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Competition favors elk over beaver in a riparian willow ecosystem

Bruce W. Baker,[1,5,†] H. Raul Peinetti,[2,3] Michael B. Coughenour,[3] and Therese L. Johnson[4]

[1]*U.S. Geological Survey, Fort Collins Science Center, Fort Collins, Colorado 80526-8118 USA*
[2]*Facultad de Agronomía, Universidad Nacional de La Pampa, Santa Rosa, La Pampa 6300 Argentina*
[3]*Natural Resource Ecology Lab, Colorado State University, Fort Collins, Colorado 80523-1499 USA*
[4]*Rocky Mountain National Park, Estes Park, Colorado 80517 USA*

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Abstract. Beaver (*Castor* spp.) conservation requires an understanding of their complex interactions with competing herbivores. Simulation modeling offers a controlled environment to examine long-term dynamics in ecosystems driven by uncontrollable variables. We used a new version of the SAVANNA ecosystem model to investigate beaver (*C. canadensis*) and elk (*Cervus elaphus*) competition for willow (*Salix* spp.). We initialized the model with field data from Rocky Mountain National Park, Colorado, USA, to simulate a 4-ha riparian ecosystem containing beaver, elk, and willow. We found beaver persisted indefinitely when elk density was $\leq$20 elk km^{-2}. Beaver persistence decreased exponentially as elk density increased from 30 to 60 elk km^{-2}, which suggests the presence of an ecological threshold. The interaction of beaver and elk herbivory shifted the size distribution of willow plants from tall to short when elk densities were $\geq$30 elk km^{-2}. The loss of tall willow preceded rapid beaver declines, thus willow condition may predict beaver population trajectory in natural environments. Beaver were able to persist with slightly higher elk densities if beaver alternated their use of foraging sites in a rest-rotation pattern rather than maintained continuous use. Thus, we found asymmetrical competition for willow strongly favored elk over beaver in a simulated montane ecosystem. Finally, we discuss application of the SAVANNA model and mechanisms of competition relative to beaver persistence as metapopulations, ecological resistance and alternative state models, and ecosystem regulation.

Key words: alternative stable states; beaver conservation; *Castor canadensis*; *Castor fiber*; *Cervus elaphus*; ecological modeling; metapopulation; Rocky Mountain National Park; *Salix*; SAVANNA model; simulation modeling; trophic cascades.

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[5] Present address: 2530 Newport Drive, Fort Collins, Colorado 80526 USA.
† **E-mail:** BruceReneeBaker@msn.com

Introduction

Simulation modeling may inform our understanding of beaver and elk competition for woody species such as willow and benefit conservation efforts that seek to restore and maintain beaver-willow ecosystems in browsed environments. Beaver are both definitive ecosystem engineers and keystone species whose dams, ponds, and canals create and maintain riparian wetlands and the species that depend on them (Baker and Hill 2003, Rosell et al. 2005). Beaver can facilitate willow establishment and survival processes, and willow can provide necessary

food and construction material for beaver, thus beaver-willow mutualism can drive the structure and function of riparian and wetland ecosystems (Baker et al. 2005*a*, Peinetti et al. 2009). Loss of beaver may change the system state from wetland to upland (Bilyeu et al. 2008). Beaver (*C. canadensis* and *C. fiber*) and willow were widespread and abundant in riparian ecosystems throughout the Holarctic region before human settlement decimated their populations via fur trapping and habitat loss. Beaver (*C. canadensis*) restoration has been successful in many areas and their populations coexist with competing herbivores in ecosystems where a diverse forage base and high productivity reduce competitive interactions (competitive exploitation; Hood and Bayley 2008); however, beaver have not thrived where competition with other herbivores has increased since predators were exterminated, livestock were introduced, or native ungulate populations have increased (competitive exclusion; Baker 2003). Beaver are central-place foragers that use woody stems to construct dams, lodges, and winter food caches (Baker and Hill 2003). Tall willow or similar woody vegetation can be *necessary* for beaver survival in cold climates where food caches provide winter forage. Elk may intensely browse willow even if herbaceous forage is available, thus willow can be *sufficient* but unnecessary for elk survival. When beaver cut tall willow they place regrowth within easy reach of elk browsing. The interaction of beaver cutting and elk browsing can create short-hedged willow that remains suitable as elk forage but unsuitable as beaver forage (Baker et al. 2005*a*). These fundamental differences in foraging requirements create the possibility of competition that favors elk over beaver.

Recent theory offers a foundation to better understand competitive interactions relative to beaver ecology. Specifically, interspecific competition for food can disrupt mutualisms that drive community organization (Stachowicz 2001, Bruno et al. 2003). The evolution of communities can depend on reduced competition via mechanisms that control the distribution and abundance of competing herbivores. Apex predators can create trophic cascades by controlling large herbivore impacts to vegetation, thus predator removal can alter the competitive environment and subsequent resource use (Ripple and Beschta 2004). If increased competition among herbivores strongly favors one species over another, then asymmetrical competition may exclude the weaker competitor and disrupt community organization. The response of communities to increased competition may be non-linear and appear as distinct thresholds that can rapidly change community organization (Briske et al. 2005). If the new community is resistant (i.e., stays stuck in the new state) after a return to the former competitive environment (e.g., via predator reintroduction) then an alternative stable state has been reached (Beisner et al. 2003, Suding et al. 2004). The application of competition theory to beaver and elk interactions has far-reaching conservation implications, but is difficult to test with empirical data.

Simulation models that integrate ecosystem processes are useful to test and apply ecological theory and predict the consequences of conservation management (Peck 2004). SAVANNA is a process-oriented ecosystem model structured in modular form where each component represents a specific ecological process, such as water balance, nitrogen cycling, plant biomass production, and the population dynamics of plants and herbivores (Coughenour 1994). Recently, we developed new beaver and willow submodels for SAVANNA to quantify how beaver foraging affects the growth and morphology of stems and plants in the willow community relative to their use by beaver. We used the model to demonstrate how the unique foraging behavior of beaver can create diverse plant architecture and increase the annual net primary productivity (ANPP) of willow (Peinetti et al. 2009). With competitors absent, the model showed how a 4-ha willow community can indefinitely sustain a beaver family (also called a colony) consisting of 2 adults, 2 yearlings, and 2 kits.

Here, we use the SAVANNA model to investigate the mechanisms of beaver and elk competition for willow in a simulated riparian ecosystem of Rocky Mountain National Park, Colorado, USA (RMNP). Specifically, we ask: (1) how beaver persistence varies as a function of elk density, (2) how the interaction of beaver cutting and elk browsing affects the size distribution of willow plants, and (3) how the presence or absence of beaver affects the recovery of tall willow as a function of elk density. We discuss

application of the SAVANNA model and mechanisms and consequences of competition relative to beaver persistence as metapopulations, ecological resistance and alternative state models, and ecosystem regulation.

Methods

Conceptual description of the SAVANNA model

SAVANNA is a process-oriented ecological model that represents the landscape as a collection of spatially explicit grid-cells (Coughenour 1994). The model is driven by monthly weather data, and has a weekly time step for most processes. SAVANNA is structured in modular form where each module represents a specific group of biophysical processes, such as water balance, nitrogen cycling, litter decomposition, biomass production, and plant and herbivore population dynamics. Water balance includes terms for precipitation, horizontal movement of water in the soil, infiltration rates, bare soil evaporation, and plant transpiration. The decomposition module is based on the CENTURY model (Parton et al. 1987) and simulates the breakdown of plant material, animal feces, urine, and the formation and turnover of soil organic matter. Vegetation types are modeled as homogeneous patches using the fractional cover of grid cells. The proportional area covered by facets is a dynamic outcome of growth and mortality for each vegetation type. SAVANNA represents ungulate herbivory via a response function (Caughley and Lawton 1975), where biomass removed depends on ungulate density, forage availability, and forage quality. Ungulate energy balance depends on the amount and quality of biomass removed, which influences their population dynamics through changes in birth and death rates. Thus, the "original" SAVANNA model is well-suited to understand many plant-herbivore interactions at larger scales (Coughenour 1994), but lacks the specificity needed to understand some complex interactions at smaller scales. In particular, it lacked (1) the ability to model herbivory at the level of an individual willow stem that could either be cut by beaver or browsed by elk and (2) the unique foraging activities and growth dynamics of a beaver colony. To meet this need, we developed new willow and beaver submodels for use with the "original" SAVANNA model, as described in Peinetti et al. (2009).

The willow submodel represents willow in terms of individual plant biomass and the number and size of individual stems. Empirically based allometric relationships are used to partition biomass into leaves, woody stems, and roots as a function of plant size. An explicit definition of individual stems is required to simulate beaver foraging in terms of the quantity and quality of stems used for food and construction activities (dams and lodges). Willow stems are characterized by 6 discrete size classes based on their height and biomass. Similarly, plants are characterized by 6 discrete size classes based on their height, canopy diameter, aboveground biomass, and belowground biomass; plant height categories for the 6 size classes were: (1) $\leq$0.5 m, (2) 0.5–1.2 m, (3) 1.2–2.4 m, (4) 2.4–2.9 m, (5) 2.9–3.4 m, and (6) 3.4–3.8 m. The aboveground characteristics of plants are ultimately derived from the sum of their constituent stems, where each stem has an associated biomass and morphology. Processes are simulated at either the plant or stem level, and then scaled to the other level. For example, plant carbon input is estimated at the plant level, but carbon is explicitly allocated into stems as a function of leaf biomass. Conversely, the biomass and morphology of a plant is derived from its constituent stems, where each stem size category has an associated recruitment and mortality rate. The number of stems can increase either by the establishment of new plants or by growth of new stems on established plants (sprouting). Stem number can decrease either by death or beaver cutting. Browsing by elk can decrease stem height, but not stem number. Moreover, stems can be transferred between size classes based on net annual biomass balance. Variation in net biomass depends on stem growth and loss (tissue death or browsing). As in the case of stems, the number of plants in each size class is a dynamic output of the model, and is determined by the establishment, mortality, and transfer of plants among size classes. Establishment can increase the number of plants only for size class 1, whereas death can decrease the number of plants in all size classes. Plants of a particular size class are comprised of a minimum number of stems in the corresponding size class. For example, a size class 3 plant must have a minimum number of

size class 3 stems. The transfer of stems among stem size classes determines the transfer of plants among plant size classes. Plant promotion to a larger size class results from stem growth; conversely, the transfer of plants to a lower size class is associated with stem death or stem loss via beaver cutting. Ungulate browsing suppresses stem height and can therefore maintain stems and plants in the same size class.

The beaver submodel simulates the growth and foraging activities of a single beaver colony that is comprised by up to 6 individuals ($\leq$2 kits, $\leq$2 yearlings, and $\leq$2 adults). Each age class has an associated body weight that represents the mean body weight of the individuals in the class and specific parameters associated with energy demands and body growth. Beaver foraging is represented via a nested hierarchy of decision rules based on stem preferences and availability relative to a comprehensive simulation model of willow morphology. Beaver foraging activities are simulated by (1) the harvest of stems for the construction of dams and lodges, (2) the storage of stems in a winter food cache, (3) the consumption of a winter food cache, and (4) the harvest and consumption of freshly cut herbaceous and woody food. The model allows beaver to select stems within plants and tissues within stems. It also considers the seasonal differences in selection for use by beaver as fresh food, winter food, and construction material. Biomass removed depends on beaver food preferences and biomass availability (Ellis et al. 1976). Beaver preferences are represented by preference indices specific for each foraging activity. Each preference index is multiplied by the available biomass and normalized by a 0–1 scale. Stem preferences by size class vary by type of beaver foraging activity. For example, the selection of willow as fresh food includes selection for stem size and selection for the type of stem tissue consumed (bark, leaves, or current annual growth). Although beaver are considered central place foragers that can vary selection with distance from distance from water, beaver dams, lodges, or food caches (Baker and Hill 2003), the beaver submodel assumes the willow community is spatially homogeneous in terms of physical conditions, vegetation, and beaver use. In other words, the model assumes all willow stems are equally available to beaver, as if the 4-ha site was a long, narrow riparian area of consistent slope. The amount of biomass removed depends on the intake rate of beaver for all foraging activities (fresh food, winter food, dam construction, and dam maintenance). Beaver are assumed to cut willow stems until all required biomass is collected. Biomass consumed by beaver is transformed to metabolizable energy intake by considering the dry matter digestibility of each plant tissue type, the gross energy content of plant tissues, and the metabolizability of digested forage. Colony energy balance is determined by comparing the energy *acquired* to the metabolic energy *required* by the number and age of beaver in the colony. Energy balance affects body weight; thus, animal performance is evaluated by a condition index calculated by comparing the actual and expected body weight of individuals in each age class. Weather inputs in the model affect plant growth and forage production through parameterized plant growth responses to temperature and water availability, which in turn affects the forage availability of willow and herbaceous plants. Thus, beaver persistence time is the emergent outcome of weather-driven plant growth and plant-animal interactions on the landscape.

Model setting and evaluation

We configured the model as in previous applications for a riparian willow community in RMNP (Peinetti 2000, Coughenour 2001, 2002, Peinetti et al. 2002). Simulations used randomly selected yearly weather data from local weather stations and SNOTEL sites in and near RMNP. Field data were collected by Peinetti (2000) from a montane riparian area of RMNP (Endo Valley, elevation 2500 m) at a site dominated by *Salix monticola*. The field site likely had received a low level of elk and beaver use in the last decade, based on empirical data and field observations.

The initial conditions of the model were generated using this field data as a baseline. Willow parameters represented riparian willows in RMNP, and simulated willow growth rates were consistent with empirical data (Peinetti et al. 2009). To generate an initial condition, we ran the model for 50 years with beaver and elk absent to remove the possible effects of past herbivory on willow. Then we then ran the model for another 50 years with elk absent and beaver

present (2 adults, 2 yearlings, and 2 kits) to create a simulated 4-ha beaver-willow community in stable equilibrium, which served as the model experimental setting (see Peinetti et al. 2009 for model configuration details). Thus, the initial model condition was a 4-ha beaver-willow community that indefinitely sustained a single beaver colony when elk were absent (Peinetti et al. 2009). We modeled the effects of elk browsing on willow as a function of elk density using a simple version of the ungulate model in SAVANNA, which did not model elk population dynamics. Elk density values corresponded with those used in a previous application of the model (Coughenour 2002), but were scaled to obtain forage intake rates similar to observed field data (as in Hobbs 1989). Elk browsing effects on willow were non-linearly related to adjusted elk density as a function of preference and availability. The model assumed that all portions of willow stems <2.0 m in height were available to browsing elk and that all portions >2.0 m in height were unavailable. Elk use of willow depended on the growth and availability of both willow and grasses, past elk use, and snow depth. The dietary preference weights for willow were multiplied by available edible biomass to estimate the fraction of willow in the elk diet (Ellis et al. 1976). Elk and beaver densities were assumed to be homogeneous throughout the 4-ha area, but varied among different simulation scenarios. We adjusted elk density levels (but not those for beaver) for observed seasonal movement patterns in RMNP, as follows: 100% of maximum during October 1 to April 30, 50% of maximum during May and September, and 10% of maximum during June, July, and August (estimated from Lubow et al. 2002). Elk densities reported in this paper refers to winter densities. Thus, we modeled the interaction of beaver and elk herbivory on willow condition, and the consequences of willow condition on beaver.

Simulation experiments

The first experiment simulated the effects of elk browsing on the persistence of a beaver family when elk density was varied from 0 to 100 elk km^{-2}, which represented the actual range of observed densities in RMNP. Energy balance for the beaver family was determined by comparing the energy *acquired* through food intake and the energy *required* by the costs of metabolism and activities. Beaver persistence time depended on a condition index (0–1 scale), which we defined as the ratio of actual weight (based on current energy balance) to expected weight (based on optimal energy balance) for the entire beaver family. We assumed that beaver were able to persist when the mean condition index of the family was steadily maintained at values $\geq$0.80. Conversely, we assumed that a steady downward trend in the beaver condition index indicated evidence of competitive exclusion by elk, with the year of exclusion defined as the first year the condition index was <0.80.

The second experiment evaluated how the interaction of beaver cutting and elk browsing altered the size distribution of willow plants. Simulations were run with the beaver family either absent or present, and elk densities of 0, 30, 40, 50, and 60 elk km^{-2}. The response variable was the proportional size distribution of willow plants. Simulations were run until the model showed steady state conditions or until the condition index was <0.80 and beaver were unable to persist.

The third experiment evaluated the effects of elk density on the recovery time of willow after beaver abandoned the site. Starting with initial condition, we ran the model with a single beaver family present and elk densities of 0, 10, 20, 30, 40, 50, and 60 elk km^{-2}, then removed the beaver family after 28 years, which was the number of years that beaver persisted under the highest elk density. We measured the response variable as the time required (in years) to recover willow size classes 5 and 6 back to their initial condition, which we assumed meant the 4-ha site had recovered enough tall willow to support recolonization by a beaver family. Thus, the experiment evaluated how elk browsing affected beaver and willow recovery under periodic beaver use.

Results

Patterns of elk density and beaver persistence

Beaver persistence was strongly affected by elk density (Fig. 1). Beaver persisted indefinitely when elk density was $\leq$20 elk km^{-2}, but persistence decreased exponentially as elk density increased from 30 to 60 elk km^{-2}. Higher elk

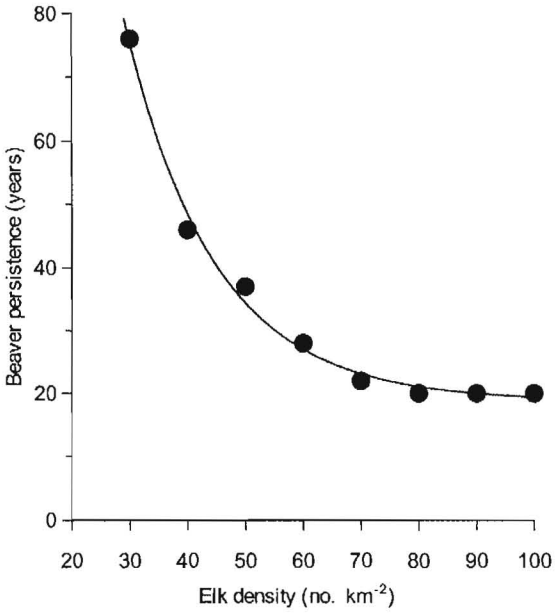

Fig. 1. A beaver family persisted indefinitely in a simulated 4-ha willow community when elk density was ≤20 elk km^{-2}. When elk densities were increased above this threshold level, then beaver persistence time declined sharply until elk densities reached ≥70 elk km^{-2}. Further elk increases did not decrease persistence time because willow habitat had already become unsuitable to beaver. Run configurations were: IC + 50 years, NB NE + 50 years, B NE + n years B E; where IC = initial condition (RMNP field data), B = beaver, NB = no beaver, E = elk, NE = no elk, and n = 20 to 100 years depending on the simulation. Beaver density was 1 family in 4 ha and elk density was 0 to 100 elk km^{-2}. $Y = 18.8 + 390 \times \exp^{(-0.064 \times X)}$; ($R^2 = 0.99$).

densities of 70 to 100 elk km^{-2} had no further effect, likely because willow biomass suitable to beaver had already been consumed by elk. These patterns suggest a threshold effect occurred at 20 elk km^{-2}, when beaver were extremely sensitive to increasing elk density. Conceptually, this density is equivalent to only 0.8 elk in the 4-ha simulated area. Thus, simulations showed competition for willow strongly favored elk over beaver.

Mechanisms of beaver and elk interactions

The interaction of beaver and elk herbivory strongly affected the structure of the willow community (Fig. 2). With beaver absent, tall willow (class 6) comprised nearly 50% of plants regardless of elk density levels (Fig. 2A–E), likely because low stem turnover rates allowed plants to reach their maximum growth potential and plants >2 m tall were out of reach to browsing elk. With elk absent and beaver present (Fig. 2F), there were fewer tall willow and more intermediate willow compared to when elk and beaver were both absent (Fig. 2A), likely because beaver herbivory increased stem turnover rates and stem selection by beaver favored taller stems (see Peinetti et al. 2009 for details). The interaction of beaver and elk herbivory had dramatic effects on plant architecture. When elk density was 30 elk km^{-2}, there was a shift toward smaller willow and beaver were excluded after 76 years (Fig. 2G). When elk densities were 40 and 50 elk km^{-2}, the proportion of shorter willow greatly increased and beaver were excluded after 46 and 37 years (Fig. 2H and 2I, respectively). When elk density was 60 elk km^{-2}, over 90% of willow were <0.5 m tall (class 1) and beaver were excluded after 28 years (Fig. 2J). Elk persisted in all cases because they were limited by herbaceous vegetation rather than by willow. Thus, the interaction of beaver and elk herbivory transformed a tall willow community into a short-hedged community and excluded beaver when elk densities exceeded 20 elk km^{-2}.

Willow recovery

The recovery of tall willow after 28 years of combined use by beaver and elk was strongly affected by the elk density that preceded and followed beaver removal (Fig. 3). Recovery time was 0 years when elk density was 0 elk km^{-2}, which represented the beaver-willow community at stable equilibrium. Recovery time increased exponentially as elk density increased from 0 to 50 elk km^{-2}, and became asymptotic when elk densities were >50 elk km^{-2}. This pattern suggests the interaction of beaver cutting *followed by* intense elk browsing continued to suppress the regrowth of tall willow even after beaver were removed. Beaver can persist longer with higher elk densities if beaver alternate their use of foraging sites in a rest-rotation or periodic pattern rather than continuously use a single 4-ha site. For example, a beaver family can persist indefinitely with an elk density of 40 elk km^{-2} if they rotate their use of two 4-ha sites every 12

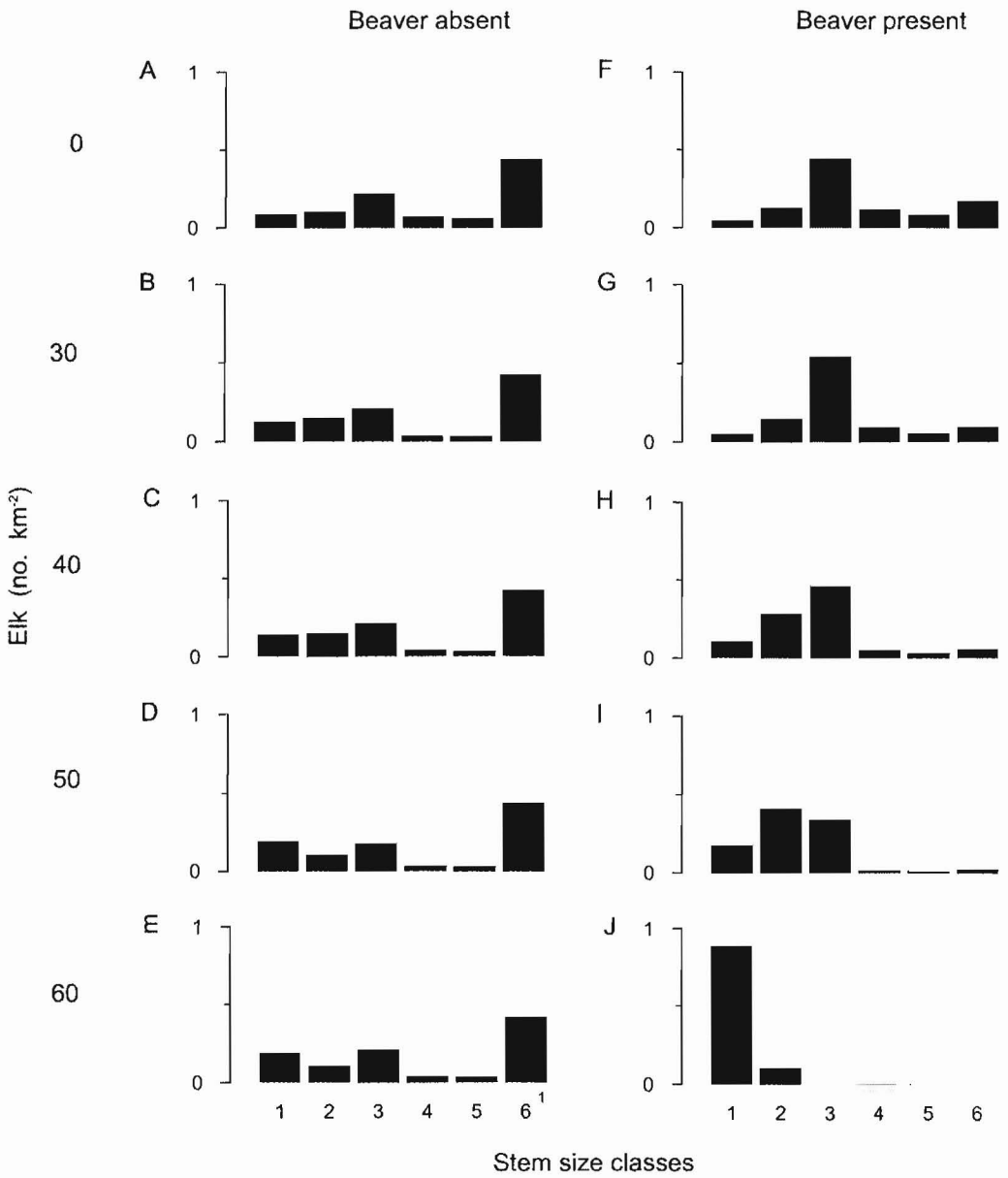

Fig. 2. The size class distribution of willow plants (see *Methods* for details of the 6 size classes) with a beaver family absent (A–E) or present (F–J) under 5 different elk densities in the 4-ha simulated willow community. Beaver persisted indefinitely when elk were absent, but were excluded in 76, 46, 37, and 28 years after initial condition when elk densities were 30, 40, 50, and 60 elk km^{-2}, respectively. Size distribution data present the status of willow 28 years after initial condition. Although not shown, the size class distribution of willow for (G), (H), and (I) became similar to (J) when simulations were run long enough to exclude beaver. Thus, the interaction of beaver and elk herbivory shifted the size structure of the willow community by increasing short willow and eliminating tall willow. Loss of tall willow was the mechanism that excluded beaver. Note that size class 6 stems with beaver absent were largely unaffected by elk browsing at all densities because the model assumed that browsing was limited to plant biomass <2 m tall. This assumption may not be realistic in all cases as foraging elk sometimes break tall stems to access the tips of leaders. Run configurations were: (1) for beaver absent

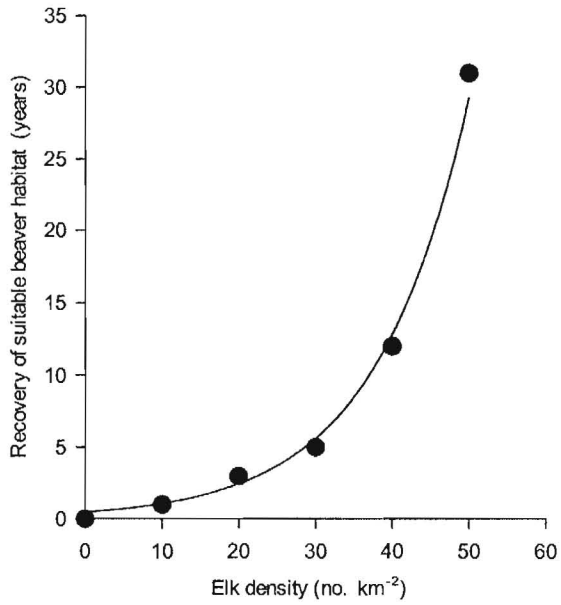

Fig. 3. Beaver recovery time (defined in years as the initial condition (in proportion) of willow in size classes 5 and 6) increased exponentially with increasing elk density after the removal of the beaver family from the 4-ha simulated area. Note that the curve becomes asymptotic when elk density is >50 elk km^{-2}, which indicates the system never recovers enough tall willow for beaver to reoccupy the site. Run configurations were: IC + 50 years NB NE, + 50 years B NE, +28 years B E, + n years NB E; where IC = initial condition (RMNP field data), B = beaver, NB = no beaver, E = elk, NE = no elk, and n = ≤31 years (depending on simulation conditions). Beaver density was 1 family in 4 ha and elk density was 0 to 50 elk km^2. $Y = 0.47 \times \exp^{(0.082 \times X)}$; ($R^2 = 0.99$); (for x = {0–50}).

years, which allows time for willow plants to recover their initial condition (Fig. 3). In contrast, beaver were unable to occupy a *single* 4-ha site longer than 46 years when the elk density was 40 elk km^{-2} (Figs. 1 and 2), as the interaction of continuous beaver and elk herbivory suppressed the recovery of tall willow. Thus, the cumulative effects of beaver and elk competition for willow can be reduced if beaver foraging sites are used in a cyclic pattern of occupation, abandonment, recovery, and reoccupation.

Discussion

We simulated beaver and elk competition for willow via the SAVANNA ecosystem model. We found a 4-ha healthy willow community indefinitely sustained a beaver family of 2 adults, 2 yearlings, and 2 kits when elk were absent or density was ≤20 elk km^{-2}, but densities of ≥30 elk km^{-2} eventually excluded beaver via food limitation. The interaction of beaver cutting and elk browsing strongly suppressed the proportion of willow in the taller size classes, which were required by beaver as food and construction material. Recovery of tall willow under intermittent beaver use allowed beaver to persist when elk densities were higher than under continuous beaver use. Thus, simulation modeling showed how asymmetrical competition can favor elk over beaver in a montane willow community.

Mechanisms of beaver and elk competition for willow

Elk populations were not regulated by the size or availability of willow in our model, so elk persisted under all willow conditions (Figs. 1 and 2). When elk diets are subsidized by herbaceous forage then large herds can congregate in riparian areas at densities far beyond the carrying capacity of willow. Thus, elk browsing can create short-hedged willow that remains productive as elk forage for many decades, but is unsuitable to beaver (Baker et al. 2005*a*).

(continuation of Fig. 2 legend)

and elk density = 0, then IC + 50 years NB NE + 50 years B NE +28 years NB NE; (2) for beaver absent and elk density = 30 to 60 elk km^{-2}, then IC + 50 years NB NE + 50 years B NE +28 years NB E; for beaver present and elk density = 0, then IC + 50 years NB NE + 50 years B NE+28 years B NE; and (4) for beaver present and elk density = 30 to 60 elk km^{-2}, then IC + 50 years NB NE + 50 years B NE+28 years B E; where IC = initial condition (RMNP field data), B = beaver, NB = no beaver, E = elk, NE = no elk. Beaver density was 1 family in 4 ha.

Modeling showed beaver persistence time rapidly decreased as the willow community lost tall plants and became dominated by short-hedged plants (Fig. 2F–J). Tall stems have higher food value because they have a greater biomass of suitable bark and a larger number of small twigs (Baker and Cade 1995). Tall stems also have higher construction value because they provide better structural support and can be cut into smaller segments to add mass and patch leaks in dams. The interaction of beaver and elk herbivory strongly suppressed willow height, which regulated beaver persistence. This pattern is consistent with empirical data from RMNP, where elk browsing greatly reduced willow (*S. monticola*) regrowth after simulated beaver cutting (Baker et al. 2005*a*). Given adequate growing conditions, willow can respond to complete stem removal by beaver with rapid mobilization of belowground nutrients, vigorous sprouting, and high growth rates (Kindschy 1985, 1989, Baker et al. 2005*a*). However, this response depletes root reserves until regrowth can recover the stem and leaf tissue necessary for photosynthesis. The interaction of beaver cutting followed by intense elk browsing suppresses compensatory growth mechanisms by preventing new shoots from recovering lost tissue. Thus, elk exclude beaver by suppressing the growth of tall willow.

Beaver persisted indefinitely at 20 elk km^{-2}, but persistence time decreased exponentially as elk density increased from 30 to 60 elk km^{-2}. Rapid change suggests a functional threshold (Briske et al. 2005). Furthermore, simulations show beaver declines lagged behind tall willow declines, which suggests a structural threshold was reached in the willow community (i.e., hedged plants) before the functional loss of beaver occurred. If declining willow condition predicts future beaver decline, then managers can monitor willow to determine beaver population trajectory. The fall season is the best time to monitor willow where ponds freeze during winter and food caches built in the fall provide winter food that is the primary limiting factor for beaver. Willow architecture (leader length and number, overall plant shape) can inform browsing history (Keigley and Frisina 1998), thus it can predict beaver population trends. Our evidence suggests a downward trend if browsing has suppressed the height of more than half of the tallest willow plants (Fig. 2). Short-hedged plants around the perimeter of beaver ponds also suggest risk of beaver decline. If browsing pressure exceeds the threshold level, then a rapid decline of tall willow within the pond complex will likely precede beaver declines. Thus, managers should act to reduce browsing pressure before a threshold level of competition with other herbivores excludes tall willow.

SAVANNA model application

The SAVANNA model may elucidate beaver-herbivore interactions in many ecosystems. In RMNP, the restoration of beaver-willow wetlands is a high priority after many decades of decline. Recently, an Elk and Vegetation Management Plan/Environmental Impact Statement (EIS) was developed and implemented to address these concerns. Historical records show beaver and elk competition for willow was apparent in RMNP during the 1940s when the Park trapped 218 beaver from Moraine Park to reduce nearby landowner concerns (Packard 1947). Trapping likely initiated long-term beaver declines in RMNP, as the Moraine Park population dropped from 315 in 1939–40, to 102 in 1964, to 12 in 1980, to 6 in 1999 (Baker et al. 2004). Beaver telemetry studies in the 1990s showed low mortality and movement rates, and blood samples showed no disease agents; thus, implicating other causes for decline (Baker et al. 2004). Elk were reintroduced to RMNP in 1913, following their extirpation in the late 1800s. The elk population grew quickly in the absence of wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*), which also had been extirpated. Elk were actively controlled from 1944 to 1968 to maintain their numbers between 300 and 800. Beginning in 1969, managers ceased control in favor of natural regulation. By the late 1990s the elk population in the Park and nearby town of Estes Park had increased to over 3,000 animals (Lubow et al. 2002: Table 1). Interestingly, elk use of willow was consistently high (~85% annually) during 1968 to 1993 (Zeigenfuss et al. 1999: Fig. 11), even though elk numbers varied greatly. Field experiments showed elk browsing strongly suppressed the regrowth of simulated beaver-cut willow (Baker et al. 2005*a*). Simulation modeling showed a beaver-willow community persisted indefinitely as a stable equilibrium (Peinetti et al. 2009), but

rapidly declined when elk density exceeded 20 elk km^{-2} (this paper). Given these studies and many others, RMNP prepared the EIS to guide management over a 20-year period in order to reduce the impacts of elk on vegetation and to restore the natural range of variability in the elk population and affected plant and animal communities, including beaver and willow. The SAVANNA model was used to evaluate the population dynamics and ecological effects of elk, and to predict plant responses to potential elk management. Adaptive management is being used to balance public, resource, and regulatory needs in RMNP; monitoring of beaver and elk population levels, and willow browsing intensity, will help inform ecologists and managers about how to manage beaver, elk, and vegetation.

SAVANNA also may be applied in a variety of other ecosystems to restore and conserve beaver populations in browsed environments where competition with herbivores can reduce carrying capacity for beaver. The competitive interactions we describe for beaver, elk, and willow in RMNP likely apply at some level to Eurasian beaver (*Castor fiber*), competition with other native herbivores and introduced livestock, and other plant communities such as birch (*Betula* spp.), alder (*Alnus* spp.), cottonwood (*Populus* spp.), and aspen (*P. tremuloides*). The model is general enough to analyze these different interactions given reliable data on large herbivore and beaver diet compositions and plant growth rates. Such data can be used to parameterize the model, and to verify that the model is predicting accurate balances between herbivore utilization and plant production. Given correct off-take rates (biomass removed by browsing) and plant growth responses to herbivory, then competitive interactions between beaver and large herbivores should, theoretically, be correct. The model can predict beaver persistence at the watershed scale (10–100 km^{-2}) using weather and other data that describe the landscape in terms of soils, topography, and vegetation. It also could be adapted to conduct beaver population analyses or to more fully describe the unique foraging and engineering characteristics of beaver.

Beaver are central place foragers that can select plants depending on species and stem size availability relative to their effective distance from a food cache, dam, or lodge (Baker and Hill 2003). Central place foraging could be represented in SAVANNA either by modeling the foraging behavior of individual animals or the expected allocation of foraging effort across space, effectively distributing "beaver foraging days" spatially in relation to distance from the central place, water, or other factors. Movement cost surfaces could be constructed based upon various foraging routes across land or water, and these surfaces could likewise be used to estimate the likelihood of beaver foraging across the landscape. Although these types of modifications likely would benefit some applications, we suggest our representation here of beaver foraging as a spatial average across the 4-ha simulated habitat provides a good first approximation to the net impacts of beaver within that portion of the landscape used by beaver. Our primary question here was the degree of competition between beaver and elk for willow. As such, the mean response we used likely captured the majority of the competitive outcome in our simulations. Alternatively, incorporating fine-scaled spatial variation in either beaver or ungulate foraging patterns may benefit other applications and could be an interesting topic of future research.

SAVANNA is also appropriate for resource-based population viability analyses of beaver reintroductions in browsed environments. The animal population submodel is a traditional age and sex class model with age and sex specific birth and death rates. Importantly, these demographic rates are dynamically affected by resource availability in the model. Forage availability, which is affected by forage production as well as snow cover, affects animal intake rates, which then affect animal energetic status, which then affects birth and death rates. Thus, there is a seamless causal linkage from weather, to plant growth, to animal demographics. Variations in beaver birth and death rates could be modeled via stochastic simulation experiments to estimate the risks of population extinction under various scenarios of climate and large herbivores. Beaver metapopulations can be simulated by representing movements of animals among subpopulations across the landscape. Such movements within a metapopulation, coupled with the mosaic dynamics of willow growth following herbivory, would produce considerably different

risk predictions than models that neglect spatial dynamics. Possible effects of competition on beaver habitat quality should also be included in population viability estimates of beaver persistence following reintroduction (South et al. 2000).

SAVANNA differs from previous models of beaver population viability analysis (Nolet and Baveco 1996, South et al. 2000) in that it directly represents habitat carrying capacity and density dependent competition for resources. Resource abundance is the net outcome of plant growth rate and off-take by beaver. Rather than specifying a fixed carrying capacity, the number of sustainable beaver depends upon beaver food and construction requirements relative to resource productivity. SAVANNA represents competition directly rather than use a density dependence parameter. The model is spatially explicit in that vegetation is distributed realistically across the landscape, thus there is no need to classify habitat suitability. Suitable habitat is simply an outcome of resource abundance coupled with proximity to water and other habitat variables. Although not in the current version, SAVANNA could be modified to simulate beaver dispersal across the landscape, as does the model of South et al. (2000). SAVANNA could also be modified from its current representation of age and sex classes to an individual-based model, as are the models of Nolet and Baveco (1996) and South et al. (2000). Thus, SAVANNA can be adapted to meet many different user needs.

Beaver persistence as metapopulations

Competition with elk or other herbivores may exclude beaver where browsing intensity is high but allow beaver to persist regionally as relatively isolated metapopulations where browsing intensity is low. Beaver east of the Continental Divide in RMNP have persisted as small populations of 1 or 2 families in remnant tall willow patches that receive low elk use due to their location, topography, and historical use patterns (Wild Basin, Endo Valley), but declined dramatically from core elk winter ranges in Moraine and Horseshoe Parks (Baker et al. 2004). Metapopulation theory suggests inferior competitors (beaver) may coexist with superior competitors (elk) as metapopulations if the competitive environment varies within the larger landscape (Ricklefs and Miller 2000). Variation in elk browsing intensity creates variation in willow patch suitability to beaver as individual stems, plants, and populations reflect their particular browsing history. Variation in willow patch suitability within a region likely restricts migration among local beaver populations, which is a defining characteristic of a metapopulation (Ricklefs and Miller 2000). Colonization by beaver that disperse from natal colonies usually occurs as migration within the riparian corridor in steep mountain environments rather than as upland travel between watersheds (Baker and Hill 2003). If beaver colonies are separated by long reaches of riparian habitat made unsuitable by competition with other herbivores, then gene flow may decrease among small, isolated beaver populations. Small populations are subject to local extinction but can be easily rescued by occasional immigration or translocation from other populations (Stacey et al. 1997). Thus, beaver may persist in isolated habitat patches as metapopulations within heavily browsed environments where long-term fitness may be rescued by occasional immigration or translocation from outside populations.

Competition, resistance, and alternative state models

Ecological resistance is the amount of change that can be absorbed by a system before the processes that control its structure and function also change (Suding et al. 2004). Loss of beaver may alter community organization and create an alternative stable state, defined as system stability in the absence of continued disturbance (Beisner et al. 2003). Thus, competition with elk has moved a beaver-wetland to an alternative state of elk-grassland if the site fails to recover its former wetland state after elk are removed.

The application of alternative state theory (Suding et al. 2004: Box 2) to beaver conservation suggests the consequences of competition depend on how beaver declines alter the physical system state (Fig. 4). If the physical state remains intact, then the former biotic state should recover (Fig. 4A). For example, increased browsing intensity in a beaver-wetland (up arrows) can cause beaver to abandon the site, moving the system to an elk-grassland state (down arrows).

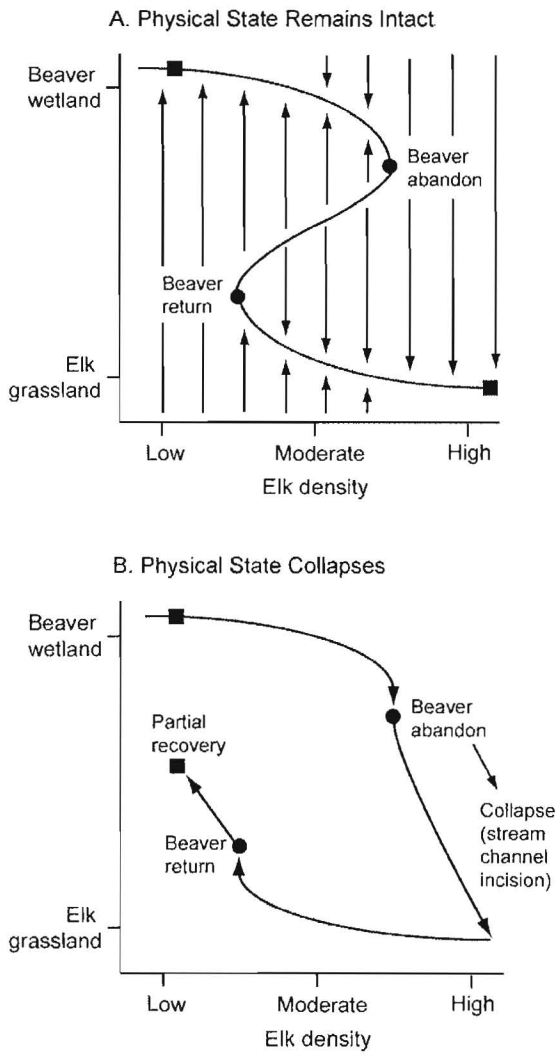

Fig. 4. Alternative state theory (Suding et al. 2004: Box 2) suggests the consequences of beaver and elk competition for willow will depend on how beaver declines alter the physical system state. The system can fully recover if the physical state remains intact (Fig. 4A) or partially recover if it collapses (Fig. 4B). In the intact system (Fig. 4A), low browsing intensity maintains the beaver-wetland state (up arrows) but increased browsing causes beaver abandonment and the system moves to the elk-grassland state (down arrows). If browsing intensity is reduced to its former low level, and hedged willow recover their former tall stature, then beaver can return and the system will move back to its former beaver-wetland state (up arrows) along a similar trajectory. If the physical state collapses (Fig. 4B) due to beaver declines, then the system may be unable to fully recover its former wetland state. For example, beaver dam failure after abandonment can cause channel incision that places the former floodplain beyond the reach of rebuilt or new beaver dams. In this case, some areas may be unable to recover their former beaver-wetland state even though elk browsing intensity is reduced to its former lower level. Thus, competition can create an alternative stable state of elk grassland if physical state changes caused by beaver declines prevent the restoration of the former wetland state.

If browsing intensity is reduced to its former low level, and hedged willow recover their former tall stature, then beaver can return and the system will move back to its former beaver-wetland state (up arrows). The black dots in Fig. 4A represent critical thresholds of environmental conditions, in this case moderate elk densities (see Figs. 1 and 2), that bound stable and unstable equilibriums. Conservation management that reduces elk browsing, such as fencing, predation, or population control, can release suppressed willow (Baker et al. 2005*b*) and restore beaver-wetlands if the physical state remains intact.

If beaver declines cause physical state changes, then the system may be unable to recover its former beaver-wetland state (Fig. 4B). Beaver can benefit willow establishment and survival processes by maintaining high water tables throughout the growing season and by placing water and sediment where floods cannot reach (Westbrook et al. 2006, Westbrook et al. 2011). Beaver abandonment can cause dam failure, channel incision, and a lower water table, which can kill existing willow and prevent re-establishment (Apple et al. 1985, Fouty 2003). In Yellowstone National Park, USA, willow that was protected from ungulate browsing and given adequate water via simulated beaver dams were taller and more vigorous than protected willow in undammed sites (Bilyeu et al. 2008). In such cases, partial recovery may occur within incised channels in areas that are sub-irrigated or watered by beaver dams. The result may be that some portions of the landscape are "stuck" in alternate physical states that forever preclude beaver colonization (e.g., high terraces beyond the reach of beaver dams) whereas other areas may recover

beaver if competition with other herbivores is reduced. Thus, competition may create a landscape mosaic of alternative physical states that vary temporally and spatially in their ability to recover and sustain beaver populations.

Competition and ecosystem regulation

The role of bottom-up vs. top-down mechanisms in ecosystem regulation has been highly controversial (Kay 1998). In 1968, the National Park Service, USA, stopped elk control and allowed natural processes (food, weather) to regulate populations. Elk thrived but beaver and tall willow declined in Yellowstone, Rocky Mountain, and other parks, which lacked apex predators such as wolves. Debates ensued about how to explain cause and restore natural processes and conditions, which is the Park Service mandate. Understanding beaver as weak competitors may inform these debates.

Beaver evolved and thrived in competitor-rich environments. The historical abundance of beaver in North America is legendary, as the number trapped for fur during 1550 to 1850 led Seton (1929) to estimate their population at 60 to 400 million. Eurasian beaver also were abundant before overharvest and habitat loss (Rosell et al. 2005). Willow evolved to dominate disturbed riverine environments with life history traits (Karrenberg et al. 2002) benefited by the dams, ponds, and foraging of beaver. Many competing herbivores (*Cervus* spp.) and apex predators (*Canis* spp.) also coexisted with beaver and willow in the Holarctic for several million years (Alroy 2001, Paquet and Carbyn 2003). What mechanisms allowed beaver to evolve and thrive in competitor-rich environments?

The trophic cascade hypothesis suggests apex predators, such as wolves, can regulate elk with effects that cascade to lower trophic levels, such as beaver and willow (Smith et al. 2003, Ripple and Beschta 2004, Fortin et al. 2005, Beschta and Ripple 2009). Apex predators may benefit beaver by reducing competition with elk for willow via direct mortality and behavioral changes due to fear of predation. Beaver dams, lodges, and canals within a matrix of dense willow may be a death trap for elk in a predator-rich landscape. Restoration of trophic cascades where apex predators have been lost may or may not help to restore beaver populations in degraded habitat. Evidence from Yellowstone National Park shows beaver have increased slightly since wolves were reintroduced in 1995–96, but cause and effect is uncertain (Smith et al. 2003). Thus, the trophic cascade hypothesis may have allowed beaver to evolve and thrive in competitor rich environments, and is consistent with our evidence of beaver as weak competitors with elk.

In conclusion, the SAVANNA model showed how competition strongly favored elk over beaver in a simulated montane willow ecosystem of RMNP. Beaver were weak competitors that were excluded when intense elk browsing suppressed the growth of tall willow, but beaver persisted under lower elk densities. The ability of beaver to thrive in competitive environments varies with the level of competition (Baker 2003, Baker et al. 2005*a*, this paper) and with the diversity and productivity of forage (Hood and Bayley 2008). Spatial and temporal variation in herbivore density, diet overlap, predator effects, and physical features of the landscape suggest the consequences of competition exist along a continuum, and are scale-dependent. At small scales, such as the 4-ha area we simulated in this paper, competition may or may not exclude a single beaver family, whereas at larger scales it may be expressed as a mosaic of both exclusion and resource exploitation (coexistence). Conceptually, in terms of competition, it may be useful to think of a large landscape, such as a National Park, as overlain with a grid of 1 m^2 cells that vary in their ability to support beaver, depending on the level of competition (e.g., elk browsing intensity) and the ability to recover if competition is reduced (i.e., they are not "stuck" in an alternative stable state; Fig. 4B). If browsing intensity exceeds the threshold level that excludes beaver at the small scale, then beaver carrying capacity will be reduced at the large scale. Thus, competition may help explain the success or failure of beaver to thrive as ecosystem engineers at the landscape scale.

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