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An ecosystem engineer, the beaver, increases species richness at the landscape scale

Abstract Ecosystem engineering – the physical modification of habitats by organisms – has been proposed as an important mechanism for maintaining high species richness at the landscape scale by increasing habitat heterogeneity. Dams built by beaver (*Castor canadensis*) dramatically alter riparian landscapes throughout much of North America. In the central Adirondacks, New York, USA, ecosystem engineering by beaver leads to the formation of extensive wetland habitat capable of supporting herbaceous plant species not found elsewhere in the riparian zone. We show that by increasing habitat heterogeneity, beaver increase the number of species of herbaceous plants in the riparian zone by over 33% at a scale that encompasses both beaver-modified patches and patches with no history of beaver occupation. We suggest that ecosystem engineers will increase species richness at the landscape scale whenever there are species present in a landscape that are restricted to engineered habitats during at least some stages of their life cycle.

Keywords Beaver · Ecosystem engineering · Habitat heterogeneity · Landscape · Plant community

Introduction

There has long been interest in the causes of habitat heterogeneity and its effects on species richness (Hutchinson 1959; Sousa 1979; Pickett and White 1985; Chesson and Huntly 1989; Huston 1994). Although geomorphology and physical disturbance are more commonly studied agents generating habitat heterogeneity, the role of organisms in creating heterogeneity is receiving increased attention (McNaughton 1985; Huntly 1991; Brown 1995; Pickett et al. 2000). Physical ecosystem engineering by organisms – the creation or modification of habitat structure – has been postulated to be an important mechanism generating landscape-level heterogeneity and thus high species richness (Jones et al. 1997).

For a physical ecosystem engineer to increase species richness at the landscape scale – defined explicitly here as a scale that encompasses multiple patch types – two conditions must be fulfilled. First, an engineer must create a patch with a combination of conditions not present elsewhere in the landscape. Second, there must be species that can live in the engineered patches that are not present in patches unmodified by the engineer. There are no a priori reasons to assume that an engineered patch should be more or less species rich than an unengineered patch (Jones et al. 1997). Previous research on organisms that modify the environment has found that modified patches can have both higher (e.g., Martinsen et al. 1990; Crooks 1998) and lower (e.g., Bratton 1975; Collins and Uno 1983) species richness than unmodified patches. Without knowing how an ecosystem engineer modifies the resource flows in a system and how all of the species in the system respond to such modifications, it is difficult to predict the effect of an engineer on between-patch richness (Jones et al. 1997). However, if the engineer creates patches that are sufficiently different from surrounding patches so that species otherwise excluded from the landscape can persist, one would predict that the addition of an engineer to the landscape should increase species richness by increasing habitat heterogeneity.

Dam-building beaver (*Castor canadensis*) are clear examples of ecosystem engineers that are abundant throughout the northern temperate and boreal regions of North America. The ponds they create by damming streams have dramatic effects on both pond and stream community structure and ecosystem functioning (Naiman et al. 1988). In the central Adirondack region of New York, beaver ponds are relatively short-lived habitats, and are typically occupied for <10 years (Remillard

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et al. 1987). When ponds are abandoned and the associated dams are breached, extensive meadows form that can persist for over 50 years (Ives 1942; Terwilliger and Pastor 1999). Beaver set the stage for the creation of these meadows by building dams that trap nutrient-rich sediment and by both directly and indirectly killing woody vegetation in the riparian zone via herbivory, felling and flooding. In contrast to forested riparian zones, beaver meadows have high light penetration and elevated soil moisture and nitrogen levels (Naiman et al. 1994; Johnston et al. 1995). Beaver foraging has been shown to have significant effects on forest succession around active ponds by decreasing densities of preferred food species (Barnes and Dibble 1986; Johnston and Naiman 1990b; Donkor and Fryxell 2000). However, surprisingly little has been published on the long-term effects of beaver on the composition and successional dynamics of beaver meadows (McMaster and McMaster 2000).

Given the significant differences in resource availability, we hypothesized that beaver-modified riparian patches are sufficiently different from the forested riparian zone to support a distinct assemblage of plant species. If so, we would expect the presence of beaver-modified patches to increase plant species richness of the riparian zone compared to a landscape consisting entirely of forested riparian zone. To test the hypothesis that ecosystem engineering by beaver increases species richness at the landscape scale, we sampled the plant community of beaver-modified riparian sites and riparian sites with no history of beaver modification to determine the degree of similarity in species composition. We then quantified the magnitude of the engineering effect on species richness at the landscape scale by using resampling techniques. Such estimates of the strength of the effect of an engineer on species richness provide a valuable tool for comparing the relative importance of different species of engineers in structuring ecosystems.

Materials and methods

The study was conducted at the Huntington Wildlife Forest (HWF), a 6,142-ha forest reserve located in the central Adirondack region of New York (latitude 44°00′N, longitude 74°13′W, elevation 457–823 m). In this area, abandoned beaver ponds develop either into open meadows dominated by the grass *Calamgrostis candensis* and several species of sedge (*Carex* spp.), or into shrubby swamps dominated by speckled alder, *Alnus incana*. Visual analysis of historical aerial photographs taken at roughly 10-year intervals between 1942 and the present indicated that in this region beaver activity is the only large-scale form of disturbance in the riparian zone. Furthermore, aerial photograph analysis suggests that all large wetland areas in the landscape are associated with active or abandoned beaver dams.

We selected sites in three different habitat types in multiple watersheds. All meadow sites (*n*=6) and alder sites (*n*=6) showed evidence of past modification by beaver, either by the presence of a beaver impoundment in aerial photographs or the presence of a collapsed dam. Meadow and alder sites differed in presence or absence of an overstory of *Alnus incana*. Beaver-modified sites were only selected if historical photographs demonstrated that they had been forested at one point over the period from 1942 to the present. Undisturbed riparian forest sites (*n*=4) that showed no evidence of

beaver modification at any point during the 60-year period covered by aerial photographs were selected to match sites that had been modified by beaver in terms of gradient, elevation, and surrounding forest type. We sampled the herbaceous plant community in 0.5×1.0-m plots and identified all vascular plants present in each plot. Three large meadow and three large alder swamp sites contained 30 plots each with the remaining three meadow and three alder sites containing ten plots each, totaling 120 plots in each habitat type. The number of plots at each forested site was limited by the length of the stream reach, with two sites containing 12 plots, one site with 36 plots and one site with 60 plots for a total of 120 plots. Plots were located randomly within 1 m of the edge of the stream. Species accumulation curves for all three habitat types reached a plateau after 50 plots, indicating that our sampling effort fully captured the richness and composition of all three habitats.

We compared the composition of the three habitats using two techniques. We performed a non-metric multidimensional scaling (NMS) (McCune and Mefford 1999) ordination based on species presence-absence data for each plot to portray the degree of species overlap between the three habitats. We also calculated Morista-Horn similarity indices (Colwell 1997) for all pair-wise comparisons of sites based on the relative abundance of species within each site. Using this quantification of similarity among habitats we tested for differences in levels of similarity within and between habitat types using a one-way ANOVA with six sets of comparisons (meadow-meadow, alder-alder, forest-forest, meadow-alder, meadow-forest, and alder-forest). To correct for the non-normality of proportional data, we used arcsine transformed values of the Morista-Horn index, with significance being determined using a Bonferroni correction for multiple comparisons.

To calculate the effect of beaver activity on species richness of the riparian zone at the landscape scale, one must first estimate the species richness of a landscape without beaver-modified habitats, and then of an equally sized area with beaver-modified habitats. The difference between the species richness of the landscape with a mix of beaver-modified and forest plots and the landscape composed of only forest plots provides an estimate of the contribution of beaver-modified areas to the total species richness of the riparian zone. Estimates of species richness of forest plots were calculated using all forest plots in the data set, and estimates for the beaver-modified plots were calculated using all meadow and alder plots in the data set. Estimates for total riparian zone richness were drawn from a data set constructed using data from all three habitat types. We used estimates of the relative abundance of each habitat type in the landscape, as generated from aerial photograph analysis (see below), to determine the relative abundance of beaver-modified habitat and forested habitat in the constructed data set. All estimates of species richness were rarefied to correct for differences in sample pool size and represent the mean richness of 50 runs of the Coleman rarefaction estimate for 120 plots (Colwell 1997).

We determined the proportion of stream length flowing through beaver-modified habitat using a GIS. We created GIS layers mapping all streams and beaver-modified areas on the HWF in ArcView (ESRI 2000) from digitized, color infrared aerial photographs taken in April 1998. Beaver sites were classified as open water, meadow, or alder sites. We used the map of streams and the map of beaver areas to generate a layer containing only stream segments flowing through beaver-modified areas. To determine the proportion of total stream length in the HWF that flowed through beaver-modified habitat, we compared the total length of streams flowing through the beaver-meadow layer to the original stream layer. We had hoped to use maps of regulatory wetlands to determine the percentage of all wetlands on the HWF that are associated with beaver activity. Unfortunately these maps were extremely inaccurate both in placing wetlands in areas where no known wetlands exist, and in mapping the boundaries of known wetlands. As a rough estimate of the percentage of wetlands that are associated with beaver, we first classified all wetlands on the regulatory wetlands map as reliable or not based on visual analysis of aerial photographs and ground truthing. We then took counts of the number of reliable wetlands that overlapped with beaver-modified areas for at least some of their extent.
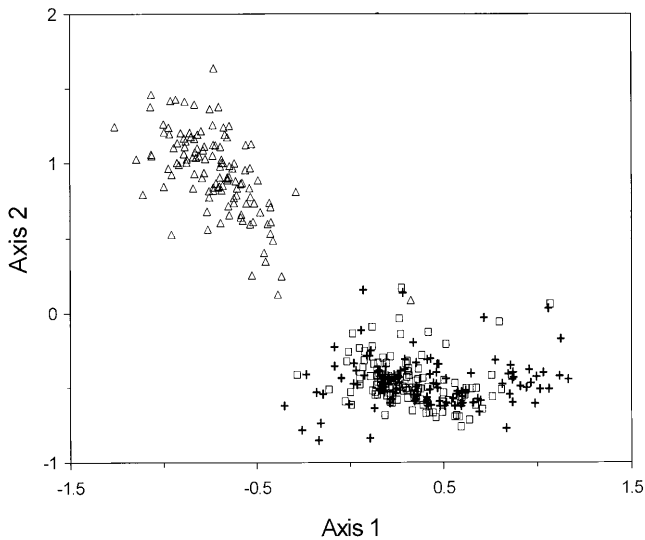
Fig. 1 Ordination of plant community composition between riparian zone habitats. Ordination of plots based on presence of species using non-metric multidimensional scaling. △ Forested riparian zone habitat, □ alder habitat, ✚ meadow habitat

Fig. 2 Similarity in plant community composition between riparian zone habitats. Mean Morista-Horn similarity index for pair-wise comparisons of sites from the same and different habitat types ± 1 SE. *Bars with different letters* are significantly different at an experimental error rate of $P<0.05$ using a Bonferroni test for multiple comparisons

Results

The number of species in each of the three habitat types did not differ at the scale of the 0.5-m^2 sampling plot [mean ± ISE: meadow (M)=8.2±2.7, alder (A)=8.8±2.5, forest (F)=8.4±2.1]. There were differences in the estimated total number of species in the three different habitat types (M=79.3±8.7, A=60.8±2.9, F=65.4±4.5), and the forest riparian habitat had a species richness intermediate to the two engineered habitat types. This indicates that engineering by beaver had no predictable effect on species richness at the patch scale.

Although beaver-modified and forested sites did not differ in species richness, the composition of these habitat types was quite different. Both meadows and alder swamps were generally dominated by sedges or grasses with an understory of herbs, and several species of shrubs in the alder swamps. Forest herbs along with several species of fern dominated forested riparian zones. Ordination of the plots indicated a striking separation in species composition between plots in engineered and unengineered sites (Fig. 1).

These differences in community composition between beaver-modified and forested habitats were reflected in significant differences in the similarity of different sites within and between habitat types ($F_{5,114}=73.378$, $P<0.001$) (Fig. 2). Comparisons of sites from engineered and unengineered habitat (i.e., meadow-forest and alder-forest) showed extremely low levels of similarity, again indicating very low levels of species overlap between the two habitat types. In total, only 17% of the 125 species recorded in the survey were found in both engineered and unengineered patches. Forested sites were all highly similar to each other in community composition, as were alder sites. Meadow sites were more variable in composi-
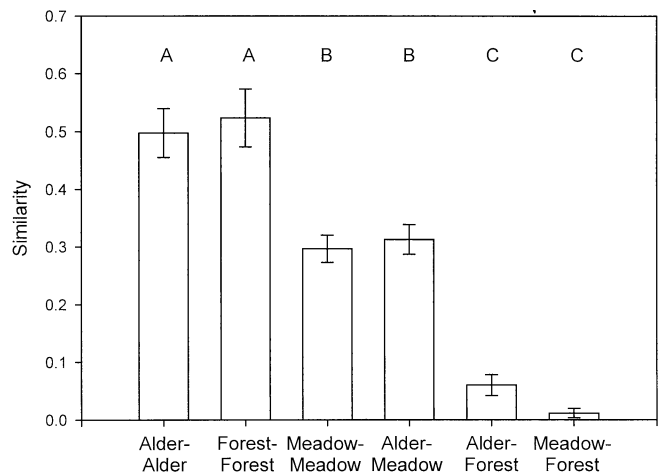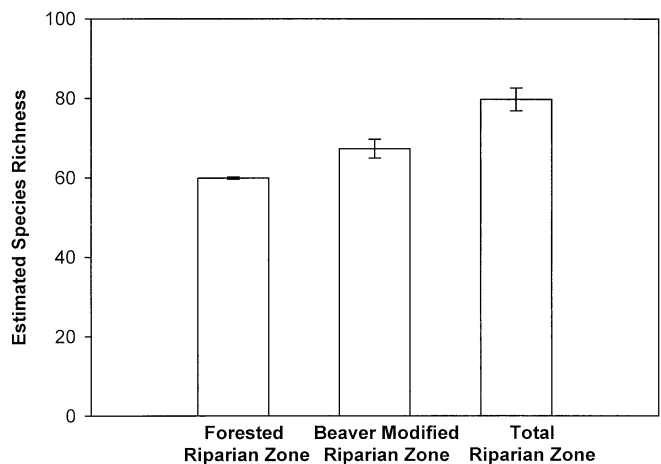

Fig. 3 Estimated species richness of hypothetical landscapes composed only of forested riparian plots, only of beaver-modified riparian plots, or of a combination of engineered and unengineered plots. *Error bars* represent ± 1 SD

tion than forest and alder sites, and were, on average, no more similar to each other than they were to alder sites (Fig. 2). Of all the 95 species found in both meadow and alder swamps, 58% were found in both habitat types.

As a result of this high degree of dissimilarity between the engineered and unengineered habitat types, species richness (S) estimated by randomly sampling plots of all three habitat types was 1.33 times higher than richness estimated when drawing only from forest or beaver-modified plots (mean ± 1 SE: S=79.7±2.9 for all plots, S=59.9±0.3 for forest plots, and S=67.3±2.4 for beaver-modified plots) (Fig. 3).

Beaver-modified habitat occupied 26.7% of the riparian zone of the HWF on a per unit length basis, with as

Table 1 Classification of species from the beaver-modified and non-modified riparian zone habitats into National Wetlands Inventory indicator categories. Only species found in >10% of plots within a habitat are included. Species classified as obligate wetland species (*OBL*) are estimated to occur with >99% probability in wetlands; highly facultative wetland species (*FACW*+) 99–89% probability; facultative wetland species (*FACW*) 88–78% probability; somewhat facultative wetland species (*FACW*–) 77–67% probability; facultative species with tendencies towards wetlands (*FAC*+) 66–56% probability; facultative species (*FAC*) 55–45% probability; facultative species with tendencies towards uplands (*FAC*–) 44–34% probability; facultative upland species (*FACU*) 33–1% probability; and upland species (*UPL*) <1% probability. Classifications are based on the region 1 regional classifications (Reed 1988)

	OBL	FACW+	FACW	FACW–	FAC+	FAC	FAC-	FACU	UPL
Meadow and alder	0.48	0.16	0.16	0	0	0.16	0	0	0.04
Forest	0.19	0.24	0.1	0	0.1	0.1	0.14	0.1	0.05

many as 4.3 sites km^{-1} stream length in some drainages. In all, 151.5 ha of the HWF were classified as being either beaver meadow or alder habitat associated with beaver disturbance in 1997. An additional 45.4 ha were classified as active ponds that are likely to eventually develop into either meadows or alder habitat. Altogether, beaver had modified 3.21% of the study area in the 1997 aerial photographs. Of the 54 regulatory wetlands on the HWF that were reliably associated with known wetlands, 83.3% were associated with beaver activity. These beaver associated wetlands accounted for 92.2% of the 333.3 ha of reliable regulatory wetlands.

Discussion

Based on our estimates, beaver-modified patches may contribute as much as 25% of the total herbaceous plant species richness of the riparian zone. This estimate of the effect of beaver-modified habitat on the species richness of the riparian zone is likely to be an underestimate as it was based on the relative proportion of stream length flowing through beaver-modified habitat. Beaver tend to occupy sites where the stream gradient is low and the riparian zone is relatively wide (Howard and Larson 1985), thus the proportion of the riparian zone that has been modified by beaver is likely to be much higher on a per unit area basis than on a stream length basis. Furthermore, this study looked at only the effects of beaver modification on the vascular plant community. Pollock et al. (1998) found that mosses were quite diverse in beaver meadows in Alaska, and contributed significantly to overall diversity. If beaver have a similar effect on moss diversity in the Adirondacks to that in southern Alaska, their effect on total plant species richness of the riparian zone might be even greater than their effect on vascular plant diversity.

Given the large changes in a number of physical conditions that occur after a site has been occupied by beaver (Naiman et al. 1994; Johnston et al. 1995), it is difficult to predict a priori whether these sites should have higher or lower species richness than sites that have never been modified by beaver. We found that patches that had and had not been modified by beaver had similar levels of species richness at the patch scale (alpha diversity, sensu Whittaker 1972). Thus, the increase in species richness at the landscape scale contributed by beaver-modified patches is not simply due to the replacement of species-poor forest patches by species-rich meadow patches. Rather, the low overlap in species composition between the two patch types means that the presence of beaver-modified habitats allows a number of species to persist in the riparian zone that otherwise would be excluded.

It is not surprising, given the likely differences in light availability, soil moisture, and nutrient availability that the species composition differs in forested and beaver-modified patch types. Interestingly, there is little difference in the species composition of the two beaver-modified habitats, meadows and alder swamps, despite apparently different light environments based on the degree of canopy cover. The lower species richness, the tighter cluster of plots in the ordination, and the higher similarity between sites in alder habitat versus meadow habitat all suggest that the species found in beaver-modified sites currently dominated by alder represent a subset of those species found in meadow sites. Thus, meadow patches may be more important than alder patches in determining the effect of beaver activity on landscape-scale species richness.

In the central Adirondack landscape, as typified by the HWF, the majority of large open wetlands are associated with beaver activity. Half of the species found in beaver-modified areas are classified as obligate wetland species, and 80% of the species are found in wetlands at least 77% of the time (Table 1) (Reed 1988). Thus, it would seem likely that the effect of beaver increasing species richness of the riparian zone extends to the landscape as a whole. In areas having wetland habitats independent of beaver activity, we would predict that beaver-modified patches would be less important in determining the total species richness, although McMaster and McMaster (2000) suggest that the combination of full sun and saturated soil found in beaver meadows is relatively rare.

The large increase in species richness caused by an ecosystem engineer appears to be due to the creation of novel habitat types in the riparian zone and the presence of a large number of species capable of exploiting the resources provided in these engineered patches. Previous research on ecosystem engineers in a wide range of natural ecosystems has indicated that engineered patches can have both higher (Martinsen et al. 1990; Crooks 1998) and lower (Bratton 1975; Collins and Uno 1983) species

richness than non-engineered patches. An increase in richness within engineered patches is typically thought to be a result of disturbance increasing resources by eliminating competitively dominant species or ameliorating stressful conditions (cf. Hacker and Gaines 1997). Alternatively, a decrease in species richness could occur if the conditions created by the engineer facilitate the growth of a competitive dominant, or are so harsh as to eliminate most species.

Comparing the richness of engineered and unengineered patches is not sufficient to determine the overall effect of the engineer on species richness at the landscape scale. Changes in richness at the patch scale can have important consequences for the evenness of the distribution of species across the landscape. However, the effect of the engineer on richness at the landscape scale will be negligible unless there are species found in engineered patches that are not found elsewhere in the landscape. Collins and Uno (1983) found that species richness was lower inside buffalo wallows than in the surrounding prairie. However, since buffalo wallows form ephemeral wetlands and thus contain an assemblage of species different from those found just outside the wallows, the authors suggest that the presence of buffalo wallows increases the species richness of the prairie. Thus, even in systems where engineered patches have lower species richness than non-engineered patches, the existence of species uniquely present in the engineered patches will result in ecosystem engineering having a positive effect on richness at the larger scale.

Several studies have suggested that engineering activities increase species richness at the landscape scale (Collins and Uno 1983; Inouye et al. 1987; Guo 1996; Ceballos et al. 1999). Only by fully sampling both patch types, as demonstrated by species accumulation curves, and by accounting for the relative area of the two patch types using methods such as rarefaction, can one properly estimate the effect of engineering on richness at the landscape scale. The estimate made in this study, along with the qualitative results of earlier studies (Collins and Uno 1983; Inouye et al. 1987; Guo 1996; Ceballos et al. 1999), support the hypothesis that ecosystem engineering can increase species richness at the landscape scale. Although we expect this result to be common across systems whenever there is not perfect overlap between engineered and unengineered patches in species composition, further testing is necessary to determine the general relationship between the activity of ecosystem engineers and species richness at the landscape scale. In particular, we would expect species richness to increase rapidly as the number of engineered patches in the landscape increase from low numbers. However, if engineered patches begin to dominate the landscape, we would predict total species richness to decrease if the number of unengineered patches drops below the number sufficient to support their full complement of species.

The results presented here have important implications for the persistence of species restricted to engineered habitats. In this landscape, where beaver-modified areas comprise the only open wetland habitat, the fates of 25% of the species found in the riparian zone are directly linked to the patches created by the engineering activities of beaver. Furthermore, some species that are present in both beaver-modified and forested riparian zone habitats may depend on engineered patches as sources of propagules if populations in forested areas are acting as "sinks" (Hanski and Gilpin 1997). As populations of the ecosystem engineer change, the amount of habitat available for these habitat-specialist species will vary as well (Johnston and Naiman 1990a). Thus, factors that control the dynamics of populations of ecosystem engineers may indirectly control the species richness of the landscape. Ecosystem engineers move about landscapes in response to resource availability and biotic interactions, as opposed to more commonly studied abiotic agents of heterogeneity such as fire and wind. As a result, the dynamics of the patches created by ecosystem engineers may be quite different from those created by physical forces (Pickett et al. 2000). Although current trends in conservation are to move away from single-species management and towards ecosystem management, these results suggest that for ecosystem engineers, it may be important to manage a single species in order to conserve landscape-level diversity.

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