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Review

Large predators and trophic cascades in terrestrial ecosystems of the western United States

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ABSTRACT

Large predators potentially can help shape the structure and functioning of terrestrial ecosystems, yet strong evidence of top-down herbivore limitation has not been widely reported in the scientific literature. Herein we synthesize outcomes of recent tri-trophic cascades studies involving the presence and absence of large predators for five national parks in the western United States, including Olympic, Yosemite, Yellowstone, Zion, and Wind Cave. Historical observations by park biologists regarding woody browse species and recently compiled age structure data for deciduous trees indicate major impacts to woody plant communities by ungulates following the extirpation or displacement of large predators. Declines in long-term tree recruitment indexed additional effects to plant communities and ecological processes, as well as shifts towards alternative ecosystem states. The magnitude and consistency of vegetation impacts found within these five parks, in conjunction with other recent North American studies, indicate that broad changes to ecosystem processes and the lower trophic level may have occurred in other parts of the western United States where large predators have been extirpated or displaced. Thus, where ungulates have significantly altered native plant communities in the absence of large predators, restoration of native flora is urgently needed to recover former ecosystem services. Following the reintroduction of previously extirpated gray wolves *Canis lupus* into Yellowstone National Park, a spatially patchy recovery of woody browse species (e.g., aspen *Populus tremuloides*, willow *Salix* spp., cottonwood *Populus* spp.) has begun, indicating that large predator recovery may represent an important restoration strategy for ecosystems degraded by wild ungulates.

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Contents

1. Introduction . . . 2401
2. Study areas . . . 2403
3. Methods . . . 2403
4. Results . . . 2404
5. Discussion . . . 2406
6. Conclusions . . . 2412
Acknowledgements . . . 2412
References . . . 2412

1. Introduction

British ecologist Charles Elton began to recognize in the early 1900s that predators could exert important "top-down" controls on underlying animal populations (Elton, 1927). Later, based on a survey of deer ranges across the United States (US), Leopold et al. (1947) concluded the loss of large predators was a precursor to the irruption (i.e., a rapid increase in population) of wild ungulates and subsequent impacts to plant communities. Hairston et al. (1960) built upon the ideas of Elton, Leopold, and others with their Green World Hypothesis (GWH) and suggested that predators maintained global plant biomass at high levels by limiting herbivore densities. Paine (1980) first used the term "trophic cascade" to characterize a progression of direct and indirect effects of native predators across successively lower trophic levels. This concept

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was further refined by Pace et al. (1999) when they defined trophic cascades as "reciprocal predator–prey effects that alter the abundance, biomass, or productivity of a population community or trophic level across more than one link in the food web."

Ecologists who agree that trophic interactions between top predators (carnivores), herbivores (consumers), and plants (producers) are important in determining ecosystem structure and dynamics have often debated the relative effectiveness of top-down and bottom-up forces. Thus, there is an increasing need to better understand how and why various factors can affect the interactions and relative strengths of these contrasting forces (e.g., Schmitz et al., 2004; Borer et al., 2005). Although top-down influences upon community structure have typically been found in both terrestrial and aquatic ecosystems (e.g., Shurin et al., 2002; Schmitz et al., 2000), a particularly troubling aspect of trophic cascades research in terrestrial ecosystems is the paucity of studies involving large predators. This may be due, at least in part, to the difficulty of assessing their effects at long temporal and large spatial scales.

Across much of the globe, humans have reduced the range of large carnivores. In the US, widespread poisoning, trapping, and hunting in the 1800s and early 1900s by Euro-Americans and a concerted effort at predator eradication by federal agencies greatly reduced gray wolf *Canis lupus* and cougar *Puma concolor* ranges (Laliberte and Ripple, 2004). Ecologically effective populations of wolves were largely gone in the western US by the early 1900s and cougar ranges became fragmented. These human-caused reductions in large predator distributions beg several questions: Have significant ecosystem adjustments occurred following the loss of large predators? Are potential effects confined primarily to prey species, or are there broader consequences to the structure and functioning of ecosystems?

In the late-1800s and early 1900s, the US Congress began establishing national parks at various locations within the diverse landscape that comprised the American West. These parks generally afforded increased protection to wildlife but not always to predators. In retrospect, these parks created a series of natural experiments (Diamond, 1983) that could be useful for assessing the historical effects of large predator presence/absence upon lower trophic levels. National parks provided experimental design benefits for undertaking such assessments since (1) confounding effects of land uses such as forest harvesting, livestock grazing, and hunting were largely absent following park establishment, (2) individual parks comprised a large contiguous area, (3) parks were established in a variety of biomes, (4) riparian ecosystems within a park typically had free-flowing streams and rivers (i.e., uninfluenced by dams or diversions), and (5) spatial controls, such as areas with a continued presence of large predators, refugia from browsing, or ungulate exclosures, were variously present.

Of all the western parks, the effects of wild ungulates on ecosystems probably have been studied the most in Yellowstone National Park (NP). Following the extirpation of wolves from Yellowstone in the early 1900s, Aspen *Populus tremuloides* recruitment (i.e., growth of seedlings/root sprouts above the browse height of ungulates into tall samplings and trees) began to rapidly decline as a result of intensive elk *Cervus elaphus* browsing (Fig. 1a; NRC, 2002a). Today, numerous aspen stands across the elk winter ranges of northern Yellowstone reflect a history of reduced recruitment spanning multiple decades (Ripple and Larsen, 2000) and, for many of these stands, only large diameter trees remain (Fig. 1b). In contrast, aspen recruitment within fenced ungulate exclosures has been ongoing (Fig. 1c). As aspen stands declined in Yellowstone NP and the foraging effects of elk became a major scientific and public controversy (NRC, 2002a), ensuing debates failed to consider seriously the possible role of large predators.

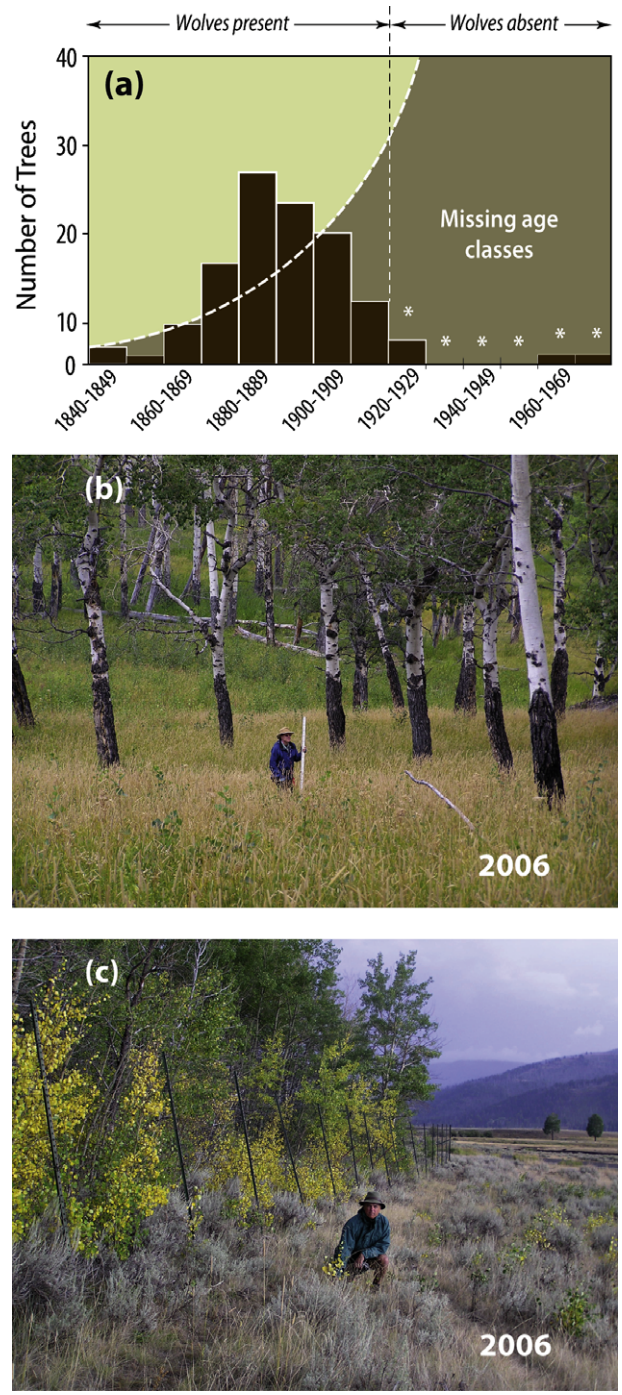

Fig. 1. (a) Aspen age structure from 1840 to 2000, (b) an aspen stand showing heavy bark damage from elk along the lower several meters of each tree and a long-term lack of recruitment (tall saplings and small diameter trees are missing), and (c) ongoing aspen recruitment within a fenced elk exclosure and an absence of recruitment outside the fence (even though root sprouts are present); all in the northern range of Yellowstone National Park. For the period following the extirpation of wolves in Yellowstone, significant decreases (95% lower CI) in aspen tree frequencies are indicated by "*". *Source*: adapted from (a) Larsen and Ripple (2003).

Herein our objective was to compare the potential influence of large predator presence (top-down forces) and absence on plant communities over a period of more than one and one-half centuries in five western US national parks — Olympic, Yosemite, Yellowstone, Zion, and Wind Cave. Each park originally supported a large carnivore guild that was subsequently altered by the

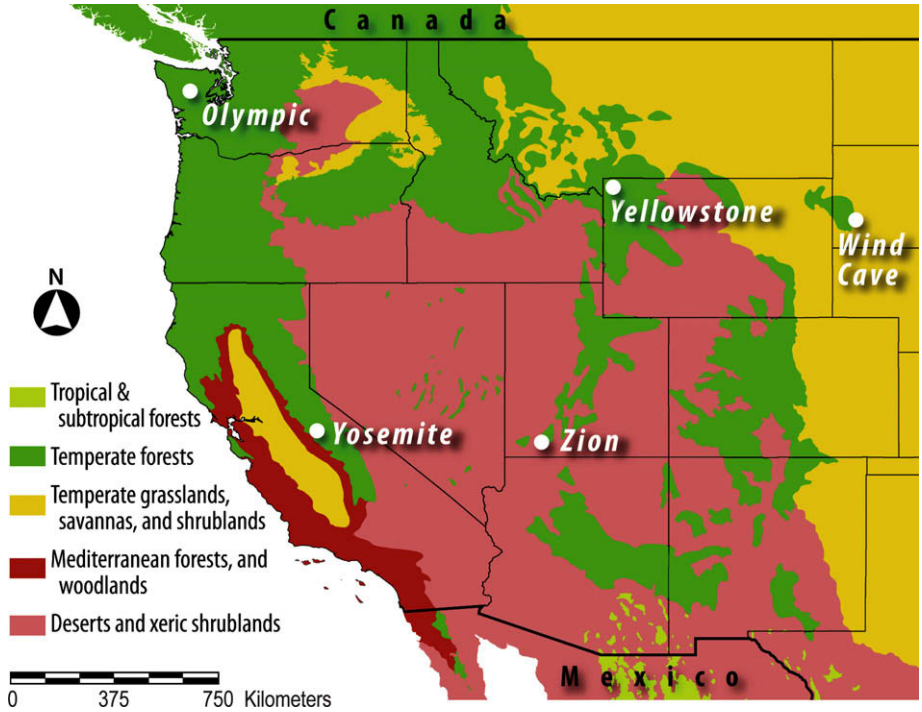

Fig. 2. Location of selected national parks and associated biomes in the western United States. *Source*: biome map adapted from Olson et al. (2001).

extirpation or displacement of one or more large predators. We assumed that tri-trophic cascades involving large predators, ungulates, and plants represented an essential model for understanding trophic level changes following large predator loss.

2. Study areas

Since the five parks were widely separated (Fig. 2), we considered each to denote an independent case study. Average annual precipitation ranged from 34 to 300 cm, average annual air temperature from 2 to 16 °C, and net primary productivity from 1.1 to 2.1 kg/m^2/yr across study sites (Table 1).

The principal predator–prey species of interest were "wolves-elk" in Olympic and Yellowstone NPs and "cougar-mule deer" *Odocoileus hemionus* in Yosemite and Zion NPs. Wind Cave NP lost multiple carnivores including wolves, grizzly bears *Ursus arctos*, and black bears *U. americanus* with potential effects on elk, bison *Bison bison*, and deer *Odocoileus* spp. Study areas within each park experienced year-round habitat use by ungulates with the exception of northern Yellowstone where seasonal elk movements occur and research was conducted only in winter ranges.

3. Methods

We evaluated historical records of each park to determine (1) when large predators were extirpated or displaced, (2) subsequent changes in ungulate populations, and (3) descriptions of native flora before and after large predator loss. We also undertook field measurements of deciduous trees in each park for assessing vegetation responses to predator–prey dynamics over time. Selected tree species represented ecologically important components of upland or riparian plant communities, were long-lived, could be easily aged *via* analysis of annual growth rings, and their leaves/twigs were palatable to ungulates. These species included: black cottonwood *Populus trichocarpa* and bigleaf maple *Acer macrophyllum* in Olympic NP; California black oak *Quercus kelloggii* in Yosemite NP; aspen, narrowleaf cottonwood *Populus angustifolia*, and black cottonwood in Yellowstone NP; Fremont cottonwood *Populus*

Table 1
General characteristics of study areas within the indicated National Parks.

National Park	Date of park establishment (yr)	Park area (km^2)	Study area elevation (m)	Study area climatic data[a]						
				Precipitation		Snowfall	Air temperature			
				Annual (cm)	Summer[b] (%)	Annual (cm)	Annual (°C)	February (°C)	August (°C)	NPP[c] (kg/m^2/yr)
Olympic	1909	3743	<100	300	7	33	9.9	5.4	16.2	2.1
Yosemite	1890	3081	1220	94	3	140	12.1	5.2	22.0	1.9
Yellowstone	1872	8983	2000	34	36	239	1.7	−8.0	13.0	1.3
Zion	1918	593	1300	38	19	23	16.3	7.1	27.8	1.1
Wind Cave	1903	115	1100	51	42	na	10.2	1.2	22.4	1.1

na = Not available.
[a] Long-term climatic data from the following weather stations: Olympic NP (Forks, WA; n = 60 years), Yellowstone NP (Lamar Ranger Station, WY; n = 60 years), Yosemite NP (Yosemite Park Headquarters, CA; n = 60 years), Zion NP (Zion Park Headquarters, UT; n = 80 years), and Wind Cave NP (Hot Springs, SD; n = 98 years).
[b] Summer precipitation (June–August) as a percent of annual precipitation.
[c] NPP = net primary productivity in kg of dry biomass/m^2/yr (Bachelet et al., 2000; Daly et al., 2000).

Fremontii in Zion NP; and plains cottonwood *Populus deltoides* in Wind Cave NP.

For the selected deciduous tree species, we determined their age structure (frequency of trees by establishment date) from field measurements of diameter at breast height for large numbers of trees in each park, in conjunction with relationships between tree age and diameter (see Beschta (2005) for methods). We used regression analysis to establish an exponential equation between observed tree frequency (X_o) and establishment date during the "pre-treatment" period (i.e., predators present). J-shaped (exponential) relationships of age structure are characteristic of forests having a diversity of stand ages (Kimmins, 1987) and can provide a quantitative estimate of contemporary recruitment levels needed to maintain historical tree densities. Each fitted curve was extended to the present and represented expected tree frequencies (X_e) during the "post-treatment" period (i.e., when large predators had become absent or scarce). Observed tree frequency (recruitment) during the post-treatment period was considered significantly reduced if it was less than the lower 95% confidence interval (CI) of the exponential equation. We also determined temporal patterns of tree recruitment for areas within or adjacent to a given park that had intact predator populations, sites protected from browsing (refugia), or within ungulate exclosures.

We assessed the general "strength" of the trophic cascade for a given park by calculating a $\log_{10}$ response ratio of tree frequencies (i.e., $\log_{10}(X_o/X_e)$) for each decade during the post-treatment period based upon the methods of Schmitz et al. (2000) and Hebblewhite et al. (2005). If the number of observed trees (X_o) was zero during any decade of the post-treatment period, we replaced it with a small number (i.e., $X_o = 1$) so that a response ratio could be calculated. We determined the average and standard error (SE) of the response ratio over time for the sampled parks to illustrate the general trend in tree recruitment following predator loss.

In Olympic, Yellowstone, and Zion NPs, we evaluated the effects of post-treatment herbivory upon streambanks, channels, and floodplains (Beschta and Ripple, 2006a, 2008b; Ripple and Beschta, 2006a). Within riparian areas of Zion NP we measured species abundance of hydrophytic plants, amphibians, lizards, and butterflies (Ripple and Beschta, 2006a).

To assess the potential role of climate in a consistent manner across parks, we obtained long-term records of the summer-season Palmer Drought Severity Index (PDSI) (Cook et al., 2004). PDSI values represent a general measure of relative drought and wetness. We used *t*-tests to identify any significant differences ($p < 0.05$) in average PDSI between pre- and post-treatment periods for each park. Additional factors that might affect temporal patterns of tree recruitment (e.g., moisture availability, fire history, climatic patterns) were also considered in each park.

Of the five parks, Yellowstone was unique in that a previously extirpated apex predator, the gray wolf, was reintroduced during the mid-1990s.

4. Results

Historical reports and publications since the mid- to late-1800s proved crucial to understanding when large predators were extirpated/displaced from the study areas in each park and when

Table 2
Summary of observations regarding ungulates and plants following the displacement/extirpation of large predators in five western US national parks.

Olympic National Park (western portion of the park)
With wolves functionally extirpated by ~1910 and a hunting ban on elk that began in 1905, the Olympic peninsula's elk population began to rapidly increase and significant browsing of riparian shrubs was observed within a decade (Bailey, 1918). As herbivory impacts continued, palatable shrub and tree species were increasingly unable to grow above the browse level of elk (Murie, 1935; Schwartz, 1939; Newman, 1954). A deterioration of plant communities led park service biologist E.L. Sumner to surmise that wolves had likely been an essential "natural check" preventing elk over-population (Sumner, 1938). He further indicated: "Unless some substitute for this now absent controlling factor is provided, serious destruction of certain plants and even their total elimination in certain places through inability to reproduce will no doubt occur."

Yosemite National Park (Yosemite Valley)
Numerous cougar were removed in the Yosemite area during the late 1910s. By 1920 cougar were scarce in Yosemite Valley and a rapid increase in the valley's mule deer population soon followed (Dixon, 1934a). The Park Superintendent's 1929 report indicated wildflowers were "becoming very scarce" and evening primroses "which once carpeted the Valley floor have almost entirely disappeared and now bloom only in very small areas where they are protected [from deer]." California black oak seedlings were also being intensively browsed (Dixon, 1934b). Deer-proof fenced exclosures, constructed in 1934, provided additional perspectives of vegetation impacts (Allen et al., circa 1970). For example, at a meadow exclosure a variety of plants comprised dense tall growth inside the fence but were entirely absent outside because of deer foraging. In his paper entitled *Wildlife Surpluses in National Parks*, Cahalane (1941) concluded: "Deer have thus increased on the floor of popular Yosemite Valley, where their ancestral enemy, the cougar dares not follow ... heavy destruction of browse plants is the result."

Yellowstone National Park (northern winter range)
By 1920, and perhaps earlier, wolves had been functionally extirpated from Yellowstone's northern elk winter ranges. Approximately a decade later, Rush (1933) found that the northern range was "badly overgrazed", sheet erosion was occurring, and much of the "rich top soil" had washed away. Subsequently, Grimm (1939) concluded that herbaceous plants became depleted each winter due to over-utilization by ungulates. His studies of aspen indicated that excessive browsing by elk threatened the "existence of aspen on the winter range." Even though the Park Service reduced elk numbers in an attempt to lessen their foraging impacts, by the mid-1950s the cumulative effects of grazing and trampling by elk had removed lush thickets of willows from meadows, impacted sagebrush, and depleted aspen stands "that cannot be replaced while elk consume reproduction" (NPS, 1956). Bunchgrasses, which normally comprised the bulk of an elk's diet, were also in "poor condition." The diminishment of northern range plant communities led A. Leopold (1949) to simply conclude: "Thus the Yellowstone has lost its wolves and cougars, with the result that elk are ruining the flora, particularly on the winter range."

Zion National Park (Zion Canyon)
As park development occurred in the late 1920s, visitation levels rapidly increased. Cougar were eventually displaced from the canyon by the late 1930s thus "causing a profound change in the delicate balance between deer and their natural predators" (Presnall, 1938). Soon thereafter deer numbers began to increase and impact plant communities (Dixon and Sumner, 1939). In the park's 1942 annual report, the Superintendent identified over-population of deer in Zion Canyon as a "major problem" and indicated that vegetation was so "over-browsed that it is in serious condition and there is danger of complete destruction."

Wind Cave National Park
Journal records of naturalist G.B. Grinnell during the 1874 Custer expedition to the Black Hills chronicled abundant large carnivores, ungulates, berry-producing shrubs, wildflowers, and beaver along their route (Ludlow, 1875). For example, serviceberry, a browse species that today is uncommon in the park, was "very abundant, both in the form of low bushes in open, dry, sparse copses and as thickets in the valleys." Grinnell also noted "almost all the streams which we passed were dammed in many places by beaver." However, discovery of gold in 1874 and a rush of miners to the Black Hills were soon followed by large herds of cattle and sheep. Thus, large predators were quickly removed from the landscape. By the mid-1880s continuous grazing by livestock had resulted in a "dangerous depletion of the range" and thus "beaver had begun to disappear and their dams began to let go" (Palais, 1942). When the park was established in 1905, it inherited not only an area generally devoid of large predators, but one where native plant communities had experienced several decades of intensive herbivory by domestic ungulates (Smith unpublished).[a]

[a] Smith J. Rare Tree and shrub survey in Wind Cave National Park. Hot Springs, SD: Wind Cave National Park Files. Unpublished.

subsequent changes in ungulate populations and vegetation began to occur. Large predator loss occurred as early as 1880 at Wind Cave NP to as late as 1940 in Zion NP. Within a decade of when large predators were estimated to have been functionally eliminated, park biologists typically began to observe increased ungulate herbivory of woody browse species and herbaceous plants (Table 2). Yellowstone, Yosemite, Zion, and Wind Cave NPs implemented ungulate culling at various times following the loss of predators in an attempt to lower ungulate populations and reduce their ecosystem impacts. While Cahalane (1941) indicated that the overall purpose of wildlife management in national parks was "to restore and conserve a normal fauna" in an unimpaired environment, he acknowledged that the widespread destruction of predators had resulted in "an abnormal increase of grazing mammals within the parks and accelerated range destruction."

Temporal patterns of tree recruitment (age structure) over a period of 160 years (1840–2000) are illustrated in Fig. 3 for the five parks. Regardless of biophysical environment or autecology of the selected deciduous trees, their age structures demonstrated (1) ongoing recruitment when large predators were present and (2) significant decreases (95% lower CI) in recruitment after large predators were extirpated/displaced. In Olympic NP, fast-growing, shade-intolerant black cottonwood characteristically colonize bare alluvial substrates whereas slower-growing, shade-tolerant bigleaf maple seedlings are better adapted to secondary succession in riparian forests. Yet both exhibited a long-term decline in recruitment over many decades (Fig. 3a and b). Patterns of decreased tree recruitment also occurred for black oak in Yosemite NP (Fig. 3c), for black and narrowleaf cottonwood growing along valley-bottom floodplains (Fig. 3d) and aspen occupying riparian and upland

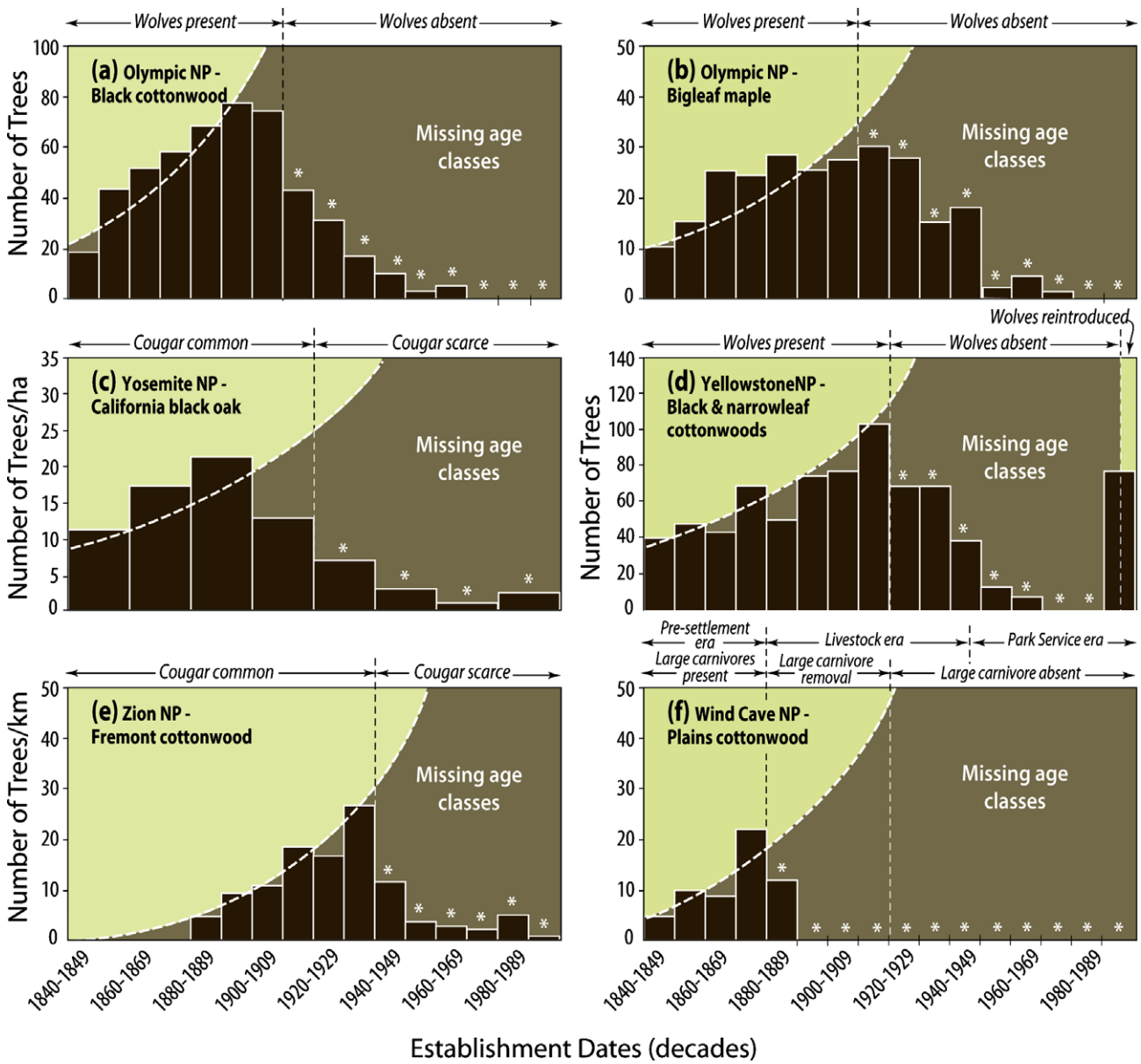

Fig. 3. Age structure from 1840 to 2000 for (a) black cottonwood and (b) bigleaf maple along river floodplains in western Olympic National Park, (c) California black oak in Yosemite Valley, Yosemite National Park, (d), black and narrowleaf cottonwood along floodplains of the Lamar River in the northern range of Yellowstone National Park, (e) Fremont cottonwood along floodplains of the North Fork of the Virgin River in Zion National Park, and (f) plains cottonwood in Wind Cave National Park. Significant decreases (95% lower CI) in observed tree frequencies following the loss of large predators are indicated by "*". *Sources*: adapted from (a and b) Beschta and Ripple (2008b), (c) Ripple and Beschta (2008), (d) Beschta and Ripple (2008a), (e) Ripple and Beschta (2006a), and (f) Ripple and Beschta (2007a).

settings (Fig. 1a) in Yellowstone NP, and for Fremont cottonwood in Zion NP (Fig. 3e).

At Wind Cave NP, livestock use began in the late-1800s (Table 2) and continued until 1946, after which only wild ungulates have had access to the park's resources. A lack of plains cottonwood recruitment during the 20th century (Fig. 3f) was found in this park, with similar results for lanceleaf cottonwood *Populus acuminata*, and bur oak *Quercus macrocarpa* (Ripple and Beschta, 2007a). Results for Wind Cave NP indicated that, in the absence of large predators, livestock and subsequently wild ungulates have had an equivalent impact upon the recruitment of woody species.

The time series of average $\log_{10}$ response ratios of tree frequency, relative to when predators became extirpated/displaced (Fig. 4), illustrates the decline in tree recruitment in our study areas generally began soon after the loss of large predators. In addition, the strength of the trophic cascade has become stronger (increasingly negative) over time regardless of whether or not a particular park undertook culling efforts following the loss of large predators.

Photographs in Fig. 5 provide visual examples of the long-term decline/absence of deciduous tree recruitment within study areas of the five parks. Not only are small diameter trees missing in these examples, but various shrub species that were historically a common component of understory plant communities are similarly absent (Table 2). Currently, grasses and other herbaceous species tend to dominate these understories.

Sites where ungulate browsing had remained relatively low over time included locations outside of park boundaries for Olympic and Yellowstone NPs and within park boundaries for Yosemite and Zion NPs (Fig. 6). The age structure of deciduous trees at these sites indicated ongoing recruitment during the 20th century. The contrasting age structures in Fig. 3 versus Fig. 6 strongly suggest that climate was not a cause of the recruitment downturn that occurred after predator loss, as all sites within or outside a given park experienced the same general climatic patterns. At Wind Cave NP, several recently installed ungulate exclosures indicated that once foraging by ungulates was curtailed, recruitment of deciduous tree species was able to occur for the first time in many decades (Ripple and Beschta, 2007a).

Where riparian plant communities have been impacted heavily by herbivory, additional consequences may extend to channels and aquatic ecosystems. For example, channel measurements from aerial photos indicated that rivers inside Olympic NP had wider active channels and a greater percent braiding than reaches outside the park where elk densities are lower (Beschta and Ripple, 2008b). Field measurements of Gallatin River channels within the elk winter range of northwestern Yellowstone NP were generally wider and floodplains had a reduced frequency of overbank flows compared to those outside the winter range (Beschta and Ripple, 2006a). At Zion NP, channels in an area where cougar were scarce had a greater percentage of eroding banks, greater width:depth ratios, and reduced fish densities than in an adjacent catchment where cougar were common (Ripple and Beschta, 2006a). Streambank photographs of the Lamar River in Yellowstone NP (Fig. 5d) and the North Fork of the Virgin River in Zion NP (Fig. 5e) illustrate ongoing streambank erosion associated with degraded riparian plant communities. Finally, species abundance measurements in Zion NP indicated that hydrophytic plants (3 genera), wildflowers (2 species), amphibians (2 species), lizards (6 species), and butterflies (10 subfamilies) were less abundant in Zion Canyon (cougars scarce) than along North Creek (cougars common) (Ripple and Beschta, 2006a).

The average PDSI during the period when large predators were present versus when they were absent/scarce was not significantly different ($p > 0.05$) for any park (Fig. 7), thus precluding climate change as a major factor affecting the observed declines in tree recruitment during recent decades. Furthermore, our evaluation of alternative factors that might influence temporal patterns of tree recruitment within each national park included: annual peak flows in Olympic NP (Beschta and Ripple, 2008b); climate fluctuations, fire suppression, conifer invasion, land use, and loss of aboriginal influences in Yosemite NP (Ripple and Beschta, 2008); fire history, hydrologic disturbances, and natural stand dynamics in Yellowstone NP (Beschta, 2005); climate fluctuations, human interventions to channels, and site differences in Zion NP (Ripple and Beschta, 2006a); and climate, land use, and fire suppression in Wind Cave NP (Ripple and Beschta, 2007a). However, none of the alternative factors explained the observed long-term declines in tree recruitment.

Thirty-one wolves were reintroduced into Yellowstone NP during the winters of 1995 and 1996. Within a few years plant measurements, at some locations, indicated a downturn in browsing intensity and a corresponding increase in heights of young willows in the upper Gallatin winter range (Fig. 8a) and young willows and cottonwoods in the northern range (Ripple and Beschta, 2003, 2006b; Beschta and Ripple, 2007). A similar pattern of decreased browsing and increased height of young aspen (Fig. 8b) was observed, primarily within some riparian areas of the northern range (Ripple and Beschta, 2007b). Additionally, for the first time in several decades, recruitment of cottonwood >5 cm diameter at breast height was documented in the northern range (Fig. 3d; Beschta and Ripple, 2008a).

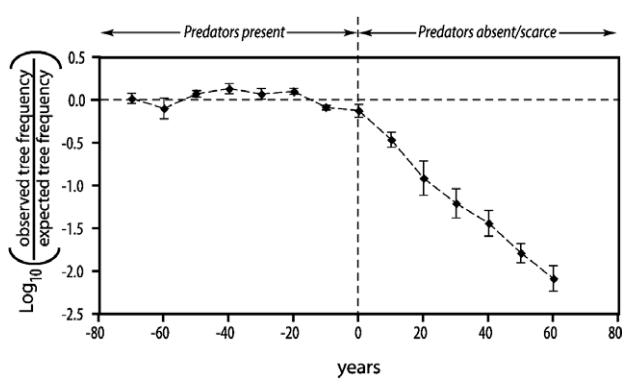

Fig. 4. Average (±SE) $\log_{10}$ response ratios of observed tee frequency (X_o) divided by expected tree frequency (X_e) [i.e., $\log_{10}(X_o/X_e)$] versus time (years). These summary statistics are based on results from five national parks (Figs. 1 and 3) for a period of time spanning from seventy years before to 60 years after the extirpation/displacement of large predators. The data were normalized temporally such that year "0" represents when large predators were estimated to have become functionally extirpated in each park. The decline in the $\log_{10}$ response ratio during the period of "predators absent/scarce" indicates a severe decrease in the recruitment of woody species following the loss of predators. Since both natural logarithm (ln) and base 10 logarithm ($\log_{10}$) response ratios are variously reported in the literature, it should be noted that the $\ln(X_o/X_e) = 2.3 \log_{10}(X_o/X_e)$.

5. Discussion

We focused on temporal patterns of age structure for upland and riparian tree species from five geographically separated and biophysically different national parks to address questions regarding the potential ecological effects of large predator removal in the western US. Since the studies reported herein only consider patterns of tree recruitment over the last 160 years, they provide limited insights regarding recruitment during earlier periods when native Americans likely had a significant presence in many western landscapes (Kay, 2007). Nevertheless, within each park the age structure of deciduous trees indicated recruitment was ongoing when large predators were present.

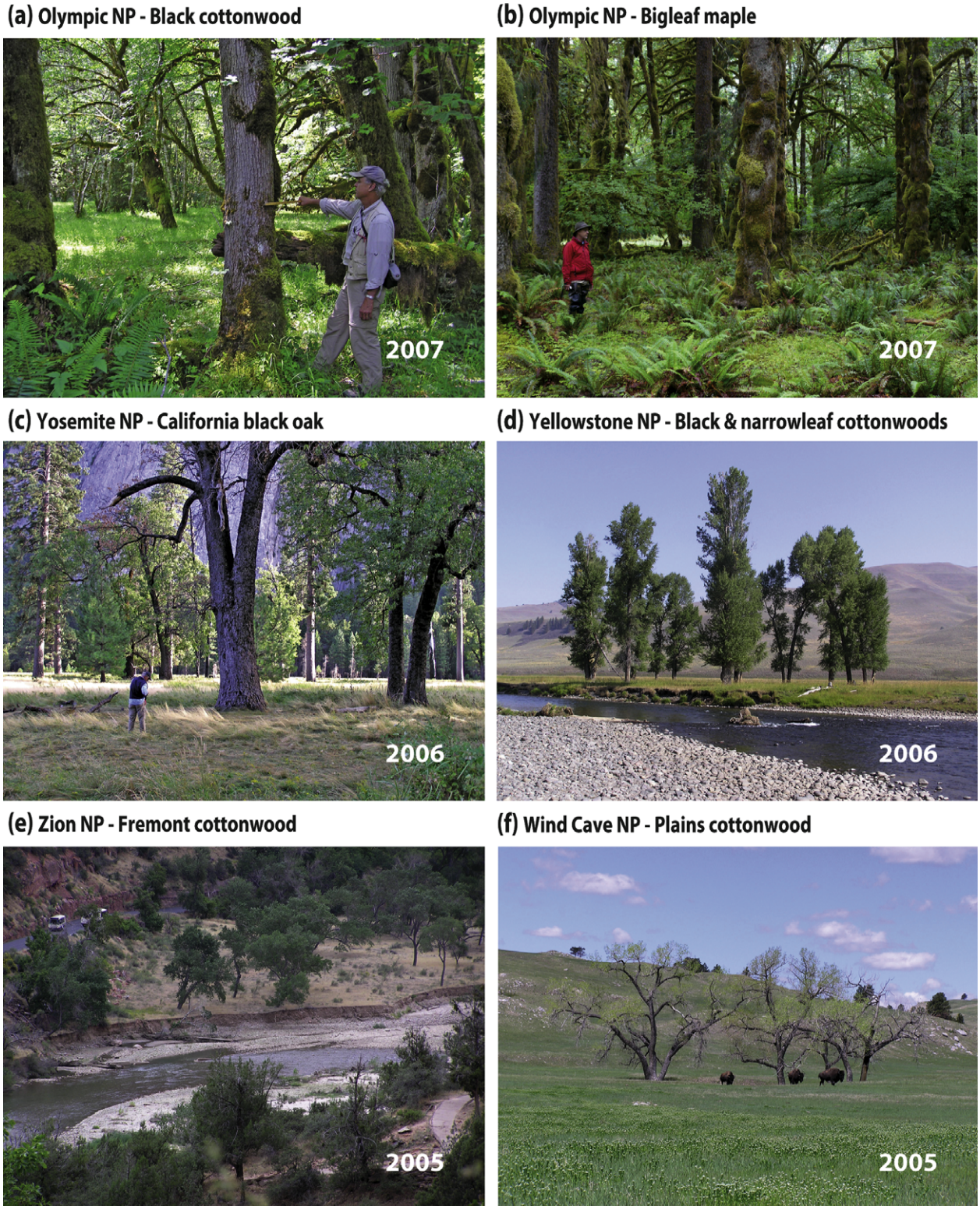

Fig. 5. Photographs of (a) black cottonwood and (b) bigleaf maple in Olympic National Park, (c) California black oak in Yosemite National Park, (d) narrowleaf cottonwood in Yellowstone National Park, (e) Fremont cottonwood in Zion National Park, and (f) plains cottonwood in Wind Cave National Park. Note the general lack of tree or shrub recruitment in all photos and ongoing streambank erosion in (d) and (e).

A dramatic reduction in the recruitment of deciduous trees was documented for study sites within each park following the extirpation or displacement of large predators. This reduction occurred regardless of on-going climatic fluctuations or whether or not park managers tried to reduce ungulate populations. The long-term decline of tree recruitment is summarized in the average $\log_{10}$ response ratios during the period when predators were absent/scarce (Fig. 4). The increasing departure of $\log_{10}$ response ratios from "0", representing increasing damage to plants and ecosystems, occurs because of (1) the observed decline in tree frequencies over time

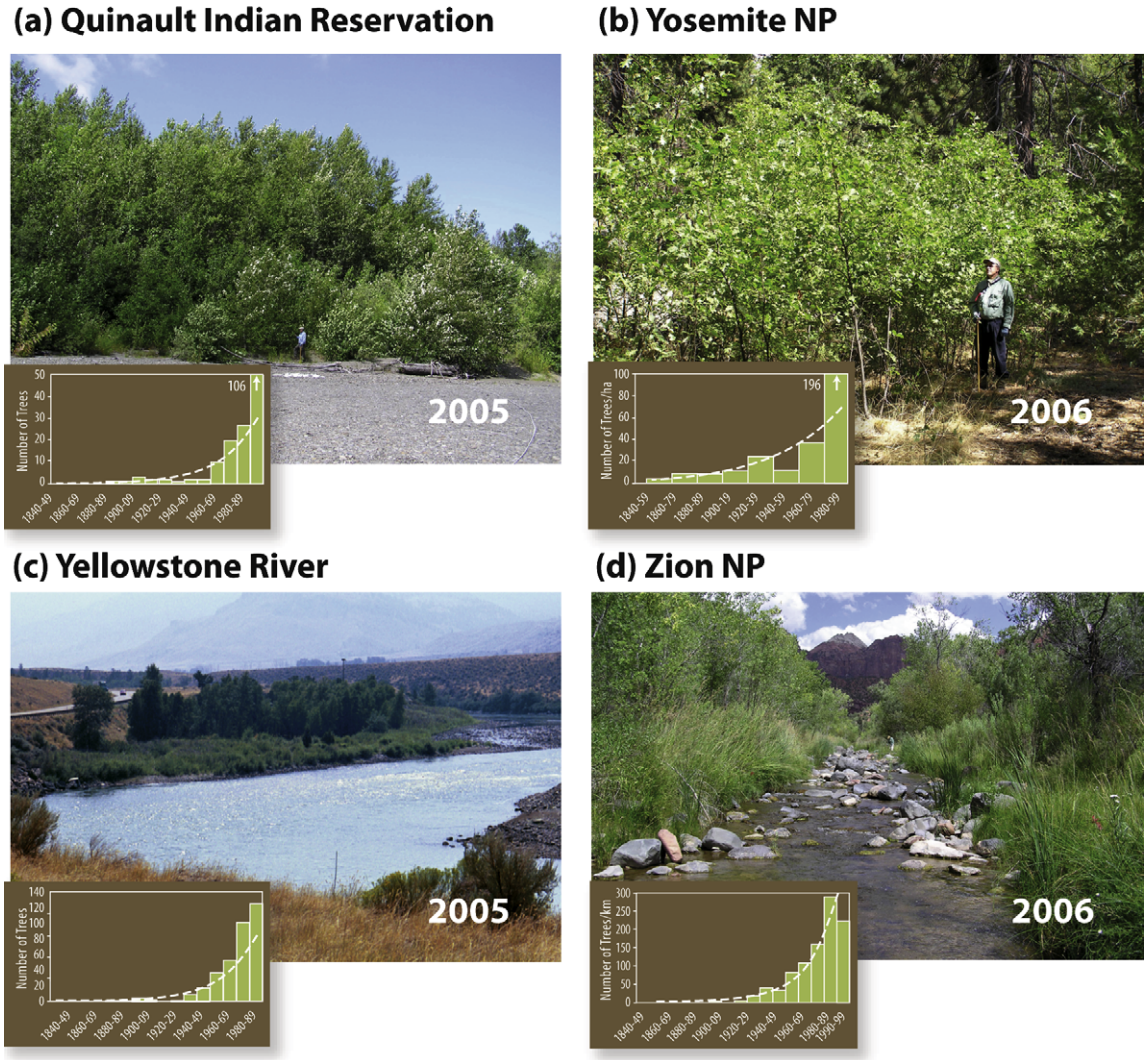

Fig. 6. Sites where deciduous trees are at low risk of herbivory by ungulates, including: (a) black cottonwood outside Olympic National Park, (b) California black oak within Yosemite National Park, (c) black and narrowleaf cottonwood outside Yellowstone National Park, and (d) Fremont cottonwood within Zion National Park. Insets show age structure (tree frequency by establishment date) indicting tree recruitment at each of these sites continues to occur in the absence of large predators. *Sources*: adapted from (a) Beschta and Ripple (2008b), (b) Ripple and Beschta (2008), (c) Beschta (2005) and (d) Ripple and Beschta (2006a).

and (2) the fact that relatively large numbers of young trees are required to maintain tree frequencies characteristic of the pre-treatment period. Within a little over two decades following the loss of large predators, tree recruitment had declined, on average, to approximately 10% ($\log_{10}$ response ratio = −1.0) of that needed to maintain historical tree communities. Within a little more than half a century, recruitment levels were at only 1% of those needed to maintain historical tree communities. Such a trend clearly indicates the functional loss of specific deciduous tree species and, if allowed to continue, their local extirpation. This trend also infers a continual transition toward decreased ecosystem services and alterative ecosystem states. The strong top-down effects exerted on deciduous tree species in each of the five parks are in contrast to recent synthesis work (Borer et al., 2005) that indicates stronger cascades in aquatic than in terrestrial ecosystems. As Borer et al. (2005) suggest, part of this apparent disparity may be due to the relative paucity of studies from terrestrial ecosystems involving large predators.

Our results indicate that the presence of large predators during the pre-treatment period was likely important for helping to sustain native plant communities in upland and riparian settings where this vegetation contributed to a wide range of ecosystem services, such as food-web support, physical habitat, soil development, streambank stability, and others. Thus, the observed decline in tree recruitment during the post-treatment period (predators absent/scarce) appears to index a broad pattern of impacts to palatable shrubs and herbaceous plants with shorter life cycles, species that historically would have been common in understory plant communities. For example, various shrub species frequently highlighted in reports by early park biologists (Table 2) are relatively uncommon today along many streambanks and floodplains of study sites in Olympic, Yellowstone, and Zion NPs. Loss of various woody browse species also has been identified at Wind Cave and Yosemite NPs as well as the reduced seasonal flower displays that were once a prominent feature of Yosemite Valley's flora. While the situations illustrated by the photographs in Fig. 5 may typify an openness associated with "park-like" settings, their collective ecological signature is one of reduced recruitment for a wide spectrum of palatable woody species due to high levels of annual herbivory over a period of many decades.

Spatial differences in the characteristics of study sites (Table 1) cannot explain the severe downturn and eventual cessation of tree recruitment following the extirpation/displacement of a park's apex predator. Similarly, the temporal patterns of PDSI illustrated

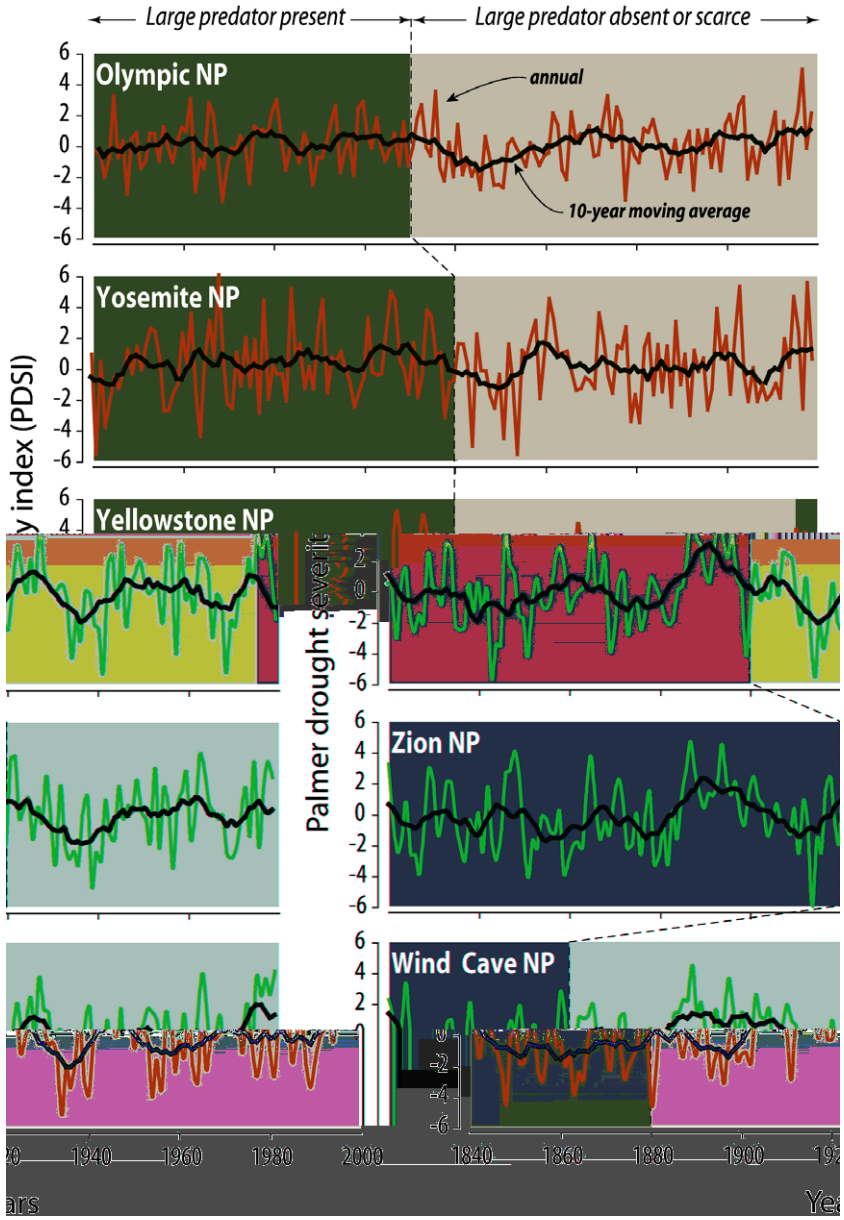

Fig. 7. Annual and 10-year moving averages of summer-season Palmer Drought Severity Index (PDSI) from 1940 to 2000 for Olympic, Yosemite, Yellowstone, Zion, Wind Cave National Parks. Positive departures of PDSI from "zero" indicate increasing wetness whereas negative departures of PDSI indicate increasing aridity (drought). Shaded portion of each panel represents period when apex predator was present. Comparison of average PDSI values for the period when a large predator was present versus when it was absent/scarce resulted in *p*-values of 0.96, 0.54, 0.40, 0.86, and 0.46 (all non-significant at $p > 0.05$) for Olympic, Yosemite, Yellowstone, Zion, and Wind Cave NPs, respectively.

in Fig. 7 have little association to the age structure of deciduous trees within each park. While temporal variations in winter severity, peakflows, drought, and other factors might reasonably be expected to exert some influence on plant community composition, ungulate foraging patterns, and perhaps other characteristics of our study sites, the presence or absence of large predators appears to have been the primary factor affecting long-term patterns of tree recruitment and other plant community impacts.

Other studies in western North America have also shown that the loss of large predators generally precedes significant plant community change. For example, Binkley et al. (2006) evaluated aspen age structure on the Kaibab Plateau of northern Arizona and found that a widespread reduction in aspen recruitment after 1910 corresponded with the loss of cougars and wolves. In Rocky Mountain NP, where elk were reintroduced in 1913 and wolves have remained absent throughout the 20th century, impacts to vegetation and soils by elk date back to the early 1930s (Hess, 1993). Park service culling of elk, that began within the park during the mid-1940s because of concerns regarding herbivory-altered plant communities and accelerated soil loss, was curtailed in 1968 (Hess, 1993). In recent decades low-elevation aspen stands on the east side of the park have experienced a reduction in recruitment due to elk browsing (Binkley, 2008).

In Canada's Jasper NP, wolves were eliminated during the 1950s and aspen regeneration in the winter range subsequently ceased due to high levels of elk browsing (Beschta and Ripple, 2006b). Reduced aspen recruitment due to elk has also been documented in other Canadian NPs, such as Banff, Yoho, and Kootenay (White et al., 1998). These are areas where large predators had been reduced or displaced by humans and historical fire management efforts directed at preventing or controlling fires. White et al. (1998) also noted that whenever fenced exclosures were installed