage rate of the plot with slow-drainage plots containing fewer species than fast-drainage plots (Table 3, Fig. 3). These differences were statistically significant following the first growing season and marginally significant

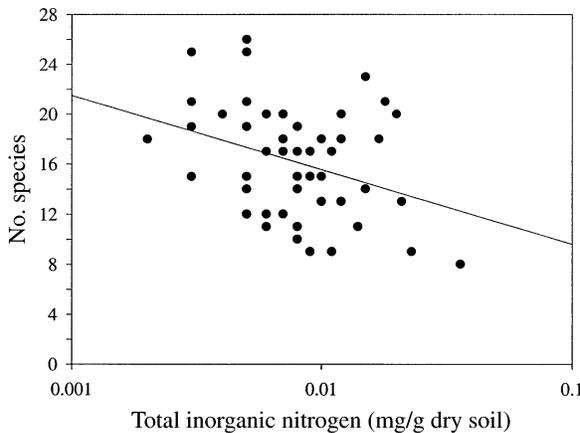


FIG. 2. Effect of total inorganic nitrogen concentrations on plant species richness in experimental mesocosms. The equation for the best-fit regression is $y = 3.266 - 2.662(\ln x)$.

TABLE 3. ANOVAs for the effects of soil drainage and sediment source on species richness in the mesocosm experiment.

Source	df	MS	F ratio	P
Year 1				
Drainage treatment	1	172.521	7.355	0.042
Sediment source	5	52.921	2.250	0.197
Drainage \times source	5	23.521	2.256	0.072
Block	3	7.706	0.679	0.571
Error	33	10.425		
Year 2				
Drainage	1	88.021	5.248	0.071
Source	5	89.071	5.311	0.045
Drainage \times source	5	16.771	1.925	0.117
Block	3	17.076	1.960	0.139
Error	33	8.713		

Notes: Years 1 and 2 of the experiment were analyzed separately. Significant treatments are shown in boldface.

after the second growing season. After one growing season, species richness in mesocosms containing sediment from different ponds ranged from 6.6 ± 1.1 (at site MIL) to 13.6 ± 1.1 (at site TRU) species per 0.39 m^2 , but these differences were not significant (Table 3, Fig. 4A). However, initial differences in species richness persisted between years and were statistically significantly different by the end of the second growing season (Fig. 4B).

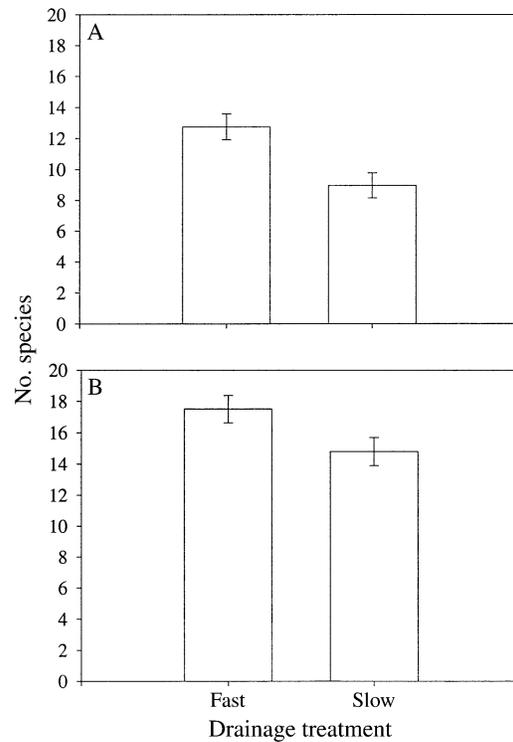


FIG. 3. Effect of drainage treatment on species richness. Bars show mean number of plant species per 0.3925 m^2 (± 1 SE) in fast and slow-drainage mesocosms after (A) one and (B) two growing seasons.

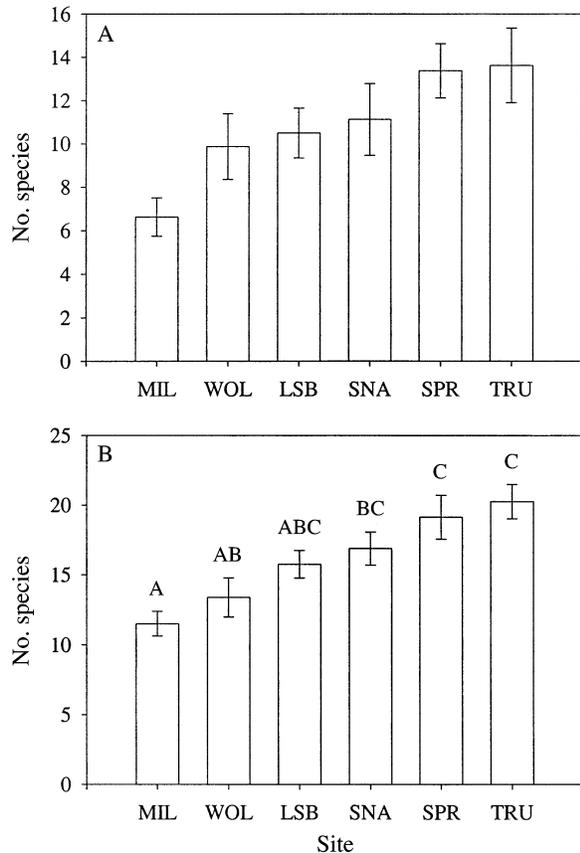


FIG. 4. Effect of sediment source on mesocosm species richness. Bars show mean number of plant species per 0.3925 m² (± 1 SE) in mesocosms containing sediments from the six different beaver ponds after (A) one and (B) two growing seasons. Means with different letters are significantly different ($P < 0.05$) using a Bonferroni comparison.

Effect of site and drainage treatments on mesocosm composition

In both years, the composition of mesocosms was strongly affected by drainage rate treatment as evidenced by the lack of overlap in the 95% confidence ellipses around the mean nonmetric multidimensional scaling (NMS) scores for fast and slow-drainage treatments (Fig. 5). The source of the seed bank did not have any significant effect on composition in either year (Fig. 6), with 95% confidence ellipses from different seed sources showing considerable overlap. Furthermore, there was little interaction between drainage rate and seed source with most sites showing parallel shifts in composition under different drainage treatments (Fig. 7).

Survey of field patterns

The beaver meadows selected for the field survey varied considerably in species richness. After correcting for differences in sampling intensity, there was a greater than two-fold range in rarefied richness between

sites, and sites showed little variability between years in their ranking of rarefied species richness (Table 1). In the year 2000, the number of herbaceous plant species found within a beaver meadow was best predicted by mean water table depth, standard deviation of water table depth, and years since abandonment ($P = 0.001$, adjusted $R^2 = 0.868$; Table 4). In 2001, the best model for predicting species richness included standard deviation of water table depth and years since abandonment, but excluded mean water table depth ($P = 0.006$, adjusted $R^2 = 0.537$). Meadow area, distance to nearest meadow, and a quadratic term for years since abandonment did not enter the best-fit model in either year (Table 4).

Sites linked by potential dispersal corridors were not more similar to each other than unconnected sites. This was true using both the "Stream dispersal" model ($F_{1,89} = 0.159$, $P = 0.478$) and the "Drainage dispersal" model ($F_{1,89} = 1.211$, $P = 0.274$).

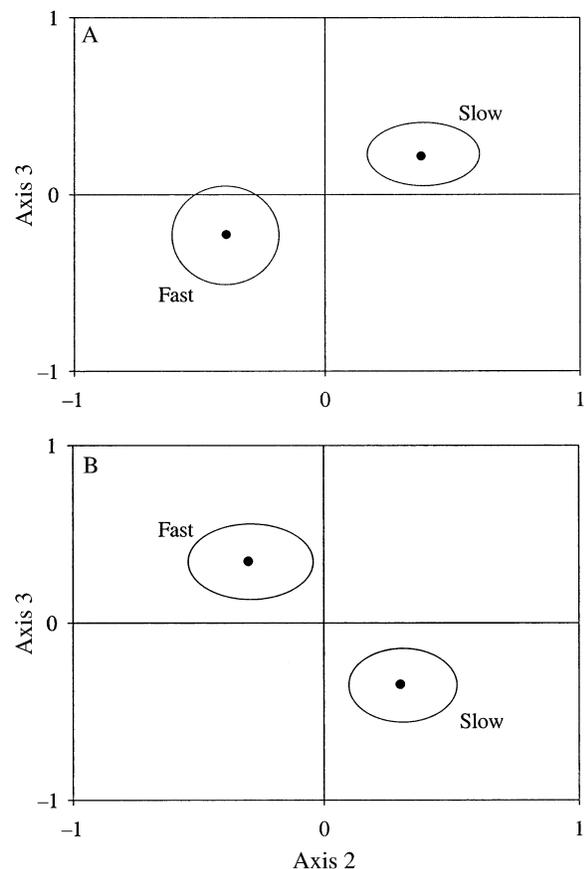


FIG. 5. Effect of drainage treatment on mesocosm composition. The figure illustrates nonmetric multidimensional scaling (NMS) ordination of plant communities in mesocosms from fast- and slow-drainage treatments based on biomass of individual species after (A) one and (B) two growing seasons. Points represent mean scores for treatments, and ellipses encompass 95% confidence intervals about means.

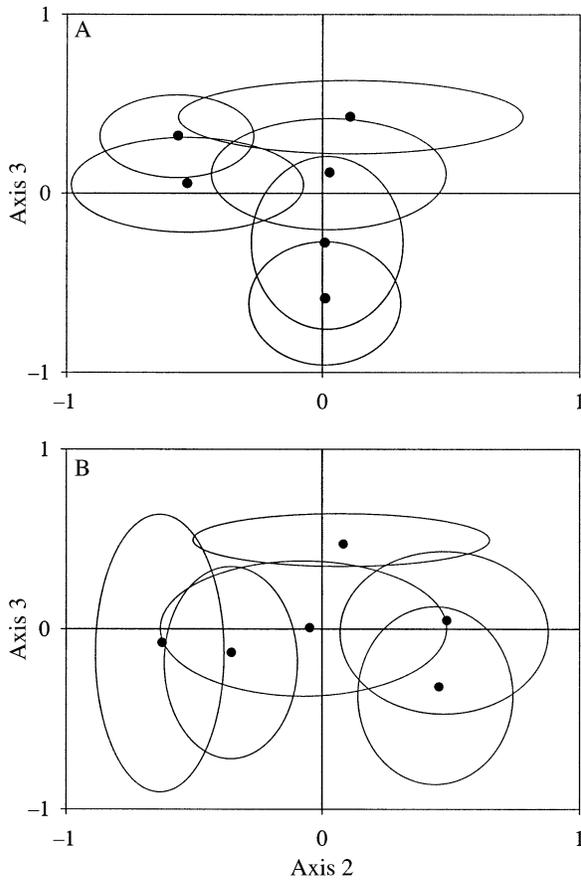


FIG. 6. Effect of sediment source on mesocosm composition. The figure illustrates nonmetric multidimensional scaling (NMS) ordination of plant communities in mesocosms with different seed sources based on biomass of individual species after (A) one and (B) two growing seasons. Points represent mean scores for treatments, and ellipses encompass 95% confidence intervals about means.

DISCUSSION

In both the experimental mesocosms and the survey of beaver meadows, soil moisture had a large effect on herbaceous plant species richness and composition. Plant communities emerging from the seed banks in sediments collected from different ponds differed in richness in the second year of the experiment, but did not differ significantly in composition. Neither isolation, represented as distance to nearest meadow, nor meadow area had a significant effect on meadow-level species richness. Sites linked by potential dispersal corridors did not show greater compositional similarity than unconnected sites. Although factors operating at local and landscape scales are both potentially important, in this system, factors operating at the local scale (i.e., drainage rate within the patch) appear to be more important in affecting local species richness than factors that operate at the landscape scale via influences on seed dispersal into sites.

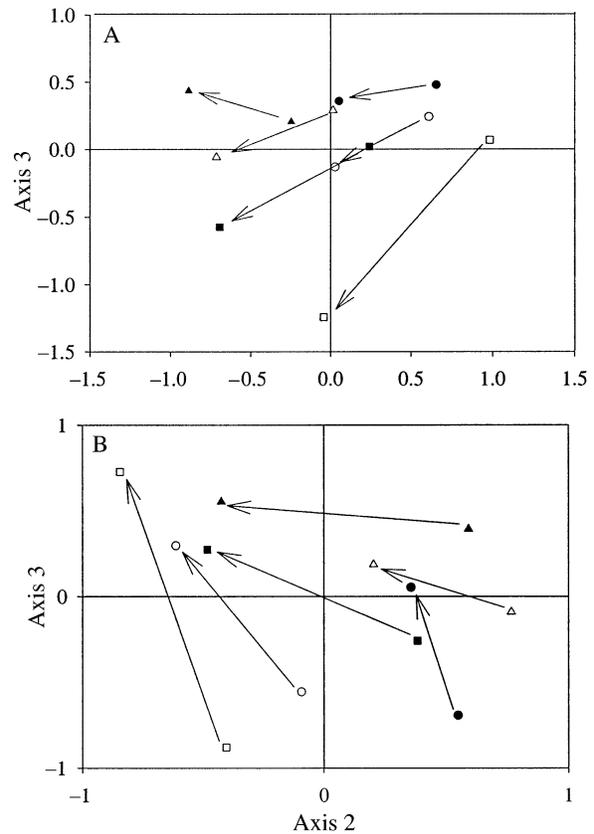


FIG. 7. Interaction of drainage rate and sediment source treatment on plant community structure in mesocosms after (A) one and (B) two growing seasons. Points represent mean nonmetric multidimensional scaling (NMS) scores for each drainage rate by seed source combination. Arrows point from the mean scores of low-drainage mesocosms to the mean scores of high-drainage mesocosms for each seed source. Parallel arrows between treatment combinations for each seed represent no interaction.

TABLE 4. Multiple linear regression analysis of predictors of rarefied meadow species richness.

Variable	Coefficient	F ratio	P
2000			
Mean water table depth	0.421	5.070	0.059
Water table depth (SD)	2.608	18.386	0.004
Years since abandonment	6.613	13.278	0.008
(Years since abandonment) ²	-0.452	1.541	0.261
Area	0.036	0.008	0.933
Distance to nearest meadow	0.276	0.497	0.507
2001			
Mean water table depth	-0.163	0.274	0.612
Water table depth (SD)	0.878	12.718	0.004
Years since abandonment	5.301	4.414	0.059
(Years since abandonment) ²	-0.364	1.530	0.244
Area	0.198	0.409	0.537
Distance to nearest meadow	-0.076	0.058	0.815

Notes: Separate analyses were performed on data from 2000 and 2001. Variables entering as significant predictors are shown in boldface.

If most plant species in beaver meadows are dispersal limited, sediments from ponds that differ in their distance to seed sources should contain seed banks that differ in composition and richness. We did not find support for dispersal limitation during the first year of the experiment. It is possible that seed input from areas adjacent to the experimental site might have overwhelmed differences between seed sources, but this is unlikely for three reasons. First, the experiment was set up in a sandpit with little nearby vegetation, and there were no proximate sources of wetland plants. Second, we observed rapid emergence of seeds from the seed bank, with most treatments being covered with a dense carpet of seedlings within two weeks of the start of the experiment. At this time, most of the common species present in beaver meadows have barely begun to flower, much less set seed (J. P. Wright, *personal observation*). Finally, if the mesocosms were experiencing significant seed input from local sources, we would have expected the significance of the sediment source effect to decrease in the second year rather than increase because mesocosms from all sites would have received more or less equal local seed inputs.

It is possible that the observed differences in species richness between sediment sources were not due to differences in the seed bank composition, which might reflect dispersal limitation, but to variation in sediment characteristics. There were significant differences in both organic matter content and total inorganic nitrogen concentrations between treatments. Although organic matter content showed no relationship with species richness, nitrogen content showed a weak but significant negative correlation with species richness in the second year of the experiment. The association between nitrogen levels and species richness could potentially explain why there were significant differences in richness between sites after the second year. Thus, it may be that nutrient levels are driving differences in species richness between treatments. However, given the strong effect of site on species richness the second year, and the rather weak correlation between nitrogen and richness, it seems unlikely that differences between sites were due entirely to differences in nutrients.

Mesocosm experiments necessarily sacrifice a certain degree of realism to test the importance of particular mechanisms. In this case, even though the variability of hydrologic conditions achieved in the experiment closely matched the variability in a natural meadow, it is possible that generalizations from the experiment to the landscape-scale might be limited. Consequently, one of the goals of this study was to determine whether the variables emerging as important factors in the mesocosm experiment could be used to predict species richness in real beaver meadows. The results of the experiment led to three key predictions. First, drier meadows should have greater species richness than wetter meadows. Second, given the compositional differences between slow- and fast-drainage

treatments, meadows with more spatially variable moisture regimes should have higher species richness than those with low variability. This would be expected, as more variable meadows should include species found in both drier and wetter microsites. Third, factors affecting dispersal into a site such as distance to nearest seed source and area of meadows should have little effect on species richness. In the 2000 survey, mean water table depth was a significant predictor of species richness, but not in the 2001 survey. In both years of the survey, we found higher richness in meadows with more variable depth to water table. There were no relationships between species richness and meadow area or distance to nearest meadow in either years.

The mesocosm experiment was not designed to detect a relationship between time since pond abandonment and meadow species richness. However, in both years, the field survey showed that species richness increased significantly with time since abandonment. This pattern of increasing richness with age is consistent with many studies of succession in old fields (Nicholson and Monk 1974, Squiers and Wistendahl 1977, Armesto and Pickett 1985). Higher species richness in older sites is typically thought to be a result of the accumulation over time of poorly dispersing, late-successional species that temporarily coexist with better dispersing early-successional species (Connell and Slatyer 1977, Pacala and Rees 1998). It is also possible that species richness increases over time due to an increase in heterogeneity within a site over time (Collins 1990). If this is the case, high species richness may be maintained in older sites by continued coexistence of specialized species with different niches rather than the transient coexistence of species with different dispersal rates. We detected no significant effect of meadow area or isolation on species richness, both factors that would influence dispersal. It seems likely that spatial heterogeneity increases over time in meadows as unconsolidated sediments erode, creating the microlandscape of pits and hummocks particularly common in older meadows (McMaster and McMaster 2001). If so, the observed increase in species richness over time may be related to spatial variation in soil moisture regimes.

Both the experiment and the meadow survey showed a strong effect of soil moisture on the composition and species richness of the plant communities found in beaver meadows in the central Adirondacks. Hydrology has been described as the master variable that controls the distribution and abundance of wetland plants (van der Valk 1987), and numerous studies have shown a strong effect of soil moisture or water table depth on wetland plant composition (Gemborys and Hodgkins 1971, Walker and Wehrhahn 1971, Collins et al. 1982, Polley and Collins 1984, Titus 1990). Soils that are waterlogged present a particularly stressful environment for plants that must deal with anoxia and problems of nutrient uptake (Mitsch and Gosselink 1993). As a

result, the wettest portions of wetlands tend to have lower plant diversity, and van der Valk and Davis (1978) found more species emerging from the seed bank of sediments that simulated conditions of an exposed mudflat than sediments placed underwater. Vivian-Smith (1997) also found that hummocks had higher species richness than hollows in an experimental wetland community. She reported that environments with spatial variability in soil moisture levels had significantly higher species richness than homogenous environments. In a survey of wetland sites across an Alaskan landscape, Pollock et al. (1998) showed that both mean flood frequency and the spatial variability of flood frequency within a site were significant predictors of species richness. These results, together with the findings of this study, suggest that the control of species richness in wetland plant communities by both the mean and the variability of hydrological factors is a widespread phenomenon.

Few of the species present in beaver meadows of the Adirondacks have seeds with obvious mechanisms for long-distance dispersal (J. P. Wright, *personal observation*). Given this, it is surprising that factors that control dispersal rates into beaver meadows had relatively little effect on species richness, both in the first year of the experiment and in the field survey. McMaster and McMaster (2001) found that beaver meadows that shared a common water source showed greater compositional similarity. Our results showed no such pattern either using the "Stream dispersal" model, reflecting dispersal via hydrochory, or the "Drainage dispersal" model, reflecting dispersal by animals such as waterfowl, which might preferentially move along stream corridors. It is possible that dispersal from adjacent upland or forested riparian zone areas might be compensating for limited dispersal between isolated beaver meadows. We feel that this mechanism is unlikely as previous research has shown that most species found in beaver meadows are restricted to these habitats in the central Adirondacks (Wright et al. 2002). It is also important to recognize that seeds in wetland seed banks often show remarkable longevity (Leck 1989). It may be that beaver, by maintaining ponds for several years, increase the period of time during which rare, long-distance dispersal events can occur, thereby increasing the species richness of seed banks, and that the mesocosm experiment represents a sample of the net effect of dispersal over multiple years. Whatever the mechanism, within the scale of this study, which covered $\sim 50 \text{ km}^2$, all sites appear to be within the same dispersal network.

The role of ecosystem engineers

Beaver meadows would not be present in the landscape were it not for the activity of beaver. In this respect, ecosystem engineering by beaver has a profound effect on the species richness of these patches as well as on the landscape as a whole (Wright et al.

2002). However, the question still remains regarding the degree to which fluctuations in the density of beaver in an area might affect species richness within a patch. In a model of the population dynamics of ecosystem engineers, Gurney and Lawton (1996) demonstrated that as the number of engineers in a landscape increased, so did the number of modified patches. However, differences in the distance between patches or the rate at which patches are abandoned and recolonized caused by changes in the number of engineers could potentially have strong effects on the number of species found within patches created by ecosystem engineering.

At the current density of patches in the Adirondack landscape, there appears to be little evidence for dispersal-related control of patch-level richness or composition in beaver meadows. In this respect, variation in the population dynamics of beaver is unlikely to affect species richness at the patch scale. However, if beaver populations declined dramatically, leading to increased inter-patch distances, it is conceivable that dispersal limitation might begin to play an important role in controlling patch-level richness and composition. Furthermore, changes in beaver population densities could also alter the species richness of patches by changing the age distribution of meadows. As populations increase, recolonization rates will increase as well (Johnston and Naiman 1990), thereby decreasing the average age of meadows in the landscape. The positive relationship between site age and species richness that we observed implies that if populations of beaver were to increase, more sites would have the lower species richness associated with early successional meadows. If some species are restricted to the abiotic or biotic environments of older meadows, these species could potentially be excluded from the landscape if beaver populations increased. Thus, in this system, the population dynamics of beaver can potentially exert a strong control on the species richness of patches.

Although the population dynamics of an ecosystem engineer are likely to influence the patch dynamics of habitats they modify, these dynamics will not always affect the species richness of engineered patches. If primarily local forces (for example, water table levels and variability in soil moisture) control species richness within patches, then the dynamics of engineers are likely to have little effect on patch-scale species richness. On the other hand, in systems that are strongly dispersal limited, or exhibit large differences in species richness along successional gradients, engineers might be expected to exert strong control on species richness by altering inter-patch distance or the age distribution of patches. These hypotheses need to be tested in other systems where ecosystem engineers are likely to affect species richness in order to develop general theories concerning relationships between ecosystem engineering and species richness. Ecosystems such as the beaver meadows in this study, where patch-scale species rich-

ness is controlled by an interaction between local and landscape-level factors, are probably the norm. Nevertheless, understanding the relative importance of these two classes of controls on species richness and how they interact allows us to understand where and when ecosystem engineers are important in shaping patterns of species richness across landscapes.

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APPENDIX

A table listing the incidence of species found at each site in the 2000 and 2001 surveys is available in ESA's Electronic Data Archive: *Ecological Archives* E084-084-A1.