

Wolves, trophic cascades, and rivers in the Olympic National Park, USA

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ABSTRACT

Gray wolves (*Canis lupus*) were extirpated in the early 1900s from the Olympic Peninsula of northwestern Washington. Thus, we studied potential cascading effects of wolf removal by undertaking a retrospective study of Roosevelt elk (*Cervus elaphus*) populations, riparian forests, and river channel morphology. For three riparian sites within the western portion of Olympic National Park, the age structure of black cottonwood and bigleaf maple indicated a pattern of significantly decreased recruitment (growth of seedlings/sprouts into tall saplings and trees) associated with intensive elk browsing in the decades following the loss of wolves. At a riparian site outside the park, which represented a refugium from elk browsing, cottonwood recruitment has been ongoing during the 20th century, indicating that climate and flow regimes, in the absence of intensive herbivory, have not limited the establishment and growth of this deciduous woody species. Using 1994 orthophotos, we also measured channel dimensions and planform morphology of 8-km-long river reaches at each vegetation sampling site and an additional reach outside the park. Channels inside the park versus those outside the park had greater percent braiding (37 vs 2%) and larger ratios of active channel width/wetted width (3.0 vs 1.5 m/m). Results for western Olympic National Park were consistent with a truncated trophic cascade hypothesis whereby ungulate browsing following the extirpation of wolves caused significant long-term impacts to riparian plant communities which, in turn, allowed increased riverbank erosion and channel widening to occur. Copyright © 2008 John Wiley & Sons, Ltd.

KEY WORDS trophic cascades; wolves; elk; riparian plant communities; channel morphology

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INTRODUCTION

Historically, gray wolves (*Canis lupus*) were common on the Olympic Peninsula, but have been absent for most of the 20th century. The presence of large predators, such as wolves, can have important effects on ungulate herbivory (via predation and predation risk), thus limiting herbivore effects on plant communities (Flueck, 2000; Ray *et al.*, 2005). This progression of effects across successively lower trophic levels represents a trophic cascade (Estes *et al.*, 2001). Alternatively, the loss of key large predators may allow greater herbivory of plant communities as ungulate populations increase, alter patterns of foraging behaviour, or both. Riparian areas and valley bottoms of the Olympic Peninsula's coastal rivers currently provide important areas of habitat and foraging for wild ungulates, principally Roosevelt elk (*Cervus elaphus*) (Moorehead, 1994).

Abundant annual precipitation along the western Olympic Peninsula, and air temperatures influenced by the Pacific Ocean produce environmental conditions that support luxuriant riparian forests (Franklin and Dyrness, 1969). Shade provided by the typically dense canopies of these forests influences understory microclimates (Kimmins, 1987) and thermally moderates aquatic environments, particularly during the summer months (Beschta

et al., 1987). Inputs of large wood from riparian forests into streams and rivers can also affect channel morphology and the quality of rearing habitat for resident and anadromous fish (Bisson *et al.*, 1987; Naiman *et al.*, 2000; Latterell and Naiman, 2007).

With regard to the morphology and dynamics of river channels, root systems of riparian plant communities impart another critical function, that of stabilizing riverbanks and floodplains (Micheli and Kirchner, 2002; Gray and Barker, 2004). In addition, the hydraulic roughness derived from above-ground stems, branches, and leaves of vegetation along riverbanks can reduce flow-induced shear stresses at the water–riverbank interface (Sedell and Beschta, 1991). Murray and Paola (2003) indicate that shrub–tree communities which normally comprise riparian ecosystems augment the deposition of sediment onto floodplains during periods of over-bank flow. They also modelled the effect of vegetation on channel pattern and found that plants, overall, enhanced the resistance of riverbanks to fluvial erosion, thus contributing to the maintenance of a single channel instead of a rapidly shifting, multiple channel (braided) pattern. The potential role of vegetation for stabilizing riverbanks and influencing the morphology of channels has become well recognized in recent years (NRC, 2002; Baker *et al.*, 2004; Bennett and Simon, 2004; Gurnell and Petts, 2006).

Since wolves had been extirpated from the Olympic Peninsula for many years, we undertook this retrospective study to investigate potential trophic-level interactions

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within the highly productive riparian forests of Olympic National Park. In doing so, we considered two linked hypotheses. Hypothesis #1 focussed on potential vegetation effects of a truncated trophic cascade: the extirpation of an apex predator (i.e. wolves), in the absence of human hunting, allowed increased ungulate herbivory to restructure riparian plant communities. Hypothesis #2 involved riverbanks and channels: increased herbivory of riparian plant communities has, in turn, led to accelerated bank erosion, thus altering long-term channel dynamics of the park's rivers (Figure 1). We also considered alternative factors that might affect recruitment (growth of seedlings/sprouts into tall saplings and trees) of riparian deciduous species and channel morphology over time.

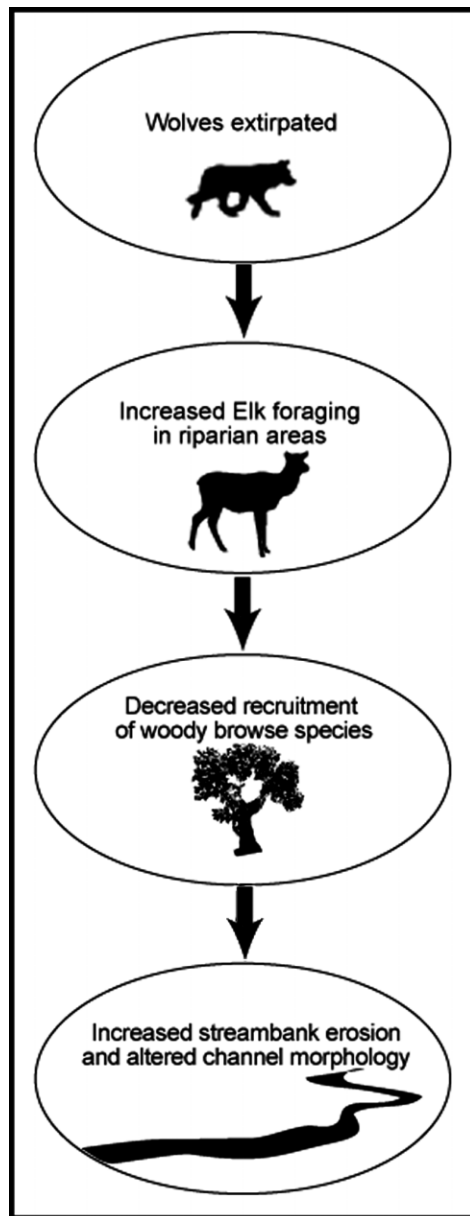


Figure 1. Conceptualized diagram of cascading ecological effects associated with elk, riparian forests, and rivers in western Olympic National Park following the extirpation of wolves.

STUDY AREA

Average annual precipitation ranges from ~250 cm/year along the west coast of the Olympic Peninsula to >500 cm/year in the Olympic Mountains. Within these mountains, the Hoh, Queets, and Quinault Rivers originate at elevations of over 2000 m, rapidly descend to ~300 m, continue westward at a decreased gradient through floodplains and broad alluvial terraces, and eventually discharge into the Pacific Ocean (Figure 2). Annual peakflows usually occur between November and January following extended periods of rain or rain-on-snow.

Riparian forests on the Olympic Peninsula typically contain red alder (*Alnus rubra*), black cottonwood (*Populus trichocarpa*), bigleaf maple (*Acer macrophyllum*), Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*) (Van Pelt *et al.*, 2006). Vine maple (*Acer circinatum*), huckleberries (*Vaccinium* spp.), salmonberry (*Rubus spectabilis*), and additional shrub species, also, frequent floodplains and terraces (Schwartz, 1939; Schreiner *et al.*, 1996). Following forest disturbance, secondary succession usually entails the development of dense shrub and deciduous tree communities that are eventually replaced by long-lived conifers (Franklin and Dyrness, 1969).

Coastal forests provide physical habitat needs and food-web support for an array of wildlife species including nearly 230 native terrestrial vertebrates (Quinault Indian Nation and US Forest Service, 1999). The contemporary large predator guild consists of cougar (*Puma concolor*), black bear (*Ursus americanus*), and coyote (*Canis latrans*), with ungulates represented by Roosevelt elk and Columbian black-tailed deer (*Odocoileus hemionus columbianus*). Resident and anadromous salmon (*Oncorhynchus* spp.) and trout (*Salvelinus* spp.) utilize the rivers of the western Olympic Peninsula for their habitat and life history needs.

HISTORICAL OVERVIEW OF WESTERN OLYMPIC PENINSULA

Hunting, fishing, and gathering by native Americans have occurred for millennia along coastal portions of the Olympic Peninsula. However, as Euro-Americans started settling along western rivers of the peninsula in the 1890s they began to harvest timber, raise domestic animals, and cultivate floodplains. Widespread Euro-American hunting of predators, ungulates, and other wildlife also occurred (Morgenroth, 1909). Wolves, originally considered common on the Olympic Peninsula, were hunted and trapped throughout the late 1800s to early 1900s (Bailey, 1918). They were eventually eliminated in the early 1920s (Ratti *et al.*, 2004) although their functional extirpation likely occurred years earlier.

Concerns about low elk populations from over-hunting led to a 1905 peninsula-wide moratorium on hunting these ungulates, a ban that continued for three decades. Mt. Olympus National Monument was created in 1909

for the primary purpose of protecting elk and their habitat (Schwartz, 1939). The monument became Olympic National Park in 1938 to preserve 'the finest sample of primeval forests in the entire United States, and to provide suitable winter range and permanent protection for herds of Native Roosevelt Elk' (from the park's enabling legislation). The Queets corridor, an area extending westward along the Queets River, was added to the park

in 1945 (Schroer *et al.*, 1993). The park currently comprises an area of 2750 km², mostly within the interior Olympic Peninsula. Outside the park, large portions of the Olympic National Forest as well as forested lands in state, private, and tribal ownership have experienced timber harvest during the 20th century (Figure 2).

With large predators suppressed and an elk-hunting moratorium in place, the elk population within the

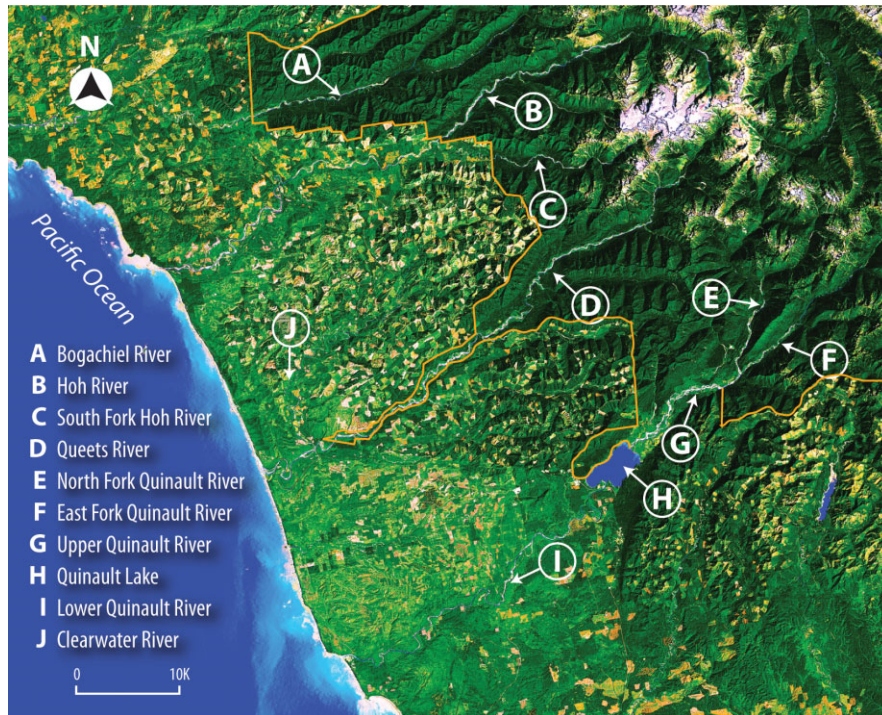


Figure 2. Satellite imagery (Landsat 5, 1996) of western Olympic Peninsula. Park boundary is shown except for the coastal portion of the park. Unvegetated alluvium (representing wide active channels) is readily visible for rivers within the Olympic National Park, as is the extensive patchwork of clearcut harvesting that has occurred on forested lands outside the park's boundaries. Imagery reproduced with permission from Advanced Satellite Productions, Inc., Kelowna, B.C., Canada.

Table I. Biologist's comments regarding elk and vegetation between 1918 and 1937, when elk populations were relatively high in western drainages of the Olympic Peninsula.

Bailey (1918) visited the Elwha and Hoh River valleys (in April and May), where '... elk were said to be most numerous and where some were reported to have died during the severe winter and spring of 1917. ... For a distance of about 15 miles along the [Hoh] river bottoms they [elk] had largely cleaned up the salmonberry, willows, blueberry, elder, and devil's-club, but vine maple (*Acer circinatum*) remains in abundance and has been well browsed.'

Riley (1918)^a found that 'The heaviest loss [of elk] ... is on the Hoh River ... the Queets [River] and Queniult [Quinault River] ... within the National Forest. The food within these limited areas, consisting of salmon berry, willows, alder, vine maple, black stemmed and licorice ferns, not extensive at best, has become extremely scarce under excessive use in recent years. Those areas where the elk have congregated and starved of late are clearly defined or traceable by the absence of these plants upon which they feed when driven down from the higher lands by snow.'

Webster (1922) observed '... a pronounced shortage of late winter or early spring feed for the elk of the upper Hoh valley, resulting, this past spring, in the loss of starvation of approximately forty animals [elk] ... Soon after leaving Spruce [heading up-valley from a settlement], on the [Hoh] river trail, one notes a scarcity of browse. There is no salal, no salmon berry, no thimble berry—practically nothing save vine maple and huckleberry. The former has been trimmed up as far as elk can reach; the latter cut down until there is little but stubby bushes remaining ... Further up river the condition becomes more acute, the timber having an open, park-like appearance, having been thoroughly cleaned to the height of about seven feet [two meters].'

Murie (1935b) concluded that 'The Hoh River is outstanding as an example of overstocking [primarily elk] and forage depletion.' Overstocking and overbrowsing were also noted for portions of the Queets and Quinault drainages.

A *Mt. Olympus National Monument Report (February 25, 1937)* indicated that 'Certain portions of the yearlong [elk] range of the Hoh, Queets, and Quinault rivers have been so heavily grazed during these [winter and early spring] periods that serious damage has resulted to the principal forage species.'

^a Riley, S. December 2, 1918. Olympic National Forest Memorandum, Olympia, Washington.

national monument began to irrupt in the early 1900s (Figure 3). As a consequence, heavy browsing of riparian vegetation and winter losses of elk due to starvation were soon reported (Table I). Although elk numbers were growing, there was an increasing tendency for them to primarily utilize riparian areas within the monument even though forage was available at downriver locations outside the monument's boundary (Bailey, 1918; Webster, 1922).

After riparian plant communities became degraded from intensive browsing (Dixon, 1943; Newman, 1953), elk numbers in the 1940s and 1950s began trending downward within the Hoh, Queets, and Quinault River drainages of the park (Figure 3). However, once woody species in riparian areas had been heavily browsed, recovery of plant communities apparently could not occur even with reduced elk numbers. For example, Newman (1953) noted that the upper Queets Valley was the 'most severely over-browsed valley in the park' and that reproduction of woody browse plants along the Hoh River was 'practically non-existent' (Newman, 1954). Elk mortality during severe winters, first reported during the 1910s and 1920s when elk populations were irrupting, has been reported as recently as 1970 (Ferry *et al.*, 2001) and 1980 (Jenkins, 1981).

From the 1930s to the 1950s, a total of 25 ungulate enclosures were established at various times within the western valleys of Olympic National Park and the Olympic National Forest to assess the effects of reduced herbivory on forest vegetation. Results generally indicated that ungulate exclusion allowed the density and size of understory shrubs and ferns to recover while grass and forb cover decreased (Woodward *et al.*, 1994). Considerable research in the park during recent decades has been directed at evaluating the effects of elk herbivory

on woody plant communities (e.g. Jenkins, 1981; Jenkins and Starkey, 1984; Moorehead, 1994; Woodward *et al.*, 1994; Schreiner *et al.*, 1996) since most shrub and tree species, with the exception of red alder and Sitka spruce, are generally palatable to elk.

METHODS

Riparian vegetation

We undertook field measurements in August 2005 and 2006 to evaluate historical patterns of black cottonwood recruitment. We focussed on sites within the park's boundary, thus avoiding issues related to logging, management of large wood in rivers, and any direct effects of elk hunting. Black cottonwood was chosen for analysis since it is highly palatable to ungulates, may live up to 200 years or more, is amenable to ageing via tree ring counts, represents an ecologically important component of riparian plant communities (Braatne *et al.*, 1996), and occurs along rivers of the western Olympic Peninsula. We inventoried all black cottonwoods along 6 km of the Hoh River (north side of the river only), 1 km of the Queets River (south side only), and 2 km of the East Fork Quinault River (both sides of the river); these distances varied owing to the availability of cottonwood stands and their accessibility. At each site, we searched floodplains and transitional fluvial terraces (Van Pelt *et al.*, 2006) for cottonwoods ≥ 1 cm in diameter at breast height (*dbh*) and measured their diameters (Figure 4).

Several stands of bigleaf maple were encountered within the Hoh and East Fork Quinault sites. Since this species is also long-lived and palatable to elk, as well as having a different autecology relative to that of black cottonwood, we measured the *dbh* of bigleaf maples ≥ 1 cm in diameter to determine its age structure. Bigleaf maple seedlings usually establish under forest canopies and seedling height growth of this shade-tolerant species is comparatively slow (Fried *et al.*, 1988). In contrast,

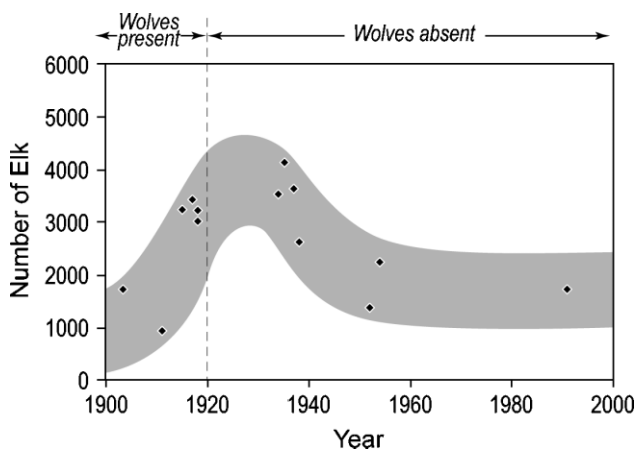


Figure 3. General elk population trends on public lands for the Hoh, Queets, and Quinault River catchments during the 20th century (the shaded band represents authors' estimate of uncertainty). Data sources: Hanson (1905); Mt. Olympic National Forest Document, Olympia, Washington (November 9, 1911); Bailey (1918); Murie (1935a,b); Mt. Olympus National Monument Report, Olympia, Washington (February 25, 1937); Schwartz and Mitchell (1945); Newman (1953, 1954); and Houston *et al.* (1990). The Houston *et al.* (1990) estimate of 3000–4000 elk for 8 northerly and westerly catchments inside the park was reduced to reflect a population estimate for the Hoh, Queets, and Quinault River catchments.



Figure 4. Measuring black cottonwood diameter at breast height (*dbh*) with a Bitterlick stick on a transitional fluvial terrace of the Queets River in Olympic National Park. Note the absence of shrubs and small-diameter cottonwoods, and the widespread occurrence of grass.

black cottonwood seedling establishment usually occurs on recent alluvial deposits where young plants are unshaded and can attain rapid height growth (Braatne *et al.*, 1996).

A fourth site was selected along the lower Quinault River on the lands of the Quinault Indian Nation. We considered this site, consisting of ~0.7-km-long pointbar on the north side of the river and located only a few kilometres from the town of Quinault, to represent a browsing refugium (i.e. a site where cottonwood seedlings could grow to tall saplings, poles, and trees without appreciable ungulate browsing) because (1) it was located between a major forest access road and the river, (2) it was immediately adjacent to a boat launching site frequently used by tribal fishermen, (3) hunting on tribal lands typically occurs throughout much of a year, and (4) elk densities are lower on tribal lands than those associated with areas inside Olympic National Park (Quinault Indian Nation and US Forest Service, 1999; Ratti *et al.*, 2004). Since high densities of small diameter cottonwoods occurred at this site, we established (using a random start) four-belt transects 30-m apart along the river. Each 4 m × 100 m transect began at the riverside margin of the riparian forest and extended directly away from the river. Within each transect, we measured all cottonwood stems ≥ 1 cm in *dbh*.

At the four study sites we selected cottonwoods across a range of *dbh* sizes for increment coring at breast height (~1.4 m). At the Hoh and East Fork Quinault sites, increment cores were similarly obtained for bigleaf maple. Cores were individually sealed in plastic straws for transport to a laboratory where they were dried, sanded, and tree rings counted with a 10× binocular microscope. We used regression analysis to develop relationships between *dbh* and the number of growth rings (i.e. tree age at breast height). Using these relationships, the establishment date of each sampled cottonwood and maple was estimated by adding 5 and 15 years (Roe, 1958; Fried *et al.*, 1988), respectively, to a calculated age at breast height. The resulting age structure (i.e. frequency histogram of establishment date by decade) of black cottonwood and bigleaf maple was used to characterize historical patterns of recruitment.

We considered temporal changes in large predator populations to represent a natural experiment (Diamond, 1983), whereby the removal of wolves represented a 'treatment'. Thus, the age structure of deciduous trees prior to and after wolf extirpation corresponded with pre-treatment and post-treatment conditions, respectively. We regarded this large predator to have been functionally extirpated by ~1910 (when few wolves remained and elk numbers began to increase) and used this date as a basis for comparing pre- and post-treatment age structures. We established exponential relationships between tree frequency (*Y*) and decade of establishment (*X*) prior to 1910 (pre-treatment data) for black cottonwood and bigleaf maple and extended each relationship through the post-treatment period (post-1910). We used the lower 95% confidence limit (CL) to determine if recruitment

had significantly decreased during the post-treatment period. We utilized the lower Quinault site (outside the park) as a spatial 'control' to illustrate recent patterns of cottonwood recruitment where ungulate herbivory appears to have remained low over time.

At each study site, we searched for patches of cottonwood seedlings ≤ 200 cm in height. Once found, we established a 2 m × 10 m (20 m²) plot to measure seedling densities and heights (cm).

Since widespread cottonwood establishment is often associated with large floods (Braatne *et al.*, 1996), we obtained available long-term peakflow records for each river. To assess the potential effects of high flows upon cottonwood recruitment, we identified annual peakflows with recurrence intervals of ≥ 10 years and compared their occurrence to temporal patterns of cottonwood recruitment.

Channel morphology

At the Hoh, Queets, and East Fork Quinault riparian sites (within the park) we delineated 8-km-long reaches on 1994 orthophotos (1-m resolution) for characterizing channel morphology (*n* = 32 measurements per reach at 0.25-km intervals). The availability of reaches outside the park for geomorphic comparisons with those inside the park was constrained by the fact that most rivers on the Olympic Peninsula originate inside the park. Thus, reach comparisons inside and outside the park become problematic since high levels of sediment input along upriver reaches can eventually influence the character of downriver reaches (Beschta, 1999). However, we considered an 8-km reach along the Clearwater River, and another along the lower Quinault River to represent 'independent' reaches for comparison with those in the park because (1) the Clearwater River catchment lies entirely outside the park (between the Hoh and Queets River catchments), and (2) the lower Quinault River is buffered from any upriver sedimentation (originating inside the park) due to Lake Quinault (Figure 2). Timber harvesting is the dominant land use along the Clearwater and lower Quinault reaches.

Measurements along each 8-km reach included the proportion of reach length comprised of multiple channels (i.e. % braided), active channel width (m), and wetted width (m). Active channel width was defined as the linear distance between vegetated banks at a given cross-section, included the wetted width of the river. From these width measurements, we calculated the ratio of active channel width/wetted width (m/m).

RESULTS

Riparian vegetation

Regression analysis of tree age at breast height (*age*, years) and *dbh* (cm) based on black cottonwood increment cores resulted in the following relationship: $age = 0.47 dbh^{1.21}$ (*n* = 32, *r*² = 0.85, *p* < 0.01). Regression analysis of bigleaf maple increment cores resulted in

the following: $age = 1.92 dbh$ ($n = 20$, $r^2 = 0.71$, $p < 0.01$). Thus, each tree's establishment date (ed) was calculated as $ed = [2006 - (0.47 dbh^{1.21} + 5)]$ for cottonwood and $ed = [2006 - (1.92 dbh + 15)]$ for maple.

For sites within Olympic National Park, statistically significant ($p < 0.01$) exponential relationships of decadal tree frequencies versus decades of establishment using pre-1910 data were obtained for both black cottonwood [$Y = 9 \times 10^{-20} e^{0.0255X}$, $r^2 = 0.90$, Figure 5(a)] and bigleaf maple [$Y = 1 \times 10^{-19} e^{0.0248X}$, $r^2 = 0.78$, Figure 5(b)]. These relationships thus provided a basis for identifying potential decreases in tree recruitment after 1910. Recruitment of black cottonwood and bigleaf maple was found to have significantly declined after 1910 and 1930, respectively, and has not occurred during recent decades. In contrast, black cottonwoods sampled at the lower Quinault River site (outside the park) show ongoing recruitment during the 20th century [$Y = 2 \times 10^{-30} e^{0.0360X}$, $r^2 = 0.73$, $p < 0.01$, Figure 5(c)]. If the number of cottonwoods sampled within the four-belt transects at the lower Quinault site is expanded to represent the entire point bar, approximately 220 pre-1910 and 7500 post-1910 trees are estimated to occur at this location.

For the three study sites within the park, considerable searching was required before we were able to find

discrete patches of cottonwood seedlings. Eventually, we measured seedlings on seven plots (four on the Hoh, one on the Queets, and two on the East Fork Quinault sites). The average density of young cottonwoods within these 20-m² plots was 8000 seedlings/ha and all plants were ≤ 32 cm in height. Numerous elk tracks were observed on alluvial deposits in and around these plots. At the lower Quinault site (outside the park), we measured seedlings on four plots along the edge of the active channel. The average density of young cottonwoods for these plots was 33 000 seedlings/ha of which two-thirds were 1–50 cm in height and the remaining third were 50–200 cm in height. Elk tracks were not observed at this site.

The Hoh, Queets, and Quinault are free-flowing rivers (undammed) that occur in adjacent catchments along the west side of the Olympic Peninsula. However, annual peakflows per unit area of catchment (m³/s/km²) for the Quinault River river gauge averaged 22 and 40% lower than those for the Hoh and Queets Rivers, respectively, likely due to the gauge's location immediately downriver of Lake Quinault. Annual peakflows with recurrence intervals ≥ 10 years were relatively common for the Hoh River from 1980 to 1991, thus potentially creating bare substrates for cottonwood establishment during that period. In contrast, peakflows with ≥ 10 -year recurrence intervals for the Queets and Quinault Rivers have been distributed throughout their historical records (Figure 6).

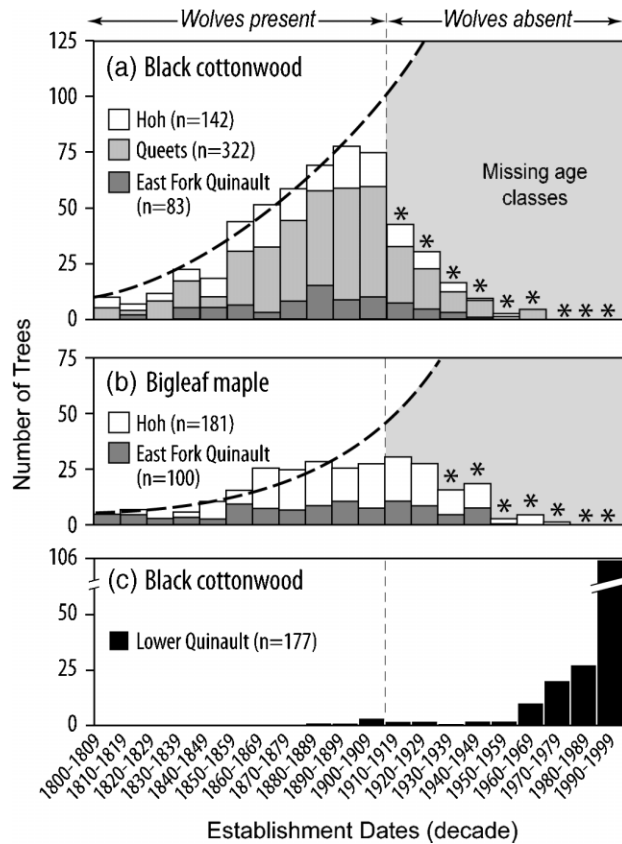


Figure 5. Number of trees by decade of establishment (age structure) for (a) black cottonwood (within Olympic National Park), (b) bigleaf maple (within the park), and (c) black cottonwood on Quinault Indian Nation lands (outside the park). Tree frequencies outside the lower 95% confidence limit are represented by *; n = number of trees measured at each study site.

Channel morphology

The 8-km-long reaches inside the park (Hoh, Queets, and East Fork Quinault) tended to occur at higher elevations as well as have steeper gradients and wider active channel widths than those outside the park (Clearwater, lower Quinault). Even so, average wetted widths for reaches inside and outside the park were similar (46 vs 44 m, respectively, Table II).

Reaches inside the park had greater braiding and larger active channel width/wetted widths relative to reaches outside the park (Figure 7). The average braiding of channels inside the park ($\bar{x} = 37\%$) was considerably greater than that of channels outside the park ($\bar{x} = 2\%$) and the average active channel width/wetted width ratio of channels inside the park ($\bar{x} = 3.0$ m/m) was double that of channels outside the park ($\bar{x} = 1.5$ m/m). Except for periods of high flow, when the entire active channel may be flooded, these measurements indicated that reaches inside the park generally had relatively large amounts of bare alluvium and less likelihood of flowing water occurring directly adjacent to forested channel margins. An example of a wide and braided reach at the Hoh River study site is shown in Figure 8(a). Since unvegetated alluvium has high reflectance in comparison to riparian forests, the wide active channels associated with rivers inside the park are readily visible from satellite imagery of the peninsula (Figure 2). In contrast, rivers outside the park tend to have narrower active channels and are thus more difficult to discern on this imagery.

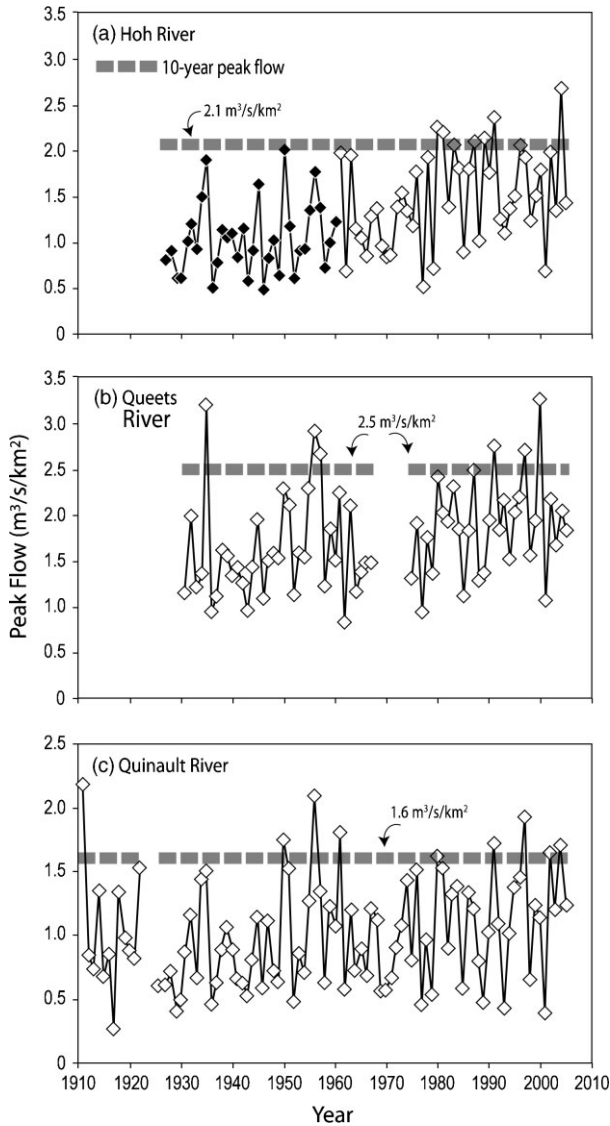


Figure 6. Annual peakflows for the (a) Hoh, (b) Queets, and (c) Quinault Rivers, western Olympic Peninsula. The dashed line represents approximately a 10-year recurrence interval flow.

DISCUSSION

Trophic cascades

Peterson *et al.* (2003) concluded that predation by large predators, especially wolves, can have a pervasive limitation on ungulate populations. Furthermore, wolves elsewhere have been found to be effective at killing ungulates

along rivers and within riparian systems (Kunkel and Pletscher, 2001; Gula, 2004; and Bergman *et al.*, 2006). Thus, with the extirpation of wolves in the early 1900s, Euro-American hunting pressure on bear and cougar, and a 1905 elk-hunting moratorium, elk populations within the park’s valley bottoms soon irrupted. Even with reduced ungulate populations in recent decades (relative to their estimated highs in the 1920s–1930s) and recovery of large predators, other than wolves (Moorehead, 1994), our age-structure data for riparian systems indicate that recruitment of palatable deciduous trees inside the park have undergone long-term decline since the early 1900s. In contrast, age-structure data at the lower Quinault site (browsing refugium outside the park) demonstrated ongoing black cottonwood recruitment throughout the 20th century.

Previous vegetation studies in the western drainages of Olympic National Park have consistently documented reduced recruitment of palatable tree species. For example, over three decades ago, Fonda (1974) found 4–30 cm *dbh* black cottonwood and bigleaf maple completely absent on Hoh River floodplains (~1 m above the river), even though bigleaf maple seedlings were common. Black cottonwood, bigleaf maple, Douglas-fir (*Pseudotsuga menziesii*) and western hemlock <10 cm *dbh* were also absent or infrequent on the first terrace (~3 m above the river) even though larger size classes of these trees were present. Along valley-floor forests of the South Fork of the Hoh River inside the park, McKee *et al.* (1982) observed few western hemlock <30 cm *dbh* while relatively unpalatable Sitka spruce <30 cm in *dbh* occurred frequently. In another study of western hemlock along the South Fork of the Hoh River, Harmon and Franklin (1983) found that a recruitment rate of ~7.5 trees/ha/decade between 1850 and 1900 decreased to <2 trees/ha/decade after 1900. While noting that poor recruitment could be affected by factors such as seasonal water stress, low nutrient availability on nurse logs, competition, and others, they also indicated that elk could kill young plants by repeated browsing as well as pulling them off of nurse logs. More recently, Van Pelt *et al.* (2006) evaluated riparian forest development along the Queets River inside the park and found an absence of black cottonwood <90 years of age. They suggested that this situation was due to a combination of factors, including a lack of ideal colonization substrates, dense elk

Table II. Catchment and channel characteristics (±standard errors) associated with 8-km-long river reaches inside and outside Olympic National Park, western Olympic Peninsula.

Characteristic	Inside park			Outside park	
	Hoh River	Queets River	East fork Quinault River	Clearwater River	Lower Quinault River
Catchment area (km ²)	280	560	205	355	1070
Approximate elevation of reach (m)	180	45	150	30	10
Channel slope (m/m)	0.006	0.003	0.005	0.003	0.001
Active channel width (m)	184 (±15)	155 (±9)	74 (±7)	43 (±2)	82 (±4)
Wetted width of river (m)	52 (±2)	60 (±3)	28 (±2)	31 (±2)	56 (±2)

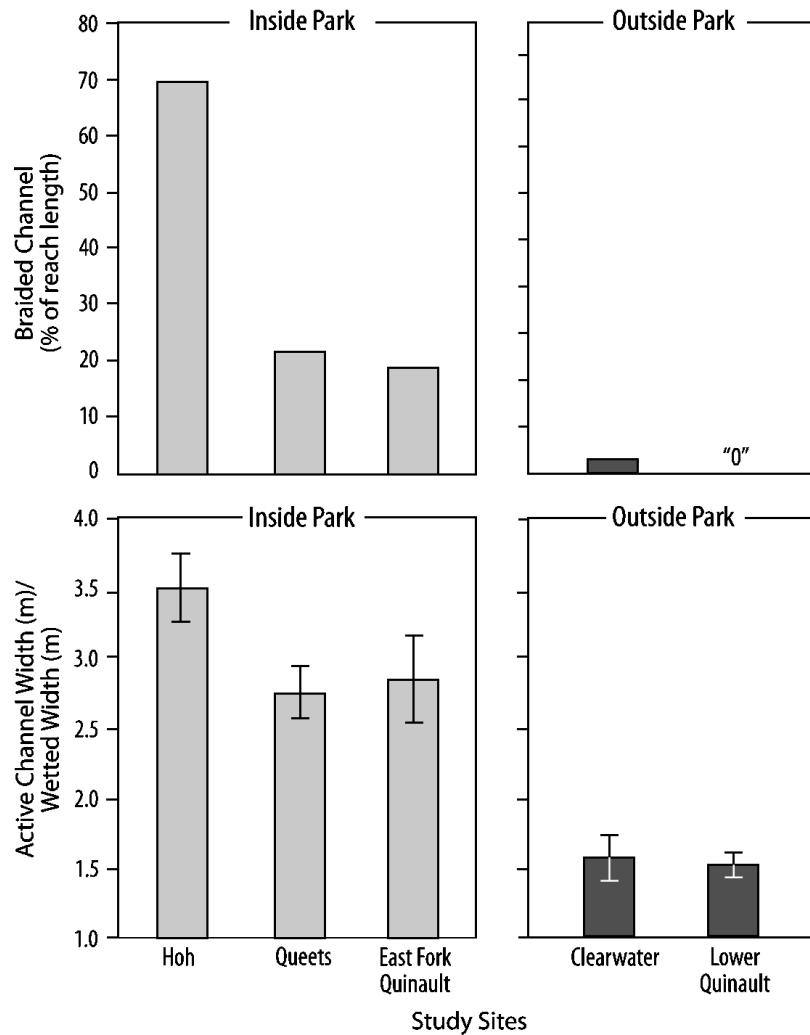


Figure 7. Proportion of reach length with braided channels (upper panel) and ratio of active channel width/wetted width (\pm standard errors, lower panel) for 8-km-long reaches inside and outside Olympic National Park.

populations, and an absence of wolves throughout most of the 20th century. Data from Van Pelt *et al.* (2006) also indicate few bigleaf maple and western hemlock occurring in stands <90 years of age.

Schreiner *et al.* (1996) assessed understory patch dynamics in old-growth forest along the South Fork of the Hoh River and concluded that ungulate herbivory was an important factor shaping vegetation patterns in coastal coniferous forests. While undertaking riparian vegetation field measurements within the park, we often found grasses, an uncommon ground cover for coastal rain forests (Franklin and Dyrness, 1969) and an indicator of long-term herbivory in this forest type (Woodward *et al.*, 1994), comprising a large proportion of the understory plant communities (e.g. Figure 4).

Balian and Naiman (2005) observed that black cottonwood seed sources were readily available from older stands along the Queets River inside the park; however, they observed no regeneration on bare alluvial surfaces. They suggested that unfavourable conditions (intermittent summer floods) for seedling establishment or preferential browsing by ungulates limited black cottonwood regeneration in most years. While we were able to find seedling

plots (20 m²) at each of our three study sites within the park, the difficulty in locating such plots indicated a general scarcity of cottonwood seedlings. Furthermore, the low densities and small stature of seedlings at these locations, as well as observed elk tracks, indicated that seedlings were sustaining high rates of herbivory. In contrast, greater seedling densities and a full range of seedling heights (1–200 cm) occurred at the lower Quinault site. Elk tracks were not observed at this site, perhaps reflecting tribal hunting pressure, nearness to human activities (roads, boat landing), and lower elk densities. On Indian reservation lands in Wisconsin, Alverson *et al.* (1988) found that year-round hunting sufficiently influenced ungulate browsing such that recruitment of palatable tree species continued to occur, whereas tree recruitment on adjacent National Forest lands, with more limited hunting, was adversely affected by ungulate browsing.

Widespread cottonwood establishment along river systems in North America is often associated with the occurrence of large peakflows that create sites (bare alluvial substrates without competing vegetation) conducive to both seed germination and seedling survival (Braatne *et al.*, 1996). Over the last several decades of

the 20th century, the Hoh River frequently experienced annual peakflows with recurrence intervals ≥ 10 years (Figure 6), yet our results indicate a lack of cottonwood recruitment during those decades [Figure 5(a)]. While high flows have occurred throughout the period of record for the Queets and Quinault Rivers, these hydrologic events also appear to have had little influence on temporal patterns of cottonwood recruitment inside the park. Furthermore, the strongly contrasting age structure of cottonwood at the three sites inside the park versus the refugia site outside the park indicate that peakflow regimes are unable to explain the paucity of cottonwood recruitment within the park's riparian systems.

With regard to bigleaf maple seedlings, disturbances that create over-story canopy gaps or generally reduce canopy densities provide important opportunities for continued height growth of bigleaf maple seedlings (Fried *et al.*, 1988). While coastal areas of the western Olympic Peninsula experienced widespread blowdown from the Columbus Day windstorm of 12 October 1962 (Lynott and Cramer, 1966), our age-structure results for bigleaf maple showed that recruitment was exceptionally low during the 1960s [Figure 5(b)].

In the Rocky Mountains, high levels of herbivory have been found to prevent recruitment of aspen (*Populus tremuloides*) following disturbance by fire (Hessl and Graumlich, 2002; Beschta and Ripple, 2007). Similarly, our age-structure data for cottonwood and bigleaf maple indicated that high levels of browsing over time have 'de-coupled' the expected recruitment of woody species that often occurs after disturbance (e.g. high flows for black cottonwood, gap openings for bigleaf maple). The general failure of palatable tree and shrub species to grow above the browse level of elk following wolf extirpation represents a major shift in the long-term structure and diversity of riparian plant communities that would normally occupy floodplains and terraces within Olympic National Park. As a consequence, low palatability tree species such as red alder and Sitka spruce are likely to increasingly dominate forest succession of the park's floodplains and transitional fluvial terraces (e.g. Van Pelt *et al.*, 2006).

Elsewhere in western North America, recent studies have increasingly linked declining recruitment of woody tree and shrub species to large predator removals or reductions. These studies include, for example, the (1) extirpation of wolves in Yellowstone National Park (Ripple and Larsen, 2000; Ripple and Beschta, 2004; Beschta, 2005; Beyer *et al.*, 2007), Banff National Park (Hebblewhite *et al.*, 2005), and Jasper National Park (Beschta and Ripple, 2007), (2) reduced cougar populations on the Kiabab Plateau (Binkley *et al.*, 2005), in Zion National Park (Ripple and Beschta, 2006), and in Yosemite National Park (Ripple and Beschta, 2008), and (3) extirpation of the large carnivore guild in Wind Cave National Park (Ripple and Beschta, 2007). We thus suggest that a truncated trophic cascade in western Olympic National Park (resulting from the loss of an apex predator), provides a plausible explanation for the changes in

riparian plant communities that have been ongoing over a period of many decades.

River channel dynamics

Diary accounts, historical photos, and survey maps of the late 1800s/early 1900s provide indications of riparian vegetation and channel morphology along the rivers of the Olympic Peninsula, prior to the availability of aerial photography in the late 1930s. For example, the Press Expedition of 1890 (Lien, 2001) found riverbanks along the Quinault River (upriver of Quinault Lake) to be 'so dense with underbrush as to be almost impenetrable'. They also observed that the river contained accumulations of driftwood (log jams) sufficiently frequent and large such that the river could not be floated. Davidson and Barnaby (1936) reported that early settlers described the upper Quinault River as a large stream that flowed 'between two rather narrow heavily wooded banks'. Today, over a century later, the situation is quite different. Understory shrub communities along floodplains and transitional fluvial terraces of the Hoh, and Queets, and Quinault Rivers inside the park are often sparse and easy to walk through (Figure 4), vertical eroding banks are common [Figure 8(b)], wide expanses of unvegetated river gravels are present and easily traversed [Figure 8(c)], and, while conducting field research during the summers of 2005–2006, we observed that accumulations of wood along these rivers seldom constituted a barrier to floating downriver.

Cadastral survey maps of 1887 and 1909 of the 'upper Quinault River' (from Lake Quinault upriver to the confluence of the North and East Forks) indicate a narrower active channel than seen on the 1939 aerial photos (Bountry *et al.*, 2005). O'Connor *et al.* (2003) compared channel migration rates over approximately the last 100 years for the Queets River (inside the park), the upper Quinault River (bordering the park), and the lower Quinault River (outside the park). They found that both the Queets and upper Quinault River had greater channel migration rates and wider active channel widths than the lower Quinault River. In a geomorphic assessment of the Hoh River, Piety *et al.* (2004) compared river reaches within the park to those immediately downriver of the park. While the downriver reaches had been logged at least once since 1939 (the year of the first available aerial photos), results indicated that reaches within the park experienced higher channel migration rates, wider active channels, greater braiding, and more frequent shifting of channel locations than those outside the park. Our results regarding braiding and active channel widths of contemporary channels are consistent with the geomorphic assessments of historical channels by O'Connor *et al.* (2003); Piety *et al.* (2004), and Bountry *et al.* (2005).

Latterell *et al.* (2006) characterized temporal patterns of loss (erosion) and establishment (deposition) for geomorphic surfaces along the Queets River inside the park. Analysis of aerial photographs since 1939 indicated a

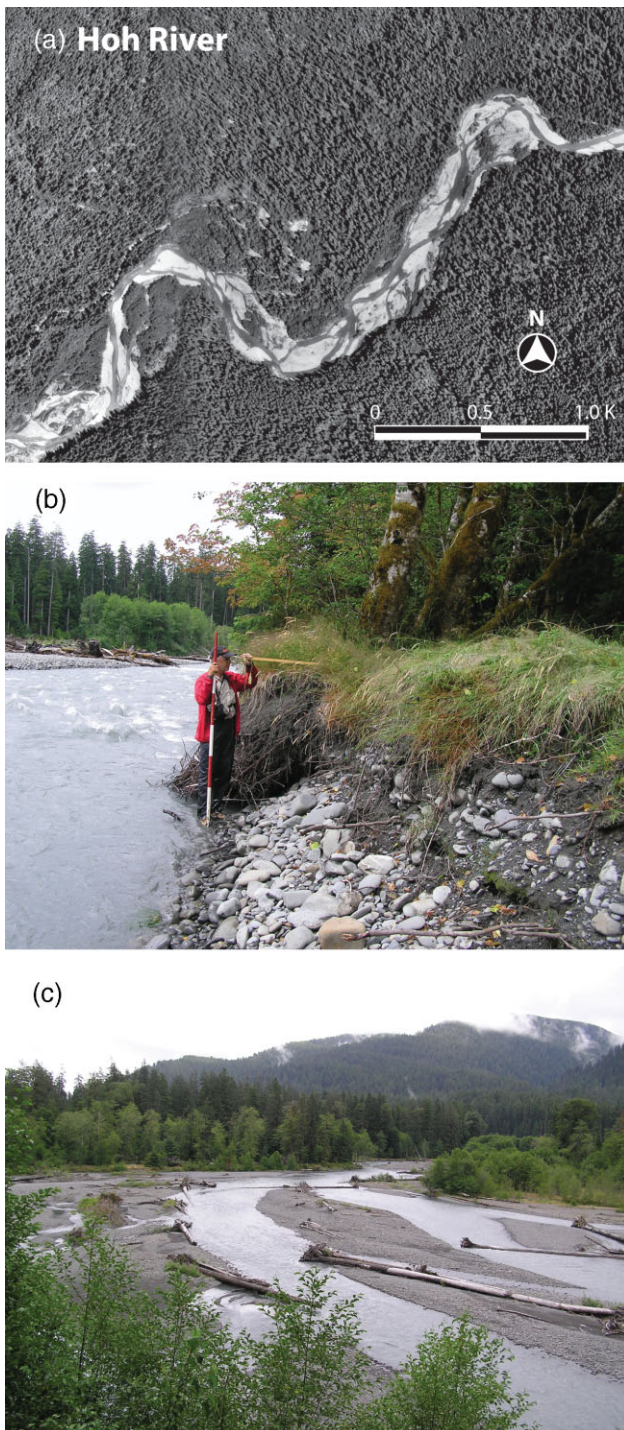


Figure 8. (a) A 1994 orthophoto showing the Hoh River and its active channel along a portion of the Hoh River study site (Olympic National Park visitor centre is located on the north side of the river near photo centre). (b) Transitional fluvial terrace 1.8-m high (above water surface) along the north side of the Hoh River near the visitor centre. The bank is comprised of coarse gravel/cobble in the lower 1.2 m grading to sand in the upper 0.6 m. Lateral erosion of these vertical banks during the periods of high flow causes large inputs of sediment and trees entering the river. (c) Upriver view of Hoh River from approximately 1 km downriver of the park service visitor centre showing a wide active channel with the large amounts of unvegetated alluvium, scattered large conifer logs, and young alders (a relatively unpalatable species) establishing on point bar (right side of photo).

mean annual channel movement rate of 13 m/year with nearly half of the transitional fluvial terraces that were

present in 1939, and which normally support stands of black cottonwood and bigleaf maple such as evaluated in this study, had eroded within the last 60 years. Cumulative erosional loss of these terraces along the Queets River is expected to approach 90% within the next 140 years (Latterell *et al.*, 2006). Such rapid rates of terrace removal by the river indicate that this geomorphic surface will likely 'disappear' (erode away) before plant communities can undergo their normal progression to old-growth coniferous forests.

Once riverbank plant communities have become degraded, fluvial erosion of alluvium below the general root zone of floodplain vegetation can easily occur and contribute to channel widening and increased channel instability (e.g. braiding) (Millar and Quick, 1998). Thus, where native riparian plant communities along rivers have been significantly affected by intensive herbivory, riverbank erosion is an expected consequence. Furthermore, recent studies have begun to connect the loss of large carnivores, via trophic cascades, to increased river erosion and channel instability. For example, following the extirpation of wolves in southwestern Montana, increased browsing by elk along the upper Gallatin River caused riparian willow (*Salix* spp.) communities to decline (Patten, 1968) followed by increased active channel widths and channel incision (Beschta and Ripple, 2006). Such changes in channel morphology effectively decrease the hydrologic connectivity (occurrence of over-bank flows) that is important for maintaining hydrophytic vegetation along riverbanks and on floodplains (Chapin *et al.*, 2002). In southern Utah, reduced cougar populations allowed mule deer (*O. hemionus*) to heavily forage upon riverside vegetation (Dixon and Sumner, 1939), thus causing greater bank erosion and significantly wider channels relative to those in adjacent catchments where cougar populations remained intact (Ripple and Beschta, 2006).

High rates of lateral channel migration during the 20th century indicate that large numbers of old-growth trees from eroding river terraces have been brought into the active channels of rivers within the park. However, Hyatt and Naiman (2001) found the half-life of large wood in the Queets River channel to only be ~ 20 years. Thus, large wood inputs from previous decades, when active channel widths were rapidly expanding (Latterell *et al.*, 2006), have likely been largely lost from this river (buried, decayed, or exported to the ocean). While large wood is currently present within the active channels of the park's rivers, during our field studies in late summer, we observed relatively few pieces of large wood in contact with water. Thus, contemporary large wood loads may be having limited influence on rearing habitat for anadromous and resident fish. If the slowing rate of cumulative erosion that has been measured for transitional fluvial terraces along the Queets River (Latterell *et al.*, 2006) is also indicative of that for comparable terraces along the Hoh and East Fork Quinault Rivers, this situation may presage a downturn in the rates at which large wood becomes available to the park's river channels during the coming decades.

A recent review of invertebrate studies (Baxter *et al.*, 2005) indicated that the riparian zones and adjacent rivers are connected by reciprocal fluxes of invertebrate prey. For example, flows of terrestrial invertebrates to streams can provide up to half the annual energy budget for drift-feeding fishes such as salmonids while the emergence of adult insects from rivers can constitute a substantial component of the energy needs of riparian consumers such as birds, bats, and spiders. In Olympic National Park, it is likely that such linkages have been increasingly fragmented along the reaches that currently support wide expanses of bare alluvium and where low-flow channels are often no longer adjacent to the riparian forest [Figure 8(a) and (c)].

CONCLUSIONS

Recruitment of black cottonwood and bigleaf maple within Olympic National Park was ongoing in the 1800s and early 1900s prior to the extirpation of wolves. Following the removal of this apex predator, and in the absence of human hunting, the collective results of this and other vegetation studies associated with the park's highly productive riparian forests indicate that the recruitment of palatable trees and shrubs have declined. This outcome is consistent with trophic cascades theory (Ray *et al.*, 2005), whereby a loss or reduction of large carnivore predation may initiate changes in herbivore densities and altered foraging behaviour that 'cascade' to lower trophic levels. Various lines of evidence further indicate that the channels within the park have significantly changed since the early 1900s. Once riverbank vegetation was heavily browsed and could no longer effectively function, accelerated bank erosion began and rapid widening of the active channel appears to have followed as rivers eroded their floodplains and ancient fluvial terraces.

In retrospect, perhaps Sumner (1938) best understood what was happening and what would happen to the park's riparian plant communities in the absence of the peninsula's apex predator (hypothesis #1), when he surmised 'unless some substitute for this now absent controlling factor (wolves) is provided, serious destruction of certain plants and even their total elimination in certain places through inability to reproduce will no doubt occur'. What Sumner apparently could not foresee was that the impacts to riparian plant communities associated with a truncated trophic cascade could also have major ramifications to the character of rivers draining the park (hypothesis #2). A shift from single-thread to braided channels, increased active channel widths, and a reduced ecological effectiveness of contemporary large wood loads within rivers draining the western portion of the park may represent some of the continuing geomorphic and ecological consequences of wolf extirpation nearly a century ago.

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