

Temporal and spatial dynamics of beaver-created patches as influenced by management practices in a south-eastern North American landscape

JOEL W. SNODGRASS

University of Georgia's Savannah River Ecology Laboratory, Drawer E, Aiken, South Carolina 29802, and Division of Life Sciences and Occupational and Environmental Health Institute, Rutgers University, Piscataway, New Jersey, 08855–1059, USA

Summary

1. Beavers create habitat diversity across catchment landscapes by impounding small streams. This increased habitat diversity leads to increased species richness of plants and animals in small streams. As managers work to balance conflicting management goals (e.g. protection of timber and human structures versus maintenance of biological diversity) the influence of beaver population management practices on habitat availability needs to be assessed. Two questions of initial concern are: (i) how do different levels of management influence the availability of beaver created habitats and (ii) do relationships developed in one region apply to other regions?

2. To address these questions, historical aerial photography was used to determine the extent and rate of impoundment of streams by beavers *Castor canadensis* over a 77 000 ha south-eastern North American landscape during a 40-year period of beaver population recovery. Between 1950 and 1983, beaver populations were protected from trapping and hunting. From 1983 to the present, beaver numbers were reduced by fatal trapping, to protect roads, railroads and timber. Trapped beavers were assigned to specific colonies associated with beaver-created patches in the landscape, and growth rates and size after management of individual patches receiving different levels of management were compared. Results from this study were also compared with previous studies conducted in Minnesota, USA.

3. Growth rate, patch size following management and the composition of habitat types within patches were not related to management activity, suggesting that the levels of management used in this study did not influence the temporal dynamics of beaver-created patches. The extent and rate of beaver impoundment on the south-eastern Upper Coastal Plain of North America was less than that reported from central North American landscapes over comparable periods.

4. These results have the following implications for management: (i) management activities should be monitored on a regional basis; (ii) conflicting beaver population management goals should be addressed, evaluated and balanced; and (iii) beavers do not present a threat to flowing-water species in south-eastern North America and need not be controlled for this reason.

Key-words: *Castor canadensis*, catchment management, forested streams, riparian habitat.

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Introduction

Understanding how physical and biological disturbances act to create patches (*sensu* White & Pickett 1985) at the landscape scale is a central tenet of landscape ecology (Forman & Godron 1986). In addition,

landscape ecologists often address questions concerning the influence of human activity (e.g. economics, forest management) on landscape characteristics. These two lines of inquiry intersect when human activities influence the rates and locations of patch-creating disturbances. An example of physical

disturbance is change in the dynamics and structure of a river floodplain-delta system following reduction of disturbance frequency due to an upstream dam. In the case of animals, control of an insect pest by humans in a forest system might influence patch dynamics resulting from insect outbreaks.

Beavers (*Castor canadensis* Kuhl in North America, and *Castor fiber* Linn. in Europe and Asia) offer an opportunity to study the indirect effects of human activity, in the form of management, on the temporal and spatial dynamics of aquatic patch creation by these species. Although beavers were extirpated from many North American streams by the late 1800's, populations are now being re-introduced or are naturally recovering from low levels in many areas (Naiman, Johnston & Kelley 1988). In Europe, beaver populations were reduced to a few scattered colonies by the nineteenth century, but have since experienced substantial recoveries in Scandinavia and the former Soviet Union (Nowak 1991). Additionally, introductions have established populations of the North American species in Finland and populations of the European species outside its historical range in Europe (Nowak 1991).

Beavers form a monogamous pair that defends a territory. Two to four kits from the previous breeding season and two to three yearlings are often associated with the breeding pair (Hill 1982). This group shares a common food supply, maintains one to several dams and is defined as a colony (Bradt 1938). In northern latitudes of North America, surveys of winter food caches are used to distinguish active colonies and estimate colony densities (e.g. Payne 1981; Brown & Parsons 1982), although this study revealed that food caches were not always constructed and bank dens are more common than lodges in South Carolina, USA.

When beavers build dams on streams, the impounded water floods the riparian forest, killing the trees and creating a distinct patch in the catchment landscape. Although these patches are readily distinguished from the surrounding forest matrix on aerial photographs (e.g. Dickinson 1971; Parson & Brown 1978), vegetation characteristics may differ greatly within and among patches (Remillard, Grundenling & Boquecki 1987; Johnston & Naiman 1990a; Feldmann 1995). While the dam is being maintained, the resulting pond is colonized by emergent, floating and submerged aquatic plants. After the dam is abandoned it deteriorates and the pond drains, exposing the riparian sediments. These exposed sediments are colonized by grasses, herbs and shrubs, forming a 'beaver meadow'. If beavers do not impound the stream again, the beaver meadow will be colonized by seedlings of riparian tree species that will grow to establish a riparian forest. The location of dam construction and temporal vegetative changes within patches, depends on local and regional geomorphology and forage availability (Slough & Sadleir 1977; Howard & Larson 1985; Beier & Barrett 1987;

McComb, Sedell & Buchholz 1990; Leidholt-Bruner, Hibbs & McComb 1992), other disturbance-generating agents, such as fire and disease (Naiman *et al.* 1988), and re-occupation rates (Remillard *et al.* 1987). Rates of pond creation, abandonment and re-occupation have been reported for populations that were not under trapping or management pressure in northern latitudes of North America (Remillard *et al.* 1987; Johnston & Naiman 1990a,b); however, these rates have not been described for southern populations in North America, for any populations of the European species or for populations under management.

Both species of beaver are frequently the target of intense management activities throughout their range (Hill 1982). The goals of these management activities vary among regions, but include the maintenance of populations for harvest, water storage and erosion control, and the control of populations to prevent damage to timber, roads and railroads. While beaver ponds have long been recognized as being beneficial to fish and wildlife (e.g. Rutherford 1955; Gard 1961), it is only recently that more extensive surveys have shown the full effects of beavers on biological diversity in streams (McDowell & Naiman 1986; Feldmann 1995; Snodgrass 1996). These surveys indicate that species diversity of plants, invertebrates and fish in headwater streams is greatly increased. In addition, the positive effects of beavers on plant and stream fish species richness has been shown to be highly dependent on the temporal and spatial dynamics of pond creation and abandonment (Feldmann 1995; Snodgrass 1996).

As scientists, and society in general, have become increasingly concerned with the loss of biological diversity, managers are being charged with monitoring and conserving biological diversity on the lands they manage. In the case of beavers, these new biological diversity management goals can present conflicts with more traditional management goals such as preservation of extractable resources (e.g. timber). For managers to make informed decisions and to balance conflicting management goals, two questions need to be addressed concerning beaver population management. First, how do different levels of management influence the availability of beaver created habitats and, thus, patterns of diversity across catchments? Secondly, do relationships developed in one region apply to other regions? Additionally, it has been suggested by some authors (e.g. Hackney & Adams 1992) that beavers may have adverse effects on biological diversity by eliminating flowing-water habitats and the species that depend on these habitats.

This paper describes the temporal and spatial dynamics of patch creation during a period of beaver population recovery at the Savannah River Site (hereafter referred to as 'the site') on the Upper Coastal Plain of South Carolina, USA. The site is a US Department of Energy nuclear production facility established in the early 1950s. In 1951, the beaver population at

the site was small (two or three colonies), but has since recovered (at least 61 colonies in 1992). In 1983, the US Forest Service began managing the beaver population to protect timber, roads and railroads. The Forest Service kept records of the location of management efforts, which allowed specific levels of management to be assigned to colonies, ranging from no management to intense management. This paper, first, addresses the relationship between management effort, growth rate and the size of beaver-created patches, and secondly, compares patterns and rates of patch creation with those from Minnesota. Ideally, levels of management effort would have been randomly assigned to patches across a number of catchment landscapes and the effects would have been monitored. Unfortunately, this approach would be too time-consuming. Managers must make decisions now, and economic considerations preclude long-term field experiments. Therefore, this study relies upon a correlative approach, and acknowledges that confidence in any cause-and-effect relationships is reduced by the lack of randomization.

Study site and methods

The site is a 77 000-ha area located on the Upper Coastal Plain of South Carolina, USA, adjacent to the Savannah River. Most of the site is characterized by 10–50-million-year-old unconsolidated sandy soils overlying Cretaceous sediments consisting of clay and sand. Stream gradients rarely exceed 20 m km^{-1} . Rainfall averages 123.5 cm annually and is distributed evenly throughout the year (Environmental Technology Section, Savannah River Technology Centre).

The streams of the site all drain from the north-east portion of the site south-west to the Savannah River (Fig. 1). Approximately 34 km of the 200 km of stream on the site have received thermal effluent from production reactors at some time in the last 46 years which has altered riparian vegetation. These altered streams are primarily confined to the lower portions of Fourmile Branch, Pen Branch and Steel Creek. For comparisons of individual patch expansion rates and vegetation structure, all beaver impoundments on undisturbed streams of the site were used; however, to determine the percentage of catchment and stream length impounded, only the undisturbed portions of six catchments were used (Fig. 1). Four of these catchments—Pen Branch, Meyers Branch, Fourmile Branch and Steel Creek—are relatively undisturbed above the downstream limits used to determine relative impoundment. The upper one-third of Upper Three Runs catchment lies outside of the Savannah River Site (SRS) and is characterized by agricultural land use. The upper portion of Lower Three Runs catchment is occupied by PAR Pond, a large cooling water reservoir, and the lower portions are outside the SRS boundary.

Beaver impoundments were identified on 1951, 1978

and 1992 aerial photographs (scale 1:16 000–20 000) with the aid of a stereoscope ($\times 3$ – 10 magnification) following the methods of previous investigators (Dickerson 1971; Parsons & Brown 1978; Remillard *et al.* 1987; Johnston & Naiman 1990a). All stream corridors were inspected for the presence of active or abandoned beaver ponds. Based on vegetation structure and hydrology, nine general landscape types were recognized within active or abandoned ponds (Table 1). These landscape types correspond closely to classification systems of beaver impoundments derived from more complicated wetland classification systems (Johnston & Naiman 1990a). When all impoundments and landscape types had been delineated on mylar over-lays of the 1992 photographs, they were visited during the summer of 1993 to verify the presence of beavers and landscape type signatures on aerial photographs.

The final beaver impoundment coverages were produced using ARC/INFO geographical information software (Environmental Systems Research Institute, Inc., Redland, California, USA). Aerial photographs were scanned using a UMAX UC1260 scanner (UMAX Data System, Inc., Fremont, California, USA) at 400 dots per inch and Adobe Photoshop software (Adobe Systems, Inc., San Jose, California, USA). Scanned images were given true latitudes and longitudes by geographically registering them to a roads coverage for the site and rectifying them using ARC/INFO software (RMS error $\mu = 12 \text{ m}$, $n = 47$). Polygons were traced on-screen with aerial photographic images displayed in the background. Final interpretation was aided by a stereoscope.

Line coverages of streams were extracted from 1:24 000-scale digital line graph (National Cartographic Information Centre) hydrography data. Digital line graph (DLG) data files were produced using manual, semi-automated or automated geographical information system methods from 1:24 000-scale US Geological Survey topographic maps (US Geological Survey 1991). Streams were coded as intermittent or perennial in the DLG files, based on information from topographic maps and then further coded to stream order (Morisawa 1968). In this stream size classification, streams originate as first-order, two first-order streams coalesce to become a second-order stream, two second-order streams coalesce to become a third-order stream and so forth. The stream coverage was also edited to reflect the general course of streams within beaver impoundments. This was necessary to ensure accurate estimates of stream length within landscape types because stream channels did not always correspond to channel locations on the scanned images. This may have been due to error associated with the original interpretation of the stream channel, production of the digital line graph files or aerial photograph registration, or to actual temporal shifts in channel position. Because of the time required to interpret and trace all stream reaches

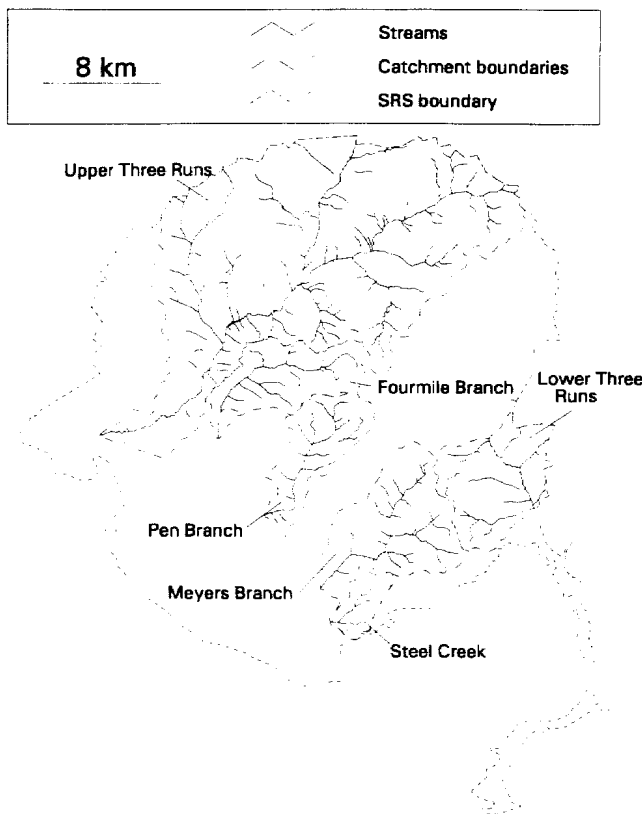


Fig. 1. Location of the six undisturbed portions of catchments in which beaver impoundment was studied.

Table 1. Hydrology, vegetative structure and characteristic plant species of the nine landscape types occurring in beaver impounded areas at the Savannah River Site

Landscape type	Hydrology	Vegetative structure	Characteristic species
Flooded hardwoods	Wet	Deciduous forest	<i>Liriodendron tulipifera</i> , <i>Acer rubrum</i> , <i>Liquidamber styraciflua</i> , <i>Nyssa sylvatica</i>
Open water	Wet	Floating and submerged aquatics	<i>Potamogeton</i> spp., <i>Myriophyllum heterophyllum</i> , <i>Utricularia</i> spp., <i>Brasenia schreberi</i> , <i>Nymphaea odorata</i>
Emergent marsh	Wet	Emergent aquatics	<i>Juncus effusus</i> , <i>Scripus cyperinus</i>
Wet shrub	Wet	Deciduous shrub	<i>Cephalanthus occidentalis</i> , <i>Itea virginica</i> , <i>Alnus serrulata</i>
Wet meadow	Moist	Herbaceous grasses	<i>Panicum</i> spp., <i>Andropogon</i> spp., <i>Carex</i> spp.
Dry meadow	Dry	Herbaceous grasses	<i>Andropogon</i> spp., <i>Erigeron</i> spp., <i>Rubus</i> spp.
Dry shrub	Dry	Deciduous shrub	<i>Myrica cerifera</i> , <i>Cephalanthus occidentalis</i> , <i>Itea virginica</i> , <i>Alnus serrulata</i>
Dry dead hardwoods	Dry	Deciduous forest	<i>Liriodendron tulipifera</i> , <i>Acer rubrum</i> , <i>Liquidamber styraciflua</i> , <i>Nyssa sylvatica</i>
Early succession	Dry	Deciduous and evergreen forest	<i>Acer rubrum</i> , <i>Liriodendron tulipifera</i> , <i>Itea virginica</i> , <i>Alnus serrulata</i> , <i>Pinus</i> spp.

in the study area, these sources of error were accepted for streams outside beaver impoundments. In addition, several impoundments occurred on drainages that were not mapped as streams. Following Johnston & Naiman (1990a) these impoundments were considered to be the source of a first-order stream, and delineated streams for the drainage based on the aerial photography images and elevation contours.

Catchment boundaries for the six catchments used to estimate the percentage of catchment area and stream length impounded were delineated based on 10' contour lines. A coverage of the contour lines for the site was extracted from digital line graph hypsography data. Catchment boundaries were then traced on-screen with the contour line coverage as a background.

Management of beaver populations at the site was initiated in 1983 by the Savannah River Forestry Station of the US Forest Service to protect road and railroad structures and timber from flooding. An individual licensed contractor is procured annually to fatally trap beavers at designated sites. All trapped beavers are returned to the Forest Station and their trapping location recorded. Information on the number and location of beavers trapped from 1983 to 1991 was obtained from the Forest Station.

To associate trapped beavers with specific clusters of active and abandoned beaver ponds (patches of beaver impoundment) the autecology of the American species was used. Estimates of territorial spacing and the presence of active ponds was used to define colonies. When territories of the American species were defined by repeated trapping of marked individuals, 93% were separated by 100 m or more of stream (Bergerud & Miller 1977). Ponds were considered active if the dam was impounding water across its entire extent. Consequently, two active ponds separated by more than 100 m were considered separate colonies. For analysis purposes, a patch was defined as a group of active and abandoned ponds that were not separated from each other by more than 100 m of unimpounded stream, but were separated from other groups of ponds by more than 100 m of unimpounded stream. Thus, a patch with no active ponds would be considered abandoned and not to contain an active colony. Trapped beavers were assumed to come from the closest patch.

Forward selection and backward elimination multiple regression analysis was used to investigate the relationship between management and growth rates of beaver-created patches, or patch size in 1992. Management effort was coded as a dummy variable. Two levels of management were recognized: (1) light management—removal of one to 10 beavers between 1983 and 1992, and (2) heavy management—removal of more than 10 beavers between 1983 and 1992. In the case of growth rates, patch growth rate before management (the period between 1951 and 1978) was

included as a covariate in the model because the limits of patch size are influenced by geomorphology (Johnston & Naiman 1990b). Therefore, decreased growth rates in managed patches may not be due to management itself, but rather to rapid growth and attainment of a larger percentage of maximum size before management. For the same reasons, patch size in 1978 was included as a covariate when testing for relationships between management effort and patch size in 1992. To meet the assumptions of homogeneity of variance and normality, all growth rates were made positive by adding the minimum growth rate to all growth rates and then applying a $\log(x + 1)$ transformation to the positive growth rates and patch sizes.

To investigate the relationship between management and landscape element composition of patches in 1992 canonical correspondence analysis (CCA) was used (ter Braak 1988). The relative abundances of landscape elements in 1992 were used as dependent variables and the relative abundances of landscape elements in 1978 and management effort were used as independent variables. Levels of management effort were coded as a nominal variable (i.e. as a dummy variable). Forward selection of independent variables was used to identify those that were significantly related to landscape element composition in 1992. A Monte Carlo permutation test following ter Braak (1988) was used to test for a significant relationship between dependent and independent variables. Significance level for entry into the model was set at $P \leq 0.10$.

Results

There was no evidence of beaver activity on the streams included in this study in 1951. By 1978, 27 patches along undisturbed streams were present. Twenty-four (89%) of these patches appeared to be associated with active beaver colonies (as indicated by the presence within patches of a dam or dams impounding water across their entire extent). By 1992, the number of patches had increased to 49 of which 37 (76%) were associated with active colonies. One patch contained two dams impounding water across their entire extent and separated by more than 100 m of stream. No management activity was associated with this patch so no effort was made to divide the patch for analysis.

All of the impounded area identified on the 1978 photographs (Table 2), and most (98% of 201.15 ha) of that identified on the 1992 photographs, was within the unimpacted portions of catchments (Fig. 1). The percentage of the total area within the six unimpacted catchments impounded by beavers was low (Table 2, Fig. 2): 0.2% of the total area in 1978 and 0.5% in 1992. For individual catchments the percentages ranged from 0.1–2.4 in 1978 and from 0.3–9.0 in 1992. The amount of catchment impounded showed an exponential decline with increasing catchment size in both 1978 and 1992 (Fig. 3). In addition, the mag-

Table 2. Catchment size and area of unimpounded land and beaver impoundments for the six catchments studied during 1978 and 1992. No numbers are listed for 1951 because no beaver activity was detected on the 1951 aerial photographs

Landscape type	Area (ha)															
	Catchment		Upper Three Runs		Meyers Branch		Lower Three Runs		Pen Branch		Fourmile Branch		Steel Creek		Total	
	Year		78	92	78	92	78	92	78	92	78	92	78	92	78	92
Unimpounded land			26223.50	26164.45	4982.49	4972.20	4022.84	4022.75	2760.03	2753.62	3400.61	3375.34	94.04	87.71	41483.51	41376.06
Open water		4.39	15.48	0.26	4.63	3.71	4.39	0.02	2.88	0.37	2.51	0.25	1.24	9.00	31.12	
Dry meadow		4.61	13.65	2.54	1.83	1.90	2.76	5.33	0.00	5.99	6.60	0.00	1.26	20.37	26.09	
Wet meadow		1.14	7.82	0.44	1.05	0.70	2.24	2.09	0.00	0.90	0.90	1.43	0.00	0.72	5.28	13.26
Flooded hardwoods		5.90	15.92	0.58	3.34	3.62	3.19	1.70	3.10	0.73	10.69	2.11	5.29	14.64	41.53	
Dry shrub		4.38	13.28	1.68	0.36	3.11	0.00	0.79	3.07	12.91	10.53	0.00	0.00	22.86	27.23	
Wet shrub		0.47	3.75	0.43	0.96	0.04	0.00	0.20	3.34	0.00	2.49	0.00	0.08	1.14	10.63	
Emergent marsh		0.86	7.23	0.24	0.84	0.99	1.98	0.12	8.60	2.23	2.10	0.00	0.10	4.44	20.84	
Early succession		0.13	9.00	0.00	3.79	0.00	0.46	4.48	0.00	3.79	13.17	0.00	0.00	8.40	26.41	
Dry dead standing hardwoods		5.71	0.52	0.32	0.00	1.00	0.15	0.54	0.68	0.00	0.00	0.00	0.00	7.57	1.34	
Total impounded Catchment size		27.60	86.65	6.50	16.79	15.07	15.16	15.25	21.66	26.92	48.70	2.36	8.69	93.70	197.65	
			26251.10	4988.99	4037.91	2775.28	3427.53	96.40	41577.21							

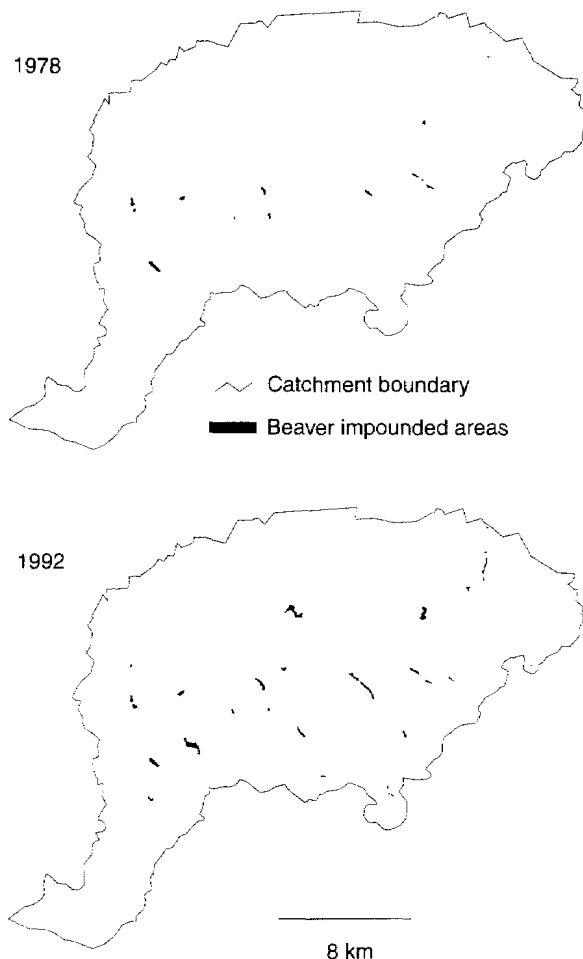


Fig. 2. Coverage of beaver impoundments in the Upper Three Runs catchment as an example of the extent and change in beaver impoundment between 1978 and 1992. No coverage for 1951 is given because there were no beaver impoundments at that time.

nitude of this exponential decline increased between 1978 and 1992. In all catchments, except Lower Three Runs and Pen Branch, the rate of increase of impounded area was greater from 1978 to 1992 than from 1951 to 1978 (Table 2, Fig. 4). In Pen Branch catchment there was a slight decrease in the amount of area impounded by beavers from 1978 to 1992, while in Lower Three Runs catchment there was little change.

In all catchments the amount of flooded (wet) and previously flooded (dry) area increased between 1978 and 1992 (Table 1, Fig. 4). The rate of increase was also greater between 1978 and 1992 in all but Lower Three Runs catchment. Wet meadow (moist), the only seasonally flooded or saturated landscape type, was rare in all catchments (Table 2, Fig. 4). In general, there were large changes in the composition of land-

scape types within the six catchments between 1978 and 1992 (Table 2). There was no correlation among the ranks (based on abundance) of the landscape types between 1978 and 1992 for Upper Three Runs, Meyers Branch, Lower Three Runs or Fourmile Branch catchments (Spearman's rank order correlation, $P > 0.05$), but there was a significant ($P = 0.0314$) negative correlation for Fourmile catchment. In these catchments instability was due to relatively large increases in open water, emergent marsh, flooded hardwoods or early succession landscape types, or a combination of these (Table 2). In Steel Creek catchment, there was a marginally significant (Spearman's rank order correlation, $P = 0.0581$) positive correlation of landscape type ranks. This was the result of low diversity of landscape types in both 1978 and 1992 (Table 2).

Overall, only a small proportion of the stream

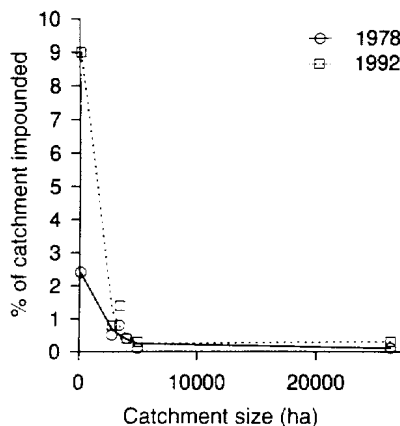


Fig. 3. Relationship between catchment size and the percentage of the catchment area impounded by beavers in 1978 and 1992.

length in the six catchments was affected by beaver impoundment; however, there was great variation between catchments (Table 3). In 1978 the percentage of stream length affected by beaver impoundment ranged from 2.1% in Upper Three Runs to 14.8% in Fourmile Branch. In 1992 this range was 6.1% to 27.1% for Lower Three Runs and Fourmile Branch, respectively. The percentage of the total stream length available for impoundment decreased with increasing stream order: intermittent, 42%; first-order, 28%; second-order, 19%; and third-order, 10%. Despite this pattern, overall and within individual catchments, the proportion of second-order streams impounded was often several orders of magnitude higher than that of other stream orders (Table 3). Between 1978 and 1992, there was actually a decline in the length of intermittent streams in Lower Three Runs, and intermittent and first-order streams in Pen Branch, affected by beaver impoundment.

Although there was a large amount of change in the landscape element composition of patches between 1978 and 1992, these changes were not predictable from the landscape element composition in 1978. The first two constrained axes of CCA accounted for only a small part of the variance in relative abundance of landscape element types in 1992 (Table 4). The relative abundance of dry shrub in 1978 was the only landscape type that was related to landscape element composition in 1992 (Fig. 5a). Patches with large amounts of dry shrub in 1978 had large amounts of early succession and small amounts of wet landscape element types (e.g. flooded hardwoods, open water, wet meadow and wet shrub) in 1992.

Consideration of the unconstrained axes of CCA (axes 3 and 4) is more suggestive of a successional series. These two axes accounted for a larger amount of variation than the constrained axes (Table 4). A plot of landscape element scores on axes 3 and 4 suggests that

Table 3. Total length of stream and percentage impounded by beavers in 1978 and 1992 for six catchments at the SRS. Fourth-order streams were present in the Upper Three Runs catchment, but are not included because there were no impoundments on these streams

Catchment	Intermittent		First-order		Second-order		Third-order		Total	
	Length (m)	% impounded	Length (m)	% impounded	Length (m)	% impounded	Length (m)	% impounded	Length (m)	% impounded
Upper Three Runs	80909	1.4	47848	0.3	26982	7.0	24391	0.0	80130	2.1
Meyers Branch	20162	0.5	9244	0.0	6590	3.4	6687	3.8	42683	6.6
Lower Three Runs	8389	7.1	16728	5.2	6415	6.8	3210	0.0	34742	5.6
Pen Branch	13752	1.6	5863	4.5	9298	3.1	0	n.a.	28913	7.9
Fourmile Branch	13354	1.9	6719	0.4	10175	15.1	0	n.a.	30248	14.8
Steel Creek	0	n.a.	5445	1.0	29	3.9	0	n.a.	8349	7.2
Total	136566	1.7	91847	1.5	62364	6.8	34288	29.2	325065	4.3

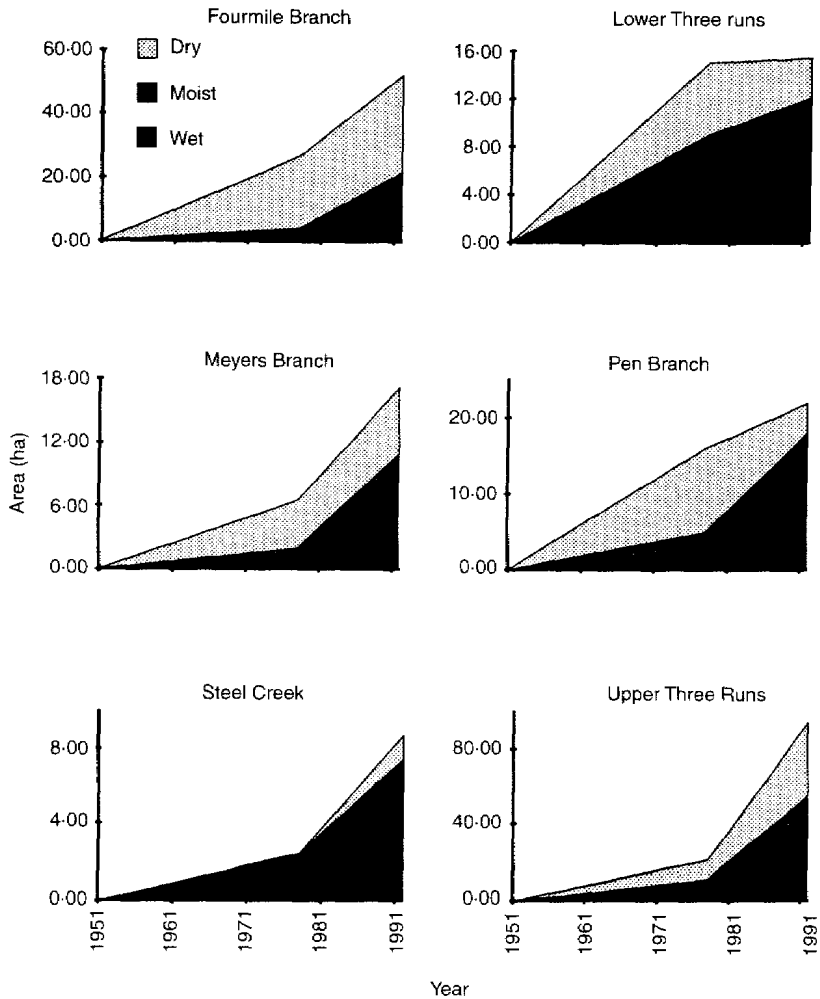


Fig. 4. Relative abundance of hydrological types between 1951 and 1992 in beaver impounded areas of the SRS. Hydrological types are defined by flooding: previously flooded: moist, seasonally flooded; wet, flooded year-round.

patches move from domination by wet landscape element types to domination by dry landscape element types along two paths that differ in temporal scale. Both paths are shown diagrammatically in Fig. 5b, and begin with flooded hardwoods or shrubs. If the dam is main-

tained, patches become dominated by open water, emergent marsh and wet meadow. Dams in these patches are eventually abandoned and the patches become dominated by dry shrub or meadow, and eventually early successional vegetation. If the dam is abandoned

Table 4. Results of CCA of relative abundance of landscape element types of patches in 1992. Note that the first two axes are constrained by the environmental variables 'relative abundance of dry shrub' in 1978 (mainly related to axis 1), and 'heavy management' (mainly related to axis 2). Axes 3 and 4 are not constrained by environmental variables

	Axis			
	1	2	3	4
Eigenvalue	0.219	0.083	0.469	0.417
% of variance in species data explained	7.5	2.9	16.1	14.3
Cumulative variance	7.5	10.4	26.5	40.8

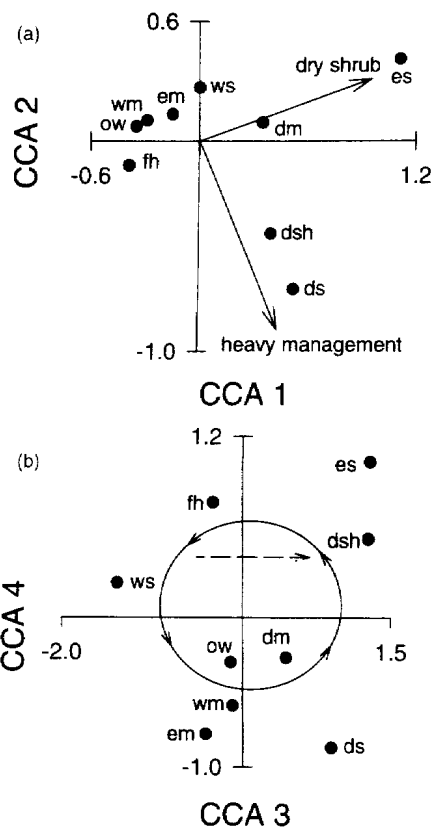


Fig. 5. Plots of landscape element scores on CCA axes 1 and 2 (a), and 3 and 4 (b). On plot (a) arrows indicate the direction of correlations between predictive variables (labelled) and the relative abundance of landscape element types in 1992 (abbreviated). A point lying near the axis of an arrow and near the arrow head is positively correlated with the environmental variable indicated by the arrow; and a point lying near the axis of an arrow, but away from the arrow head, indicates a negative correlation. Two possible paths of succession are indicated by the arrows in plot (b): a relatively short series (dashed arrow) from wet shrub and flooded hardwoods to dead standing hardwoods; and a longer series (solid arrows) from wet shrub and flooded hardwoods to open water, wet meadow, and emergent marsh to dry meadow and shrub to early succession. Abbreviations: fh, flooded hardwoods; ws, wet shrub; ow, open water; wm, wet meadow; em, emergent marsh; ds, dry shrub; dm, dry meadow; dsh, dead standing hardwoods; es, early succession.

in a shorter period, the patch becomes dominated by large areas of dry dead standing hardwoods and eventually by early succession.

A total of 277 beavers was removed from 27 colonies between 1 January 1983 and 1 January 1992. Twenty-two colonies received no management, 16 colonies received light levels of management and 11 colonies received heavy management. The majority of management effort was concentrated between 1983 and 1986 (Fig. 6). Neither method of independent

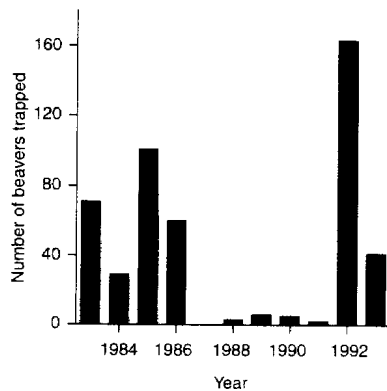


Fig. 6. Distribution of management effort, expressed as the number of beavers fatally trapped, between years at the SRS.

variable selection produced a model in which management effort was significantly related to patch growth rate between 1978 and 1992, or patch size in 1992. Additionally, patch size in 1978 was not related to patch size in 1992, but patch growth rates before 1978 were negatively related to patch growth rates between 1978 and 1992 ($P = 0.0001$; Fig. 7).

The percentage of patches occupied by active colonies was related to management. This percentage was almost identical for patches receiving no management or light management: 80.9 and 81.2%, respectively. This percentage dropped to 63.6% for patches receiving heavy management, significantly lower ($P < 0.0001$) than the percentage for patches receiving no management. CCA selected heavy management as being related to landscape element composition in 1992; however, this relationship was only marginally significant ($P = 0.09$). The analysis suggested that patches associated with colonies receiving heavy management between 1978 and 1992 contained more dead standing hardwood and dry shrub, and less emergent

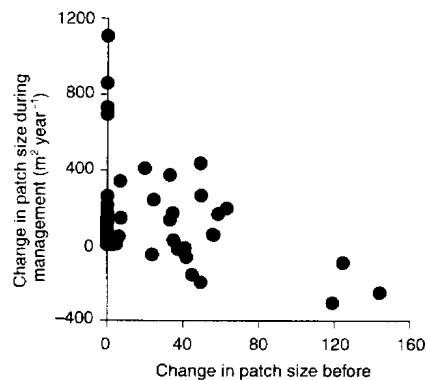


Fig. 7. Relationship between growth rate of beaver-created patches before management and growth rate during management.

marsh and wet shrub than patches associated with colonies receiving no management or light management (Fig. 5). The above analysis of landscape types does not include the transition of previously impounded areas back to riparian forest. This occurred when patches decreased in size between 1978 and 1992. One of 22 (4%) unmanaged patches, two of 16 (12%) lightly managed patches, and six of 11 (55%) heavily managed patches had negative growth rates between 1978 and 1992, suggesting that management increased the probability of forest recovery.

Discussion

PATTERNS IN SOUTH-EASTERN NORTH AMERICA

Beaver impoundment influenced a small proportion of the landscape and stream length on the Upper Coastal Plain of South Carolina, USA. After a 41-year recovery period, beavers had only influenced 0.5% of the area and 9.1% of the stream length in six catchments of the Savannah River. There was, however, a large degree of variation in the relative influence of beavers among the six catchments. The degree of influence of beaver impoundments declined exponentially with increasing catchment size suggesting that the influence of beavers within a catchment may be predicted by catchment size, and is fairly constant and low for catchments larger than 5000 ha.

Beavers showed a preference for second-order streams as indicated by their disproportionate impoundment of these streams throughout the study and across all catchments. In addition, beavers were limited to third-order or lower streams in small catchments and second-order or lower streams in larger catchments. Furthermore, beavers impounded substantial lengths of intermittent streams, effectively converting these streams from intermittent to permanent. During the field survey conducted in the summer of 1993, the annual low water period of the south-eastern Upper Coastal Plain of North America, small streams were observed below $\approx 60\%$ of the impoundments on intermittent streams. In one case there was no flow below an impoundment. Flow below the other impoundments was large enough to suggest that these stream reaches were misclassified on the USGS quadrangle maps. Nevertheless, beaver impoundments appeared to increase the proportion of perennial streams within catchments.

Beaver-created patches in the south-eastern North American landscape studied appeared to follow a successional series beginning with flooding of hardwoods and shrubs followed by either development of open water, emergent marsh and wet meadow areas, or early dam abandonment and development of areas of dry shrub or dead standing hardwoods. In both cases, early forest succession developed in some patches. Changes in landscape element composition was not

predictable from past landscape element composition. These results are in agreement with other studies conducted in North America (Remillard *et al.* 1987; Naiman *et al.* 1988) in which the stages of a successional series could be recognized. However, due to the influence of a large number of exogenous factors, present patch vegetation structure was not predictable from past vegetation structure.

COMPARISON WITH OTHER REGIONS OF NORTH AMERICA

The patterns of beaver impoundment in this study differ from those reported from more northern latitudes of North America. Johnston & Naiman (1990a) found that over a 46-year period, beavers impounded 13% of the area of a 250-km² boreal forest landscape in Minnesota, USA. In a 38-km² catchment of this same landscape they also found beavers impounded 53% of the length of first-order streams, 55% of the length of second-order streams, 87% of the length of fourth-order streams and 55% of total stream length. Only 0.5% of the landscape was impounded over the 40-year period of this study. In one catchment at the site, beavers impounded 67% of second-order streams; however, in other catchments, no more than 36%, and often substantially less, of any stream order was impounded. Furthermore, beavers preferred fourth-order streams in Minnesota, but second-order streams in South Carolina.

Rates of impoundment were found to be substantially lower in this study than those reported by Johnston & Naiman (1990a). Over the 40-year period of this study, the rate at which land area and stream length were impounded was 0.01 m² ha⁻¹ year⁻¹ and 0.7 m km⁻¹ year⁻¹, respectively. These rates for Johnston & Naiman's study were 0.28 m² ha⁻¹ year⁻¹ and 12.0 m km⁻¹ year⁻¹, respectively. Impoundment rates had also begun to decline during their study while rates were still increasing at the end of this study, despite similar study durations.

Vegetative changes involved the establishment of seedlings of riparian and upland species (young forest) and the reforestation of previously flooded riparian zones. Thus, in some cases, patches exhibited negative growth rates, decreasing in size between 1978 and 1992. These decreases in area involved the re-establishment of a forest canopy that was structurally indistinguishable from the surrounding matrix of undisturbed riparian forest on aerial photographs. Therefore, the species composition of these areas may differ from that of an undisturbed riparian forest. Again, these results contrast with previous studies from other regions of North America. Remillard *et al.* (1987) studied 37 pond sites over a 40-year period in the Adirondack State Park of New York and found that, while there was a successional series from open water to emergent marsh to shrub and back to open water, no areas returned to forest after being

impounded. Studies in Voyageurs National Park in Minnesota did not find a successional series (Naiman *et al.* 1988), but also did not observe the return of forest after being impounded.

RELATIONSHIP TO MANAGEMENT EFFORT

Originally, the differences between studies conducted in northern latitudes of North America and the results of this study were thought to be the result of management, prompting the analysis of the effects of management presented in this paper. However, over the range of temporal and spatial scales, and management levels considered in this study, management was not related to the growth rate of patches or patch size. There was a reduction in the number of patches occupied by a colony of beavers, although this apparently had little effect on the size or composition of landscape types within heavily managed patches. It is possible that management activities have not been conducted sufficiently long to allow vegetative changes to take place; however, the relative instability of vegetation within catchments between 1978 and 1992 suggests that a 9-year period is sufficient for substantial changes to occur.

The large difference in the effects of beavers in boreal forest landscapes and Upper Coastal Plain landscapes of North America may arise from differences in the geology and geomorphology of the two regions. In the boreal forest landscape studied by Johnston & Naiman (1990a) geology is characterized by poorly drained loamy to clayey soils. On the Upper Coastal Plain, soils are sandy to a depth of ≈ 200 – 600 m and well drained. As a result of high rates of recharge to groundwater in well drained soils, the density of streams on the Coastal Plain should be lower than in the boreal forest. Indeed, this is the case: stream density in the Shoepack Lake catchment studied by Johnston & Naiman was 1.23 km km^{-2} while stream densities averaged 0.86 km km^{-2} for the six catchments included in this study. This lower density of streams may inhibit dispersal and colonization, resulting in slower rates of beaver impoundment across the Upper Coastal Plain landscape.

Other hypotheses for differences between the effects of beavers in boreal forest and Upper Coastal Plain landscapes include differences in food resources and the availability of trees for dam construction, predation rates, autecology and the ability of beavers to impound streams. Food resources and trees were abundant, and predator densities low during the study period in Minnesota (Naiman *et al.* 1988). Similarly, food resources and trees were abundant, and the primary predator of beavers, the wolf *Canis lupus*, was absent during the period of study on the Upper Coastal Plain; however, American alligators *Alligator mississippiensis* occur in many coastal plain beaver ponds. The extent of predation by alligators on beavers and its influence on the population dynamics of beavers is

unknown. The fecundity of beavers in south-east North America is lower than that found in more northern latitudes of North America (Hill 1982), but no studies have documented reproductive success (number of offspring dispersing, establishing territories, and reproducing) in any location. Finally, no studies have documented the energetic costs of dam construction and maintenance in any system. Thus, differences between boreal forest and the Upper Coastal Plain in geomorphology, beaver population autecology, and the energetics of dam construction and maintenance are probably responsible for differences in the influence of beavers on the landscape of the two systems.

Recovery of the riparian forest may also be a result of the well-drained nature of the Upper Coastal Plain soils and the effects of management. Because of these well-drained soils, abandoned ponds may drain more quickly and, subsequently, soils may quickly become suitable for the establishment of saplings of riparian species. In addition, beavers were not managed or trapped from populations in studies from northern latitudes as they were in this study. Heavy management was found to increase the probability of negative patch growth rates. Negative growth rates indicate the return of forest to previously impounded areas. Thus, both mechanisms play a role because negative growth rates also occurred within patches that received no or light management.

MANAGEMENT IMPLICATIONS

Management activities should be monitored on a regional basis

All of the following management implications should be prefaced by the statement 'large differences in the effects of beavers on catchment landscapes, and the effects of management, can be expected among different regions of North America and Europe'. The results presented in this paper are only applicable to the Upper Coastal Plain of south-eastern North America; studies in other regions are needed to quantify relationships in those regions. The methods outlined in this paper could provide guidelines for using historical data to evaluate past management efforts and monitor future efforts. If economics and management goals allow, an experimental approach in which management effort was assigned randomly to colonies would permit the effects of management to be more clearly assessed.

Conflicting beaver population management goals should be addressed, evaluated and balanced

The goals of management at the Savannah River Site are to protect roads, railroads and timber. To date, management efforts are effectively protecting roads and railroads (F. Brooks, US Forest Service, personal

communication), without significantly reducing the ability of beavers to create habitats that increase biological diversity in headwater streams (Feldmann 1995; Snodgrass 1996). Clearly, some timber resources are being lost to beaver impoundment. The numbers presented in this paper could be used to estimate the economic value of lost timber; those values could be weighed against the cost of management and the loss of biological diversity that may result from management, and informed decisions concerning future management practices could be made.

Beavers do not present a threat to flowing-water species and need not be controlled for that reason

It has been suggested that beaver impoundment of south-eastern North American streams may result in the loss of strictly lotic species (Hackney & Adams 1992). For example, Rohde & Arndt (1991) list beavers as a threat to the sandhills chub *Semotilus atromaculatus* and pinewoods darter *Etheostoma mariae*, two fishes endemic to the Carolina sandhills. The results of this study indicate that beavers only impound a small portion of the stream length in small catchments of south-east North America. While the rate of impoundment was increasing in four catchments at the end of this study, in two catchments rates had begun to plateau, suggesting that the amount of stream length impounded was near the 'carrying capacity' of the catchment as determined by its geomorphology (Johnston & Naiman 1990b). In both catchments, less than 10% of the stream length had been impounded, leaving more than 90% for habitation by lotic species.

In conclusion, beavers appear to have a relatively small influence on south-eastern Coastal Plain landscapes when compared to similar-sized northern landscapes over similar periods. Additionally, beaver management efforts were not related to beaver-created patch growth rates or sizes, but did promote the re-establishment of forest within patches, suggesting that patch size is still ultimately determined by local geomorphology. Thus, management efforts met the objective of protecting roads and railroads, but not timber, while allowing the temporal and spatial dynamics of beaver impoundment to continue in some portions of the landscape.

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