

Trophic Cascades without Large Predators: Terrestrial Ecosystems of the Western United States

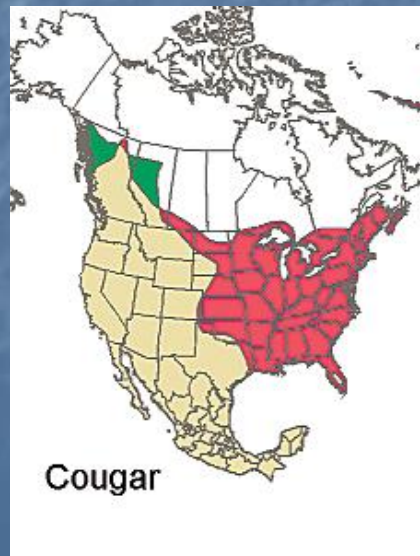


(Photos - Left, National Park Service; Right, WJ Ripple)

Gray Wolves and Cougars: Then and Now

Gray wolves and cougars once ranged over nearly all of the conterminous 48 states. However, as EuroAmericans spread across the continent in the 1800s and early 1900s, the range of these predators contracted in turn.

By the mid-1990s, wolves had been extirpated from nearly all 48 states except for small areas along the Canadian border. And cougars — except for a small holdout of survivors in the cypress swamps of southern Florida — were driven from the eastern states, persisting in the most rugged hideouts of the West despite relentless persecution.



The question of how these top predators' disappearances have impacted ecosystems is the subject of this presentation. To answer this question, we looked to our national parks.

(Graphs - Laliberte & Ripple 2004)

Predator Loss Studies in western National Parks

Olympic National Forest¹

Ecoregion: Central Pacific Coastal Forest
Predator-prey: Gray wolf - Roosevelt elk
Woody species: Black cottonwood and bigleaf maple

Yosemite National Park²

Ecoregion: Sierra Nevada forests
Predator-prey: Cougar - mule deer
Woody species: Fremont cottonwood

Yellowstone National Park³

Ecoregion: Central Rockies forests
Predator-prey: Gray wolf - Rocky Mountain elk
Woody species: Black and narrowleaf cottonwoods

Zion National Park⁴

Ecoregion: Colorado Plateau shrublands
Predator-prey: Cougar - mule Deer
Woody species: Fremont cottonwood

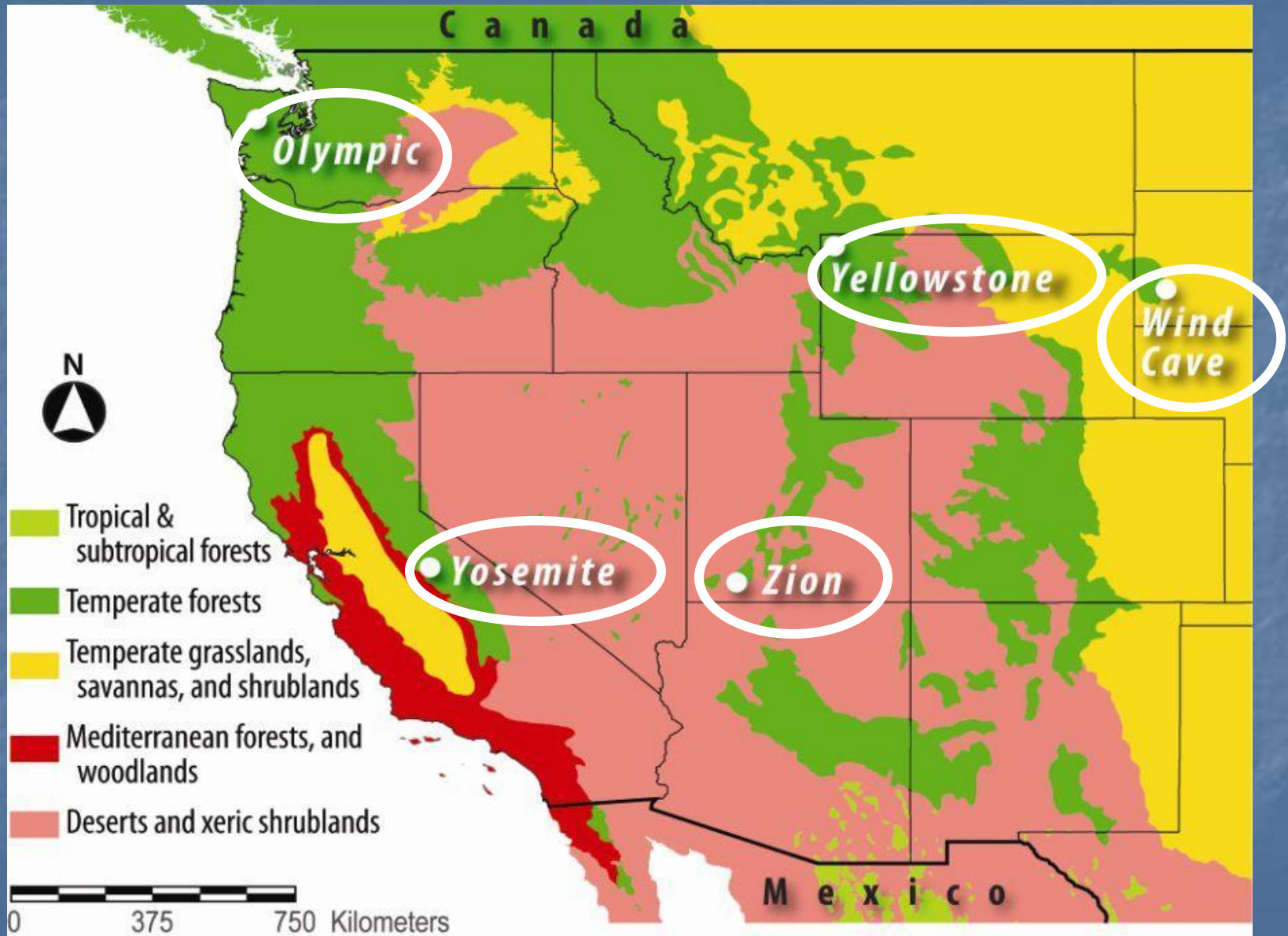
Wind Cave National Park⁵

Ecoregion: Temperate grasslands, savannas, and shrublands
Predator-prey: Multiple large predators - multiple ungulate species
Woody species: Plains cottonwood

(¹ Beschta & Ripple 2008; ² Ripple & Beschta 2008; ³ Beschta 2003, 2005;

⁴ Ripple & Beschta 2006; ⁵ Ripple & Beschta 2007)

National Park Locations



National Parks: Natural Laboratories of Missing Large Predators

For studying the ecological effects of large predator loss, national parks provide several research advantages:

- The timing of wolf and cougar loss was similar across parks, generally occurring in the early 1900s.
- Long-lived trees and shrubs palatable to native deer and elk were present in each park and their age structure could be used to evaluate plant dynamics over time.
- Historical reports and photographs were available to help reconstruct changes in predator, prey, and plant populations during the 20th century.
- Parks often occupied large areas spanning various ecoregions.
- The potentially confounding effects of various land uses (e.g., hunting, livestock grazing, roads, logging) were usually absent.

A Trophic Cascade from Predator to Plants

Ecosystem with Wolves

Wolves affect elk behavior and numbers.

Foraging on woody plants is relatively minor.

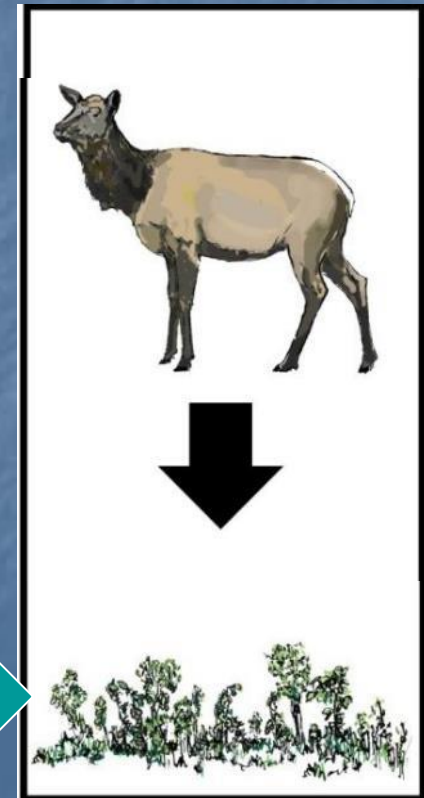
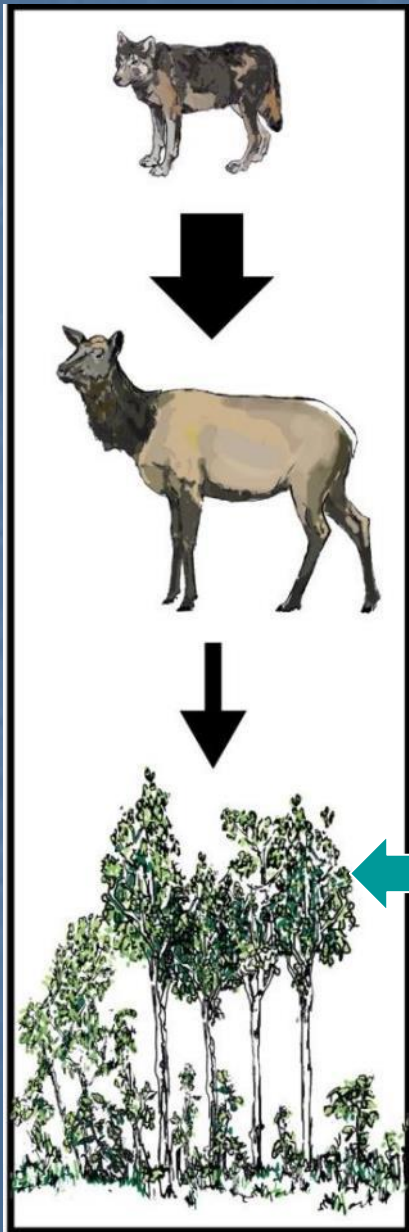
These plants thus thrive.

Recruitment of these plants is suppressed.

(Figures - Beschta et al. 2016)

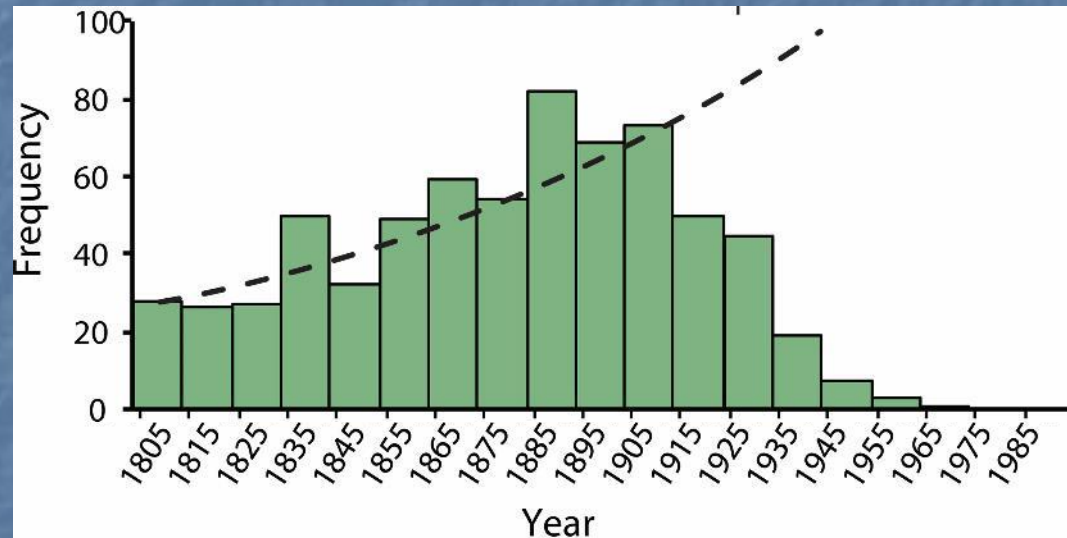
Ecosystem without wolves

Unhindered elk browsing prevents young woody plants from growing taller and surviving.



Answers from Trees

If the frequency of trees by decade of establishment is graphically presented (green bars shown below), the result is an “age structure” graph.



Normally, the frequency of trees increases from the oldest to the youngest, as occurs here during the 1800s. And, if this trend continued (as represented by dashed line) a relatively large number of young trees would be present in the mid-late 1900s.

In the above example, however, the frequency of trees declines after about 1905 indicating it was becoming increasingly difficult for them to establish and grow.

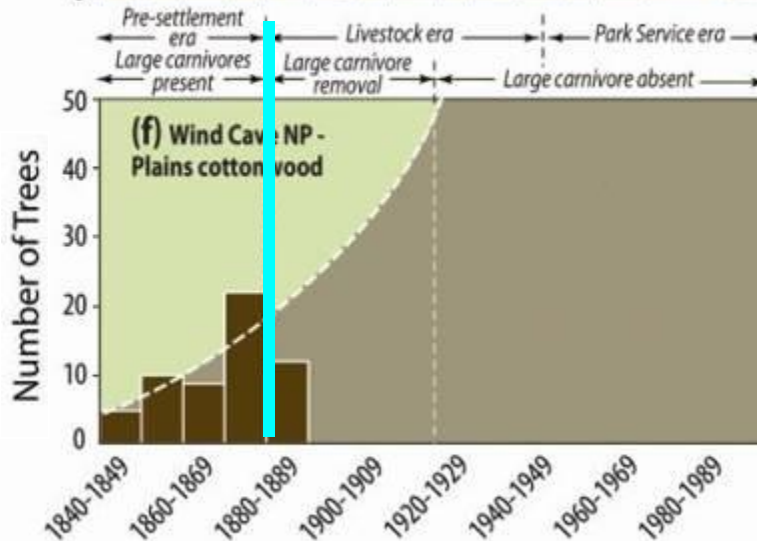
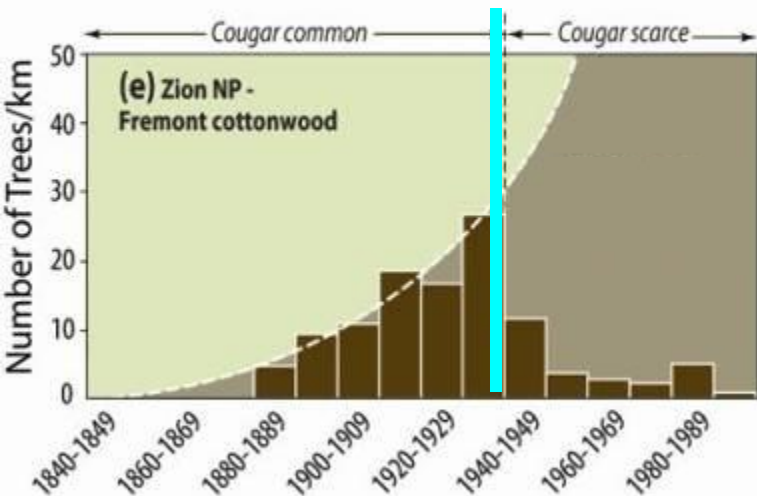
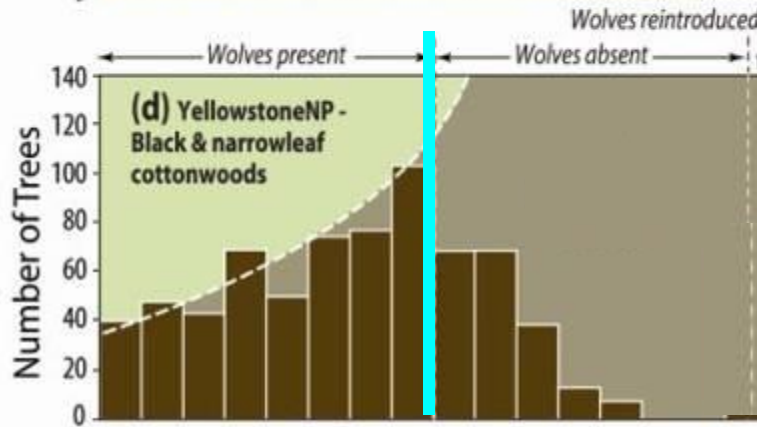
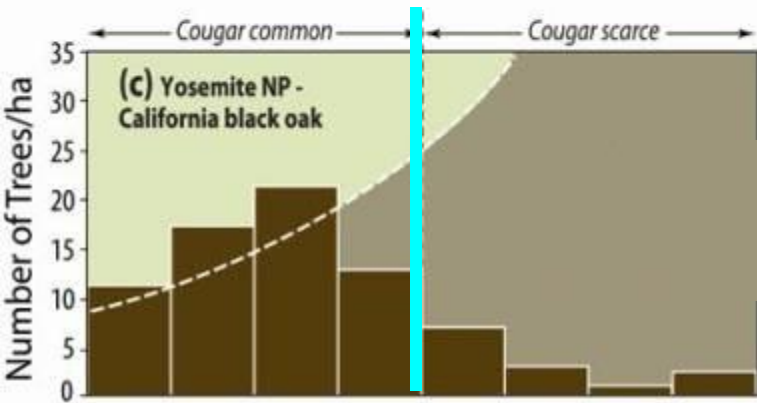
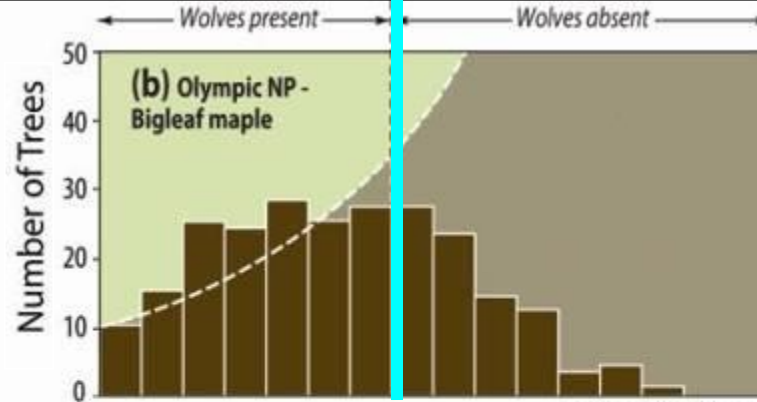
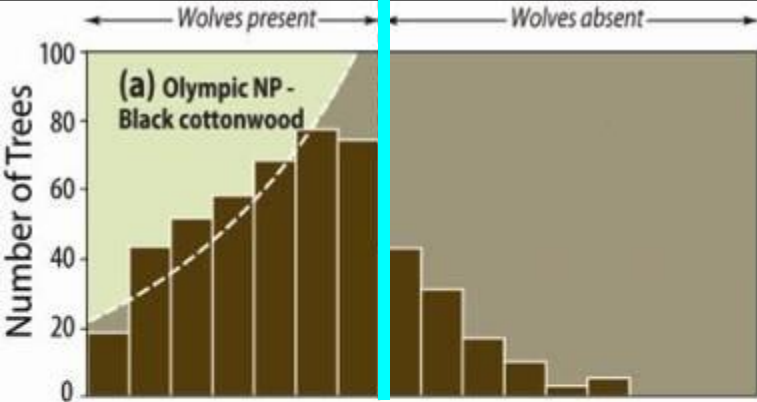
Age structure represents an important tool for identifying the effects of large predator loss upon plant community dynamics in various ecosystems of the American West.

Results

In the five western national parks that were studied, a major decline in the recruitment of woody species occurred after the extirpation or displacement of large predators, such as wolves or cougars. On average, recruitment of woody plants declined to only 10 percent of expected within two decades, and to less than 1 percent of expected within five decades.

Such dramatic reductions in recruitment, due to increased herbivory by native ungulates, signify major effects on the composition, structure, and function of native plant communities.

On the following page, age structure results for five western national parks are provided, indicating the general pattern of recruitment decline in each park.



Establishment Dates (decades)

Age Structure Results from five Parks

Vertical blue lines identify when large predators were lost.

Darker shaded areas to the right of the blue lines indicate a major loss in recruitment in each park.

(Graph - Beschta & Ripple 2009)

Results (continued)

The photographs that follow visually demonstrate some of the changes that plant communities incurred in each park. Despite representing distinctly different ecosystems, they show a remarkable consistency of impacts from increased herbivory by elk and deer.

In all photographs, relatively old and large trees are present, whereas younger, smaller trees are absent. In addition, there is a near total lack of understory shrubs. The lack of younger, smaller trees and shrubs indicate heavy browsing has occurred over many years.

Riverbanks are visible in panels (d) and (e) and accelerated erosion is evident.

(a) Olympic NP - Black cottonwood



(b) Olympic NP - Bigleaf maple



(c) Yosemite NP - California black oak



(d) Yellowstone NP - Black & narrowleaf cottonwoods



(e) Zion NP - Fremont cottonwood



(f) Wind Cave NP - Plains cottonwood



Photographic of Missing Predators

Each photo shows large, old trees and a lack of smaller, younger trees or shrubs beneath them. Most of the large trees established at a time when large predators were still present.

The lack of smaller trees and shrubs is due to heavy browsing by ungulates after the loss of large predators.

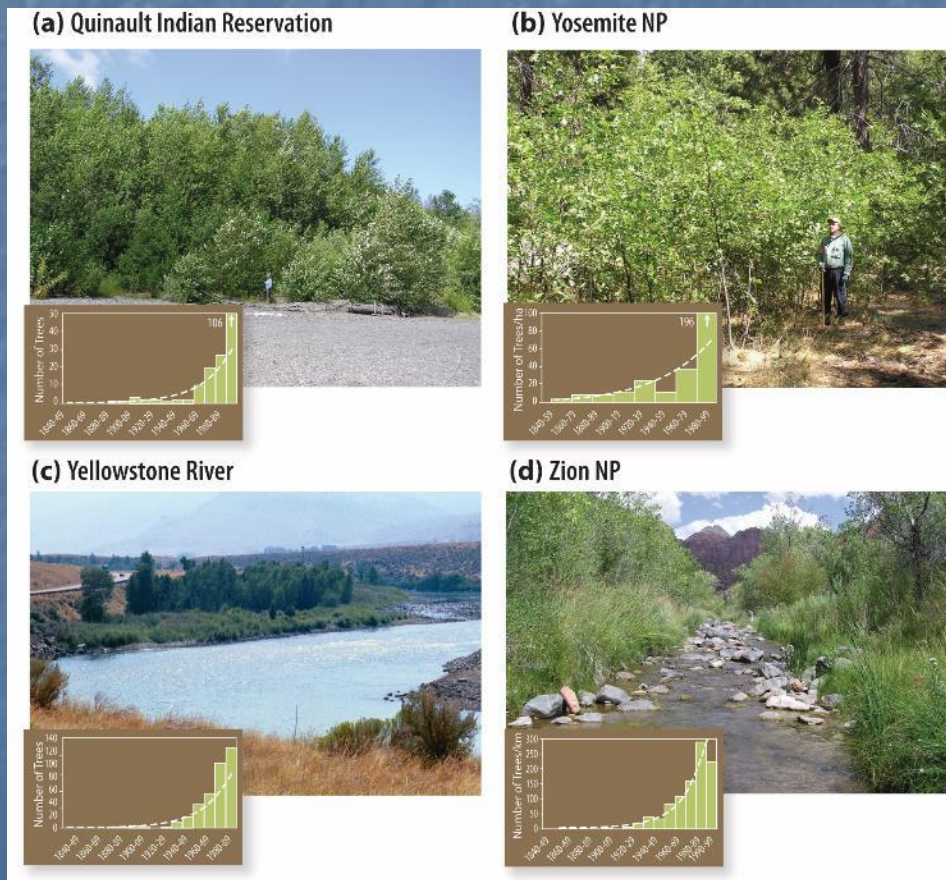
Increased ungulate herbivory has dramatically altered these plant communities, with detrimental effects on habitat for a broad spectrum of wildlife.

The eroding channels in panels (d) and (e) are likely due to a loss of streamside vegetation after increased ungulate herbivory.

(Figure- Beschta & Ripple 2009)

Plants Grow Well in Refugia

Refugia are sites where plants are relatively free of foraging ungulates such as the sites below which show dense woody plant communities in riparian areas. Age structure data (inset graphs) indicate recruitment of woody species has been ongoing at these sites, at the same time recruitment was declining in areas of high ungulate use.



Dominant tree species and refugia locations:

(a) Cottonwoods on the Quinault Indian Reservation outside of Olympic National Forest

(b) California black oaks in Yosemite National Park

(a) Cottonwoods outside of Yellowstone National Park

(b) Fremont cottonwoods inside Zion National Park

(Graph - Beschta & Ripple 2009)

Alternative Hypotheses

Various hypotheses, in addition to that of a trophic cascade, were considered in each national park (NP) to see if they might explain the observed decline in recruitment of tree species over time. These included the potential effects of any changes in various environmental factors:

Olympic NP - climate and flood frequency

Yosemite NP - climate, flood frequency, and land use

Yellowstone NP - climate, fire, and flood frequency

Wind Cave NP - climate, fire frequency, and land use

Zion NP - climate, human disturbance, and site differences

These alternative hypothesis were unable to explain the major decline in recruitment of woody species that followed the loss of an apex predator.

Conclusions

- (1) **The long-term recruitment of plants coincided with the presence of large predators** - Prior to extirpation or displacement of large predators, ungulate herbivory was relatively low, allowing sprouts and seedlings of woody species to continuously grow tall and reproduce over time.
- (2) **Ungulate herbivory increased following loss of large predators, thus affecting plants** - Due to increased ungulate herbivory following the extirpation or displacement of large predators, trees and forests began to decline
- (3) **Effects of increased herbivory extended beyond woody plants** - Highly altered riparian plant communities contributed to accelerated riverbank erosion and changes in channel morphology. Park Service reports, historical photos, and other studies indicated that the effects of intensified ungulate herbivory often extended to many plant species whose losses in turn degraded wildlife habitats.

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Related Literature

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Scientific literature associated with wolves, elk, and vegetation in northern Yellowstone, as well as other literature on trophic cascades and related topics, can be accessed at:

<http://trophiccascades.forestry.oregonstate.edu/publications>

Scientific Names of Plant and Animal Species

Plants

California black oak - *Quercus kelloggii*

Quaking aspen - *Populus tremuloides*

Animals

Cougar - *Puma concolor*

Gray wolf - *Canis lupus*

Mule deer - *Odocoileus hemionus*

Rocky Mountain elk - *Cervus canadensis*

Glossary of Selected Terms

Herbivory - The feeding or foraging of animals on living plants; browsing is used in reference to their feeding on woody plants.

Large predator - A predator is an animal that lives by killing and eating other animals. A "large predator" is one that normally exceeds 15 kg (33 lbs) at maturity.

Plant community - A group of interacting plants sharing a common environment, for example: aspen community, willow community, sagebrush community.

Recruitment - Growth of a woody plants above the normal upper browse level of ungulates.

Ungulates - Hooved animals, such as elk, deer, moose, and bison.