ASPEN FOREST COMMUNITIES: A KEY INDICATOR OF ECOLOGICAL INTEGRITY IN THE ROCKY MOUNTAINS

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SUMMARY
Aspen forests in the Rocky Mountain national parks are an excellent indicator of ecological integrity because they have maintained their presence for thousands of years through vegetative regeneration, and because these communities contain a high biodiversity of indigenous species. Further, stand conditions are easily measured, and are indicative of long-term ecosystem states and processes through a four-level trophic model that links aspen to elk, bison, wolves and humans through the processes of predation, herbivory, and fire. Most aspen stands in national parks of western Canada and United States are declining in vigour. Two competing hypotheses attempt to explain this change: 1) Food Limitation ("Bottom-up") Hypothesis: a long-term stable state occurs when aspen is browsed extensively by abundant, food-regulated elk, 2) Predator Limitation ("Top-Down") Hypothesis: Aspens' decline is a deviation from the long-term range of variation, and is due to unusually high elk densities due to release from predation, and fire suppression. We review existing evidence for the latter hypothesis and suggest further needs for research.

1. INTRODUCTION
Trembling aspen (*Populus tremuloides*) forests are a unique community type in the Rocky Mountain national parks of Canada and United States. In Banff, Jasper, Yoho, and Kootenay, aspen distribution is generally confined to low elevations where large stands occur on alluvial fans , or small stands are dotted through lodgepole pine (*Pinus contorta*) forests (1,2). In Yellowstone and Rocky Mountain national parks, aspen is limited to less than 1 percent of the area, and occurs mostly on seeps and swales in grasslands at low elevations (3,4,5). Because current conditions for establishment from seed are not favourable, the clones constituting these stands may be several thousand years old (6). Frequent (<50 years return interval), low intensity fires (7,8) regenerated large clones by removing competing conifers, top-killing the aspen, and stimulating suckering from surviving roots (9,10,11,12,13). Small aspen stands in conifer forests may survive through long fire-free intervals by periodic sucker release in forest gaps (2,14).

Because aspen stands occupy moist, nutrient-rich sites at low elevations, they sustain a high biodiversity of indigenous species, exceeded in the Rocky Mountains only by riparian zones (6). Holroyd and Van Tighem (15) rate montane aspen types in Canada as high quality habitat for large mammals such as elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*) and a diverse range of small mammal species. Bird surveys in the Bow Valley near the town of Banff, Alberta record 35 breeding species in aspen stands, compared with fewer than 15 species in nearby conifer forests (16).

Trembling aspen stand condition is easily evaluated by methods such as repeat photography, wildlife exclosures and belt transects (3,4,5,12,17). Numerous studies report that aspen stands in Rocky Mountain national parks are declining in vigour (3,4,5,18,19,20,21,22,23). Stands have low densities (<500 stems/ha), trees are intermediate to mature successionally (60–120 years old), and new suckers are browsed off by elk before reaching 2 meters in height.

2. ALTERNATE HYPOTHESES TO EXPLAIN LONG-TERM ASPEN STAND STATES AND PROCESSES
Two competing hypotheses attempt to explain the decline of aspen forests.

2.1 Food Limitation ("Bottom-up") Hypothesis.
A long-term stable state of montane aspen forest occurs when aspen is browsed extensively by abundant, food-limited elk. This is termed "natural regulation" in Yellowstone National Park (4,24,25,26). Under this hypothesis, heavily browsed aspen persists in the ecosystem due to regeneration by fire (4,27,28), chemical defence of aspen suckers against herbivory (29), or a complex interaction of factors such as fire, elk starvation, winter severity and climate change (13,25). The current degeneration of aspen is due to an increase in elk numbers back to a normal food-limited equilibrium following intense human hunting during the late 1800s. Wolf (*Canis lupus*) or other predation on elk is considered a "non-necessary adjunct" (24), which removes animals that will die anyway due to starvation, and thus cannot substantially lower elk populations below food-limited levels (30).

2.2 Predator Limitation ("Top-Down") Hypothesis.
This hypothesis considers heavily browsed aspen to not be a long-term stable state. Aspen decline is a recent condition due to unusually high elk populations (3,5,11,18,19,22). However, the long-term mechanisms for holding elk populations at low densities had not been identified, and factors affecting fire occurrence had not been integrated into explanations. Recently, the "top-down" hypothesis has been synthesized with a trophic model (Figure 1) that links humans, wolves, elk, and aspen through the processes of predation, herbivory, and fire (2,5,14,21,22). We hypothesise that the current dieback of aspen clones inside parks is due to recent human-caused changes in long-term ecological conditions which favoured aspen survival including: 1) release of

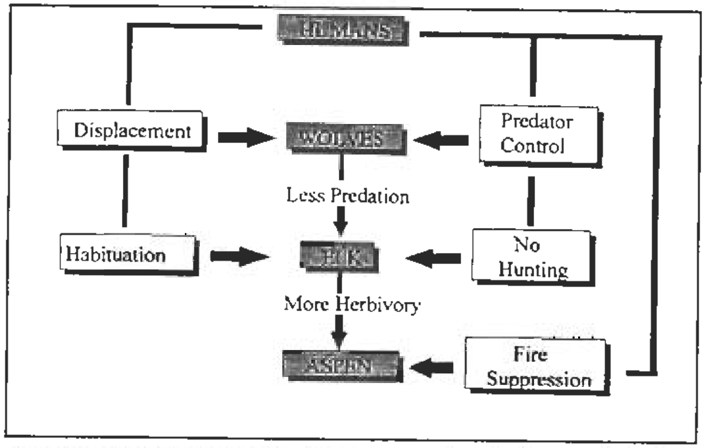

Figure 1. A simple ecosystem model that links humans, wolves, elk and aspen through the processes of predation, herbivory, fire, and animal behavioural responses to humans within Rocky Mountain national parks.

elk from intense additive predation by humans, wolves and other carnivores, 2) habituation of non-hunted elk to human presence, and 3) decrease in fire occurrence due to elimination of native cultural burning and suppression of current human- and lightning-caused fires.

3. EVIDENCE FOR THE "TOP- DOWN" HYPOTHESIS

Three subfields of ecology and anthropology provide most the theoretical framework for predicting community conditions within the aspen trophic model: 1) keystone species analysis (31), 2) optimal foraging (32), and 3) human foraging and fire-use ecology (33,34,35,36,37). The top-down hypothesis for aspen decline is supported by evidence from several independent lines of inquiry. We summarize these below, with brief reference to theoretical predictions.

3.1 Archaeology.

Zooarchaeologists use two methods to quantify animal remains recovered in study sites: minimum number of individuals (MNI), and the number of individual specimens (NISP). Both methods have recognised biases, but in conjunction, they can be used to rank the relative abundance of faunal remains per taxon (38). Kay (5) and Kay et al. (12) summarise MNI and NISP data from over 400 archaeological sites throughout the Rocky Mountain west. In Banff's Bow Valley, bison (*Bison bison*) and bighorn sheep (*Ovis canadensis*) constitute over 80% of the bones identified (Table 1), while elk constitute only 7% of NISP. For Alberta's eastern slope sites, bison dominate ungulate

Table 1. Relative abundance (percent) of ungulates in the Canadian Rocky Mountains as recorded at prehistoric sites, in first-person historic journal accounts, and recent wildlife census. For details and citations see Kay et al. (12) and White et al. (67).

Time Period	Elk	Bison	Deer	Bighorn Sheep	Moose	Goat
Prehistoric*	7	47	7	39	<1	<1
Historic**	7	22	4	39	15	13
Current***	55	0	19	21	1	4

* = From number of individual bone specimens (NISP) recovered in six archaeological sites in the Bow Valley that date from 10,700 to 100 years BP.
** = From animals observed by early explorers in the Canadian Rockies from 1792 to 1872.
*** = From the Banff National Park wildlife census for the Middle Bow Wildlife Management Unit, 1991 from White et al. (67).

remains recovered (95% NISP, 76% MNI), with elk bones constituting only a minor component (2% NISP, 9% MNI). Of over 52,000 ungulate bones identified at nearly 200 archaeological sites in the Intermountain West of the United States (Idaho, Utah, Montana, Wyoming, Washington and Oregon), only 3% were elk. The ungulate bones most frequently found were deer and bighorn sheep (5). These results support optimal foraging theory predictions that elk were a favoured prey species for wolves (39) and Native Americans (40), and were hunted to very low densities in the Rocky Mountains (5,12,40). Bison maintained relatively higher populations by long distance migration, and bighorn sheep by use of steep escape terrain, but these populations were also not food regulated (12,41,42).

3.2 Historic Analysis.

Observations of all large mammals found in first-person historical accounts by European explorers were tabulated by Kay (5,40) for Yellowstone for the period 1835 to 1876, and by Kay et al. (12) for the Canadian Rockies for the period 1792 to 1872. Only first-person journals, penned at the time of the event, or written soon afterwards, were used in these analyses to minimize biases. Journal observations were tallied as either sighted, killed, or sign, and were summarized by expedition, number of party members, date of party, and location of travel route. Historical observations from the Canadian Rockies (Table 1) and Yellowstone (5) are similar, and are consistent with the archaeological record. First, wildlife was not abundant, and many expeditions reported a lack of game or a shortage of food. Secondly, bison and bighorn sheep were the animals most commonly observed, killed, and recorded for animal sign. For example, in the Canadian Rockies, bighorn sheep represent 39% of the ungulates historically observed, bison 22%, and elk only 7% (Table 1). Consistent with our knowledge of declining bison populations, this species was commonly seen in the early 1800s, but was not directly observed after 1845

(12). Kay (5,40,41,42) reviewed these results, and concluded that population limitation by native people, wolves, and other predators provides the best explanation for historical wildlife observations in both Yellowstone and the Canadian Rockies. In addition, early explorers recorded incidents of grassland and meadow burning by native peoples (see below).

3.3 Fire History Studies.

In the Rockies, prehistoric and historic human use was greatest on valley bottom areas that provided the most favoured travel routes and year-round food resources and campsites (43). Tree-ring studies report that prior to about 1900, there were frequent, low intensity fires with intervals of between 20 and 50 years in low elevation areas (44,7,45). These fires occurred in spring and fall, outside the main lightning season, when grasslands and aspen stands are most flammable (5,8,12,14). This is in contrast to the 100- to 300-year fire cycles in higher elevation areas where mid-summer lightning fires are today more prevalent (7,8,46,47,48). Short fire intervals in high human-use areas are consistent with observations from human ecology that people commonly use fire for numerous objectives relating to hunting, foraging, and warfare (33,34,37). During the winter of 1792/93 for instance, Peter Fidler was the first European to reach the Canadian Rockies (49), and he observed uative peoples burning large areas of the foothills and plains both by accident and on purpose.

3.4 Historical Photographs.

Numerous photographs taken before 1920 in the Jackson Hole (Wyoming) area (27,50), Yellowstone (4,5,50), Idaho and Montana (17), and the Canadian Rockies (12) show no ungulate browsing of aspen or willow. Photographs of low elevation areas show evidence of frequent fires, similar to historic journal observations and fire history studies (22).

3.5 Fire Effects on Heavily Browsed Aspen.

Fire suppression is an important hypothesis for aspen decline (4,27). In lightly browsed clones, fire removes conifer competition and stimulates suckering (6). However, researchers have reported that burning of heavily browsed aspen caused severe decline, and in some cases, even death of the clones (11,12). In contrast, Dekker et al. (51) reported vegetation recovery in areas of northern Jasper National Park heavily browsed by elk in the 1950s, but repopulated by wolves in the 1960s (52). Repeat photography shows dramatic suckering of aspen since that time dating to approximately 1975, but no fires had occurred on these sites since the 1800s (53). Thus, with reduced ungulate browsing, aspen will regenerate even in the absence of fire. Protection from fire is actually necessary to slow the loss of heavily browsed aspen stands (2,3,14). Given fire's high historic frequency and usual beneficial affect on aspen stands, the current circumstances are clearly outside the long-term range of variability to which aspen is adapted.

3.6 Wildlife Exclosures.

Some researchers posit that recent climate change may have negatively effected aspen (4,13). The simplest way to test this hypothesis is to compare aspen condition inside and outside of wildlife exclosures. If climate change, not wildlife, is the main factor in aspen decline, both sides of exclosure fences should show similar stand conditions. Exclosures in both Banff (2,54) and Yellowstone (5) show large differences between the heavily browsed aspen outside the exclosures and the unbrowsed aspen inside. This provides strong evidence against the climate change hypothesis (5,12,14).

3.7 Current Ungulate Effects on Other Communities.

If aspen is impacted by elk browsing, optimal foraging theory would predict that other communities with highly palatable species should also be at risk. Probably the most susceptible communities would be low elevation, riparian willow (*Salix* spp.), also utilised by beaver (*Castor canadensis*). In Yellowstone, Chadde and Kay (55) reported strong declines of tall willow and beaver. Kay and Platts (56) concluded that beaver is 'ecologically extinct' in northern Yellowstone. In southern Banff National Park, beaver populations have decreased by over 90 percent, attributed to elk competition with beaver for willows (57).

3.8 Current Wildlife Distribution Analyses.

We believe that humans and wolves are keystone species in the aspen trophic model. Keystones are most easily identified by the effects of their removal on communities (31). All Rocky Mountain national parks have conducted partial or total removal treatments at the landscape level on wolves and human hunting. The most relevant information for understanding species removal effects on aspen stand community ecology comes from current observations of elk and wolf in Jasper (51) and Banff (58,59,60), and elk in Yellowstone (4,61), Jackson Hole (28), and Rocky Mountain National Park, Colorado (20,62). These studies show that park elk, released from hunting by humans, habituate to people, and have high densities (20 elk/km²) on winter ranges near heavily used roads and facilities. In contrast, wide-ranging wolves usually experience substantial human-caused mortality, and tend to avoid high human-use areas (52,59). In parks recolonized by wolves, but where they are not displaced by high human use, elk numbers are low or decreasing, partially attributable to wolf predation (21,51,58). The result is a partial separation of trophic layers. Wolves are common in low prey-density areas, and elk are common in predator-refugia areas near humans (59,60). This is unlike normal long-term conditions where humans, wolves, elk and aspen usually overlapped. Further, today's trophic segregation is highly stable due to stationary human developments and park boundaries. Thus, it is not surprising that within parks, aspen communities near developed areas are often in serious decline (2,5,20,21), although aspen may be vigorous in remote areas where wolves have helped reduce elk populations (51,53).

4. CONCLUSIONS AND ONGOING RESEARCH

Evidence from a variety of fields provides a new and highly defensible viewpoint on the role of top-down processes (predation and human-caused fires) in the long-term structuring of trembling aspen communities. This 4-level trophic cascade may not be unlike the key role human harvesting of sea otters played in structuring kelp forests along the North American west coast (63,64). However, in the aspen case, there remains a substantial need to test the generality of the model over broader temporal and spatial scales. Further, in western national parks, public pressure will continue to limit human predation on elk (e.g. elk culls). Therefore, it is important to fully explore whether non-human predation (mostly by wolves) can limit elk populations to a point where aspen stands can regenerate. Finally, if the significance of the ecological relationships of trembling aspen can be demonstrated and quantified, there are implications for defining ecological integrity required by national park management plans (65,66). The Banff-Bow Valley Study recommended that increasing carnivore densities, reducing elk densities, and conducting prescribed burns are essential to restore aspen communities and to help maintain ecological integrity in Banff National Park (59).

Ongoing research by the principal author on the eastern slopes of the Canadian Rockies is testing the top-down humans-wolves-elk-aspen hypothesis, and evaluating the value of aspen community condition as an indicator of ecological integrity in national parks. Work includes repeat photography at the locations of over 200 historic photographs of aspen in 15 watersheds, determining the frequency and seasonal timing of historic fires in aspen, identifying thresholds for aspen regeneration under various conditions of herbivory, fire, and conifer competition, and quantifying aspen regeneration in areas repopulated by wolves.

We conclude by stating that the Rocky Mountain national parks contain diverse environments from valley-bottom ungulate winter ranges to remote, rocky peaks. We believe that long-term top-down forces, such as human and wolf predation, and human-caused fires were most prevalent at low elevations, and decreased with increases in elevation. The challenge for science is to delineate and quantify this gradient.

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