

Plant community succession following ungulate exclusion in a temperate rainforest

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Abstract. Ecosystem structure and processes of coastal temperate rainforests of the Pacific Northwest are thought to be strongly influenced by herbivory primarily of Roosevelt elk (*Cervus elaphus roosevelti*) and secondarily of Columbian black-tailed deer (*Odocoileus hemionus columbianus*). Two large (0.5-ha) exclosures were built in old-growth coniferous rainforest communities in Olympic National Park, Washington, during 1979 to study these effects. Cover of shrubs, ferns, herbs, and graminoids and numbers of tree seedlings were described over 36 yr. Results show a sequence following ungulate exclusion of early release of shrubs, ferns, and herbs followed by eventual dominance of shrubs as other vegetation layers become shaded. Short-term responses of individual species reflected functional traits related to ability to avoid or tolerate herbivory. Over the longer term, effects reflected changing competitive relationships among vegetation layers and other ecosystem dynamics such as the provision of fallen trees in the appropriate decay class to serve as establishment substrate for tree seedlings. In aggregate, vegetation composition shifted after 36 yr from a system dominated by herbaceous cover with a major graminoid component to one dominated by shrubs (5- to 6-fold absolute increase) and ferns (5–7% increase in absolute cover), less absolute herb cover (15–20% loss), and almost no graminoids (<1.5% cover remaining in any plot) after 36 yr. These changes represented a substantial loss in plant community diversity with a loss of 46 of 74 species. Elk abundance outside of the exclosures began to decline in the 1990s leading to parallel changes in plant community trajectories outside of exclosures to those initially seen inside. While this suggests plant community responses inside the exclosures were also driven by elk exclusion, the strength of this response depends on elk abundance.

Key words: biodiversity; Columbia black-tailed deer; forest succession; herbivory; Olympic National Park; Roosevelt elk; Sitka spruce; ungulate exclosures; western hemlock.

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INTRODUCTION

As in other ecosystems with large ungulates, ecosystem structure and function of coastal temperate rainforests of the Pacific Northwest are thought to be strongly influenced by herbivory. Ungulates have consequences for forest structure, nutrient cycling (Hobbs 1996, Persson et al.

2000), and habitat for other species (Rooney and Waller 2003). Ungulate herbivory directly affects plants through biomass removal and trampling (Danell et al. 2003), and indirectly (Rooney and Waller 2003) through habitat alteration (e.g., changes in light, nutrient, and bare mineral soil availability [Hanley and Taber 1980, Hobbs 1996, Persson et al. 2000, Rooney and Waller 2003,

Mysterud 2006, Krueger et al. 2009]) and mediation of plant competitive interactions (Augustine and McNaughton 1998, Kuiters and Slim 2003). Moreover, plant species are differentially susceptible to herbivore damage based on palatability (Hanley 1997), physical structure (Diaz et al. 2001), and ability to recover from herbivore damage (Coley et al. 1985, Oesterheld and McNaughton 1991, Augustine and McNaughton 1998, Danell et al. 2003, Rooney and Waller 2003). At larger spatial extents, the density and social organization of ungulate populations and their temporal and spatial migration patterns (White et al. 2003) plus plant community distribution and availability of refugia from herbivores (Schreiner et al. 1996) determine the landscape pattern of plant community composition (Weisburg and Bugmann 2003). Over long time periods, herbivory interacts with other drivers such as succession, climate, and disturbance (Hobbs 1996, Wisdom et al. 2006). Consequently, the complexity of driver interactions and temporal variability hamper prediction of ecosystem response to changes in herbivore density and can result in contradictory outcomes (Milchunas and Lauenroth 1993, Rooney and Waller 2003, Schutz et al. 2003, Singer and Schoenecker 2003). Discerning the unique role of herbivory from other ecosystem drivers has proved daunting in forests and other biomes.

Ecologists have long used fenced exclosures to examine the influences of grazing and trampling by large herbivores on vegetation composition and processes (Hester et al. 2000). Yet despite an extensive application of ungulate exclosures (Milchunas and Lauenroth 1993), significant methodological problems make the interpretation of their results equivocal. Many exclosure studies have used plots too small to examine large-scale phenomena and to minimize edge effects such as the potential of fences to alter microclimate (Daubenmire 1940, Lodge 1954, Smoliak et al. 1972, McInnes et al. 1992). Many studies are also of too short duration to adequately describe ungulate–forest relationships (Wisdom et al. 2006, Pekin et al. 2014, Bernes et al. 2018). Another major limitation to the interpretation of results occurs when exclosure and control plots are not compared before and after treatment. This eliminates the possibility of testing whether the initial communities were similar.

In the few studies where such comparisons have occurred (e.g., Harlow and Downing 1970), differences that might have been assigned to the exclosure treatment were found to represent initial differences in spatial variation. Interpretation is further complicated by the enclosed area having a history of herbivory that may have altered species pools and seed banks, which can affect recovery. Hence, the results of ungulate exclusion will not necessarily describe a community without herbivore influence (Bergstrom and Edenius 2003, Rooney and Waller 2003). Finally, the treatment difference is usually unknown because exclosure studies compare zero herbivore density inside fences with a level outside that is often not quantified and quite possibly changing over time. Even if the level outside is known, it has been demonstrated that understanding the effects of herbivory on vegetation requires evaluating a range of herbivore densities rather than a binary comparison of zero vs. some herbivores (Endress et al. 2012, 2016). However, despite the complexity of plant responses in exclosure experiments, comparing exclosure and control plots through time can help identify the effects of initial conditions, exclusion of ungulates, and successional or cyclical changes. Hence, exclosures, if used properly, can provide a great deal of insight into the role of animals in controlling community structure (Hester et al. 2000, Bergstrom and Edenius 2003).

On the Olympic Peninsula, Washington, herbivory is predominantly due to Roosevelt elk (*Cervus elaphus roosevelti* Merriam) and secondarily to Columbian black-tailed deer (*Odocoileus hemionus columbianus* Richardson). Elk numbers and distribution have varied due to changing human activities since at least the arrival of European settlers late in the nineteenth century (Houston et al. 1990, Jenkins and Happe 2018). Hunting regulations for elk since this time have ranged from no restrictions to a total moratorium; moreover, changes in levels of predator control, intensity of logging, and the establishment of Olympic National Park as a protected area have led to fluctuations in elk density and a long history of debate over the level of elk browsing that is “healthy.” Concern that elk herbivory was damaging forest vegetation arose in the 1930s as the elk population rebounded due to protection from hunting and decline in predators

beginning at the turn of the 20th century (Schwartz and Mitchell 1945). Grazing and browsing pressure from ungulates has remained high under protection from hunting in Olympic National Park since 1938, resulting in periodic debate over the appropriateness of current browsing levels relative to poorly understood historical conditions that preceded EuroAmerican settlement (Jenkins and Happe 2018). Perceptions of “overbrowsing” by ungulates that prevailed in the 1930s gradually gave way to the perspective that elk densities had diminished by the late 1950s reflecting an ecologically acceptable equilibrium between elk numbers and vegetation conditions (Newman 1958, reviewed in Jenkins and Happe 2018). Recent evidence that elk browsing has likely affected recruitment of riparian tree species has rekindled the “overbrowsing” debate giving rise to the hypothesis that wolf extirpation has created a trophic cascade whereby elk numbers are adversely impacting river morphology through their negative effects on riparian forest vegetation (Beschta and Ripple 2008). This hypothesis is the subject of current ecological debate (Beschta and Ripple 2017, East et al. 2017, 2018) highlighting the need to better understand the role of elk in coastal forest ecology.

Ungulate exclosure studies have a long history in Olympic National Park (Schwartz and Mitchell 1945, Woodward et al. 1994). Twenty-five exclosures were built either in or adjacent to Olympic National Park in the 1930s and 1950s. Most were small (0.01–0.19 ha) and were measured regularly for 3–13 yr. Other published results from four exclosures built in forests of western Washington come from Hanley and Taber (1980). These exclosures also were small (0.01–0.06 ha) and were established in clear cuts of various ages, post-cut treatments, and ungulate use. Whereas the methodology employed in these collective studies would no longer be considered adequate, together these studies indicate that ungulate herbivory results in an increase in graminoids, a decrease in shrubs, and either gains or losses in tree seedling density dependent on tree species.

More recently, two large (0.5-ha) exclosures were built in an old-growth coniferous forest ecosystem in Olympic National Park, Washington. Happe (1993) studied these exclosures and

found that intensive herbivory increased biomass and nutrient concentration, thereby creating a better foraging environment on an annual basis in grass-dominated understory patches analogous to the “grazing lawn” described by McNaughton (1984) within the forest environment. Schreiner et al. (1996) described short-term (8-yr) changes in understory patch dynamics in response to ungulate exclusion. In this study, we report long-term vegetative changes spanning 36 yr. The study design improves on previous exclosure studies by using exclosures large enough to minimize edge effects and include gap dynamics, siting them in representative rather than heavily used areas, and describing plant communities both inside and outside exclosures at the onset of the study. We also measured overstory and understory plant responses over multiple decades, and we had access to data estimating elk abundance for much of the measurement period, which provided the opportunity to assess vegetation changes associated with changes in elk density concomitantly both inside and outside the exclosures. Thus, our objective was to describe immediate and long-term changes in plant community structure, including phenomena such as seedling establishment and growth that require years to manifest along with changes in community trajectory due to changing relationships among plant species. We recognized that the ecosystem is hierarchical with elk numbers acting on a forest template that is ultimately driven by climate, succession, and episodic disturbance. A long time series of measurements is required to capture the effects of dynamic factors and a changing context of treatment and control plots. While many exclosure studies have focused on specific species or species groups (e.g., key browse species or management targets, but see Pekin et al. 2015), our study encompassed the entire plant community over the long term and necessitated broadly stated hypotheses and predictions aimed at improving understanding of community-level changes related to variations in ungulate herbivory levels.

1. The initial response of vegetation will reflect direct elk effects (i.e., biomass removal and trampling), plant vulnerability to herbivore effects (e.g., palatability, plant physical characteristics), and plant ability to recover (e.g.,

- growth rate, locations of meristems and reserves). Consequently, we expect differential responses of individual species and species groups that can be explained by these characteristics.
2. Over the long-term, responses will reflect indirect effects of elk on plant competitive interactions, both among species and species groups, due to differences in plant size, community structure, substrate availability, and species tolerances to grazing, shade, and limits of resources.
 3. The strength and/or nature of system drivers, including ungulate density, will vary over time independent of exclosure treatments and be reflected in vegetation structure so that results must be interpreted relative to a changing ecological context.

STUDY AREA

We studied long-term trends in vegetation associated with two exclosures in the South Fork Hoh River in Olympic National Park, Washington ($47^{\circ}47'$ N latitude, $123^{\circ}56'$ W longitude, Fig. 1). Exclosures were built within two 2.0-ha plots that were established on two different elevational levels of alluvial terrace, hereafter called the upper and lower terraces. These plots were intensively studied the year before exclosure construction (Franklin 1982). The lower terrace corresponds to surface "4," the upper terrace corresponds to surfaces "5" and "6" of Swanson and Lienkaemper (1982). Elevations are 313 and 319 m for the upper and lower exclosures, respectively.

The climate is maritime characterized by relatively mild temperatures and abundant rainfall. Total precipitation averages 355 cm/yr with 75% falling between November and April. Mean temperatures fluctuate between 8° and 27°C in summer and between -2° and 4°C during winter, with a mean annual temperature of 8.9°C . Annual potential evapotranspiration (PET) and annual actual evapotranspiration (AET), using the method of Pastor and Post (1984), are 537 and 524 mm, respectively.

Soils on the lower terrace are of the Hoh series (McCreary 1975), whereas soils on the upper terrace are more developed and are of the Queets

series. Both soil series are Typic Dystrochrepts that are strongly acid (pH 4.0–4.4) and moderately well-drained silt-loams (Fonda 1974, McCreary 1975). The winter water table for both terraces averages 1–2 m below the soil surface (McCreary 1975), although surface water occurs in areas of both terraces during winter.

The forests at both exclosure sites are within the *Picea sitchensis* Zone (Franklin and Dyrness 1973) and typical of those on alluvial terraces approaching the climax stage of succession (Fonda 1974). The structure and age of the communities within the two plots have been summarized by McKee et al. (1982). The lower forest was relatively open in overstory structure compared to the upper terrace and was dominated by *P. sitchensis* (Bong) Carr. (Sitka spruce) and *Tsuga heterophylla* (Raf.) Sarg. (western hemlock), with basal area of $66.3\text{ m}^2/\text{ha}$, a density of 64 trees $>5\text{ cm}$ diameter at breast height/ha, and a maximum age of 205–258 yr. In contrast, the forest overstory on the upper terrace was denser with *P. sitchensis*, *T. heterophylla*, and scattered *Pseudotsuga menziesii* (Mirbel) Franco (Douglas-fir) and *Thuja plicata* Don ex D. Don (western red cedar). Basal area, stem density, and ages were $81.1\text{ m}^2/\text{ha}$, 142 trees $>5\text{ cm}$ diameter at breast height/ha, and 220–266 yr, respectively. Under-story composition also differed between the two terrace levels, with the lower terrace dominated by the shrub *Acer circinatum* Pursh (vine maple), herbs, and graminoids. The upper terrace was dominated by the shrubs *Vaccinium alaskaense* Howell (Alaskan huckleberry) and *Vaccinium parvifolium* Smith (red huckleberry), plus herbs, ferns, and mosses.

Roosevelt elk and Columbian black-tailed deer are the dominant large mammalian herbivores in the Olympic rainforests. We focus on elk because of their greater ecological impact due to their greater numerical abundance and body size (Leslie 1983). Historical data (summarized in Schwartz and Mitchell 1945, Taber and Raedeke 1980, Jenkins and Happe 2018) suggest elk were plentiful over the Olympic Peninsula until the late 1890s when rapid settlement and a subsequent increase in hunting greatly reduced elk population levels. By 1905, elk numbers were so low on the Peninsula (as few as 1800–2000 elk) that a 10-yr moratorium on elk hunting and a bounty system for wolves and cougars were

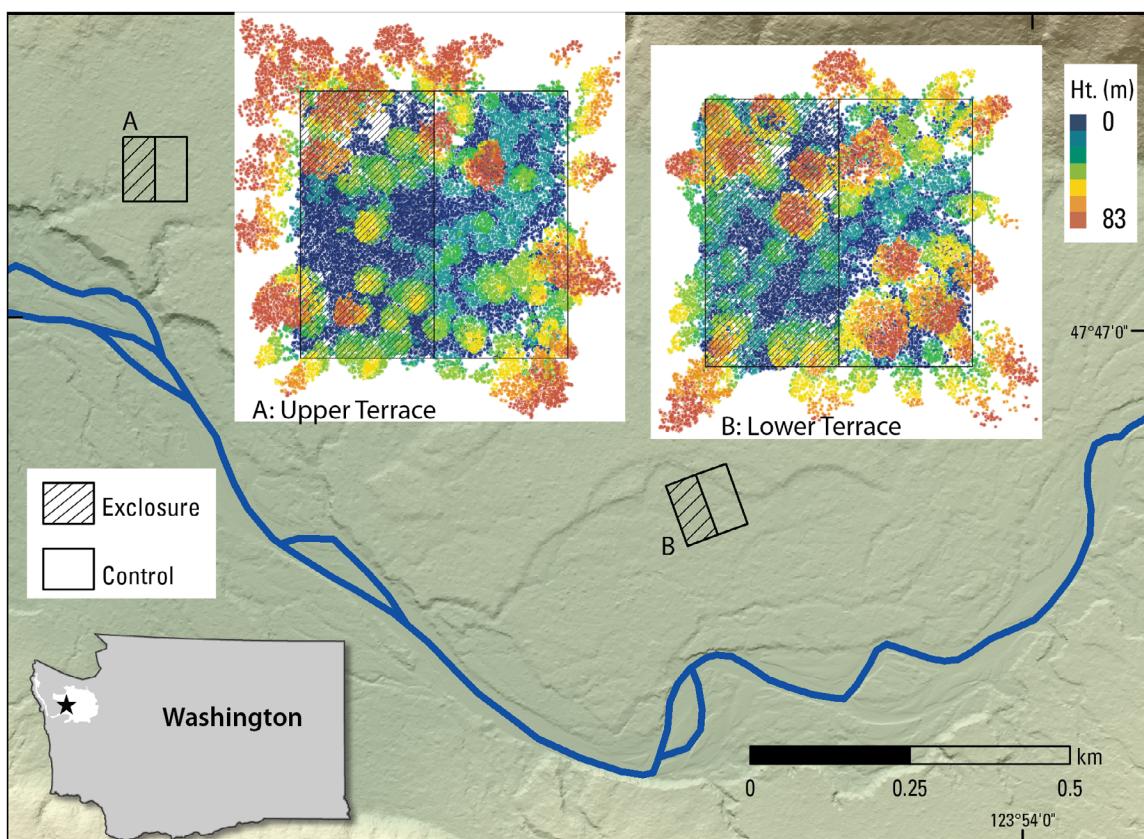


Fig. 1. Study plot locations on South Fork Hoh River, Olympic National Park, Washington, and lidar-based images (2012) showing canopy structure.

established by the Washington State legislature. In 1909, the Federal Government set aside Mount Olympus National Monument and eventually Olympic National Park (1938) to protect elk and their habitat. Elk population response to these protective measures was sufficiently rapid (increasing to as many as 7000 elk in 1917) that heavy browsing and die-off of elk was reported due to severe winter weather during the 1916–1917 winter (Schwartz and Mitchell 1945). Overbrowsing was still evident in the Hoh valley in the 1930s (Sumner 1938, Schwartz and Mitchell 1945) but elk seemed to be in balance with range conditions by the 1950s (Sumner 1952, Newman 1958). Elk populations appeared to be relatively stable in Olympic National Park from the 1950s through the 1980s, with most estimates of the Park's population ranging from 3000 to 4000 elk during summer (Houston et al. 1990, Jenkins

and Happe 2018). In the late 1980s, Houston et al. (1987) estimated elk density in the South Fork Hoh Valley to be 12 elk/km², or about 100 elk, when elk were most concentrated on the alluvial floodplains during spring green-up.

METHODS

Exclosures

Two 0.5-ha exclosures were constructed during the summer of 1979, each within one of the 2.0-ha study plots established on each of two alluvial terrace levels. Each exclosure was paired with an adjacent 0.5-ha control area to create four subplots: upper terrace in and out of exclosure (UTIN, UTOUT) and lower terrace in and out of exclosure (LTIN and LTOUT). Each exclosure was 50 × 100 m (0.5 ha) and 3 m tall. Wooden posts 10 × 10 cm were placed in the ground at

4-m spacing to support the galvanized wire fence which had 10 × 20-cm mesh. The exclosures were visited regularly during the study to repair damage caused by falling trees. For example, the upper terrace exclosure was damaged during the winter of 1986 and an elk was found inside before repairs were made. However, browsing caused by this episode appeared to be minimal. Over the years, additional repairs were occasionally needed.

Tree regeneration and understory sampling

Field crews measured tree reproduction, and woody and non-woody understory plant cover along 4, 50-m-long transects within each of the exclosures and paired subplots. The location of these transects was marked at 12.5-m intervals with wooden stakes during 1981 to reduce errors in relocation. Eventually, these were replaced with 1.5-m tall white polyvinyl chloride (PVC) pipe. Initial sampling was conducted in April 1980, but these data were not analyzed because plants had not yet full expanded. Subsequent sampling occurred in early June to mid-July in 1980–1984, 1986, 1988, 1992, 1996, 2007, and 2016. Sampling was timed to correspond with peak understory biomass.

Crews estimated cover of all herbs and small-stature shrubs within 25, 20 × 50 cm microplots systematically spaced at 2-m intervals along each 50-m transect. Six cover classes were used: (1) present but <5%, (2) 6–25%, (3) 26–50%, (4) 51–75%, (5) 76–95%, and (6) 96–100% (Daubenmire 1959). These classes were converted to cover values by using the midpoint of each class (e.g., class 1 equaled 2.5% cover). All vascular non-woody plants were identified to species level when possible. From 1980 to 1983, cover for mosses and liverworts was combined; thereafter, the cover of common bryophyte species was estimated separately. In 1982, indications of standing water and canopy directly overhead within a 10° sector was noted for each microplot.

We estimated shrub cover along each of the 50-m transects by the line intercept method. The point at which shrub species started and stopped covering the transect was recorded. In the case of *A. circinatum* Pursh (vinemaple), it was difficult to judge consistently whether a plant was a small tree or in the shrub category. Therefore, we excluded from the analysis large patches that

appeared to have been inconsistently remeasured. The mean percent of transect length for each shrub species at each time for each treatment was used in the analysis.

We measured the abundance of *T. heterophylla* and *P. sitchensis* seedlings (i.e., tree regeneration) within 1 × 50-m belt transects established along the shrub and herb transects. Seedlings >10 cm tall but less than 5 cm diameter at breast height (dbh) were tallied in six height classes: (1) 10–25 cm, (2) 26–50 cm, (3) 51–75 cm, (4) 76–100 cm, (5) 101–150 cm, and (6) >150 cm. The smallest height class (10–25 cm) represents established regeneration that survived the first few years of high mortality. We used this class as an indicator of seedbed availability. We computed the mean density of each species and size class, and total seedling density for each time and terrace-exclosure treatment. Enumeration of trees >150 cm tall and 5 cm dbh is described in "Tree measurements" section.

Tree measurements

Periodically during the study, field crews inventoried the live trees present in each of the 2.0-ha study plots (data website). Live trees >5 cm dbh were individually tagged with uniquely numbered aluminum tags. During each inventory, the status of tagged trees was assessed (i.e., live vs. dead) and dbh was determined. When trees <5 cm dbh in 1978 grew sufficiently to be counted, they were tagged as ingrowth and followed as with previously tagged trees. Total live trees at the time of an inventory were the sum of the trees surviving the previous period and the new ingrowth at the time of the inventory. Data are available from Franklin et al. (2020).

Statistical analysis

Although the study was originally conceived as a split-plot experimental design, we found that many of the assumptions for this type of analysis were not met. Specifically, initial differences in vegetation composition between terraces and between plots at each terrace meant that plots were not truly replicates. Also, trends in elk numbers outside of exclosures caused "control" conditions to vary over time. Moreover, the sample size of two sites is insufficient to generate sufficient statistical power. Consequently, we chose

to interpret changes in absolute and relative cover of plant species groups and selected species based on graphical representations of time series rather than analysis of variance. This approach exemplifies the observation of Hobbs (2003) that achieving traditional statistical power is often not feasible when collecting plot data to describe large spatial extents. Nevertheless, the usefulness of the study to inform policy and management is also a valid reason to value the study.

We examined distributions of understory plants along environmental gradients using detrended correspondence analysis implemented using the “vegan” package in R (R Core Team 2018), which uses the DECORANA methodology (Hill 1979a). Results are expressed using axes scaled in units of average standard deviation of species turnover; a change of 1 standard deviation is roughly equivalent to a 50% change in species composition. We used the mean cover of all understory species (herbs and shrubs) measured in understory microplots at each sample period for each of the two terrace and two exclosure treatments. Cover of individual moss and liverwort species from the 1984, 1986, and 1988 samples were combined into an overall moss category. *Acer circinatum* was excluded because it was not consistently measured. The only observation of *Agrostis stolonifera* L. (creeping bentgrass) was combined with *Poa trivialis* L. (rough bluegrass) because it appeared that *A. stolonifera* was misidentified. The importance of rare species was down weighted in the ordination using the default method. All other ordination options (i.e., rescaling axes, transformation, number of segments) were run on default settings.

Due to differences in canopy openness and soil moisture, several distinct communities occurred in each subplot. We used TWINSPAN, a divisive classification algorithm, to identify community types present the summer after exclosure construction in the June 1980 microplots ($N = 400$) (Hill 1979b). We excluded shrub species from the analysis because their high cover in individual microplots (cover class 6) made them distinctive regardless of the other species present. We also excluded most mosses as their abundance was high in all the microplots. However, we found that *Sphagnum girghensohnii* Russow abundance corresponded to one of the community types;

therefore, we used records of *S. girghensohnii* to assist in distinguishing that community. Although 4 divisions were used in the classification leading to 16 community types, only four were common enough to be used in the final classification. All other options (i.e., maximum indicators per division, maximum number of species, weights of pseudospecies, and indicator potentials for cut levels) were run on default settings.

To help distinguish factors most associated with vegetation trends, we examined correlations between understory vegetation response and trends in annual precipitation, temperature, elk populations indices, and tree overstories. Trends in annual precipitation and temperature measured at the Clearwater weather station (GHCND:USC00451496, 47.571 N latitude, -124.292 W longitude, approximately 30 km from plots) were described using linear regression. We calculated Pearson correlation coefficients to compare values of ordination axes with potential drivers of vegetation change and cover of vegetation.

The National Park Service conducted helicopter surveys to index the relative abundance of elk in the South Fork Hoh valley annually from 1985–1988 and again in 1991, 1998, 2006, 2008, and 2010 (Jenkins and Happe 2018). We fit a logarithmic regression curve to describe the relative trend in elk abundance outside of exclosures. We examined correlations between the index of elk abundance (logarithmic scale) and cover of vegetation classes and selected plant species outside exclosures beginning in 1984. Because we were not sure which regression model was most appropriate to describe changes in elk abundance, we also tested linear regression and two spline regressions to describe the elk index and found that our conclusions were not affected by the regression model selected.

RESULTS

Plot environmental characteristics

Environmental data collected in 1982 (Table 1) indicate that lower terrace subplots generally had more open overstory canopy and greater frequency of standing water than upper terrace subplots, which had greater canopy cover. Greater evapotranspiration due to higher tree density on

Table 1. Environmental characteristics inside and outside of two ungulate exclosures in the South Fork Hoh Valley, Washington, established in 1979.

Subplot	Open canopy† (% microplots)	Humus cover‡ (% microplots)	Log cover§ (% microplots)	Standing water¶ (% microplots)	Tree density# (trees/ha)
LTIN	38	90	7	22	68
LTOOUT	30	84	14	17	84
UTIN	11	88	11	0	130
UTOUT	18	68	27	0	186

Notes: Subplot abbreviations are for inside lower terrace, LTIN; outside lower terrace, LTOOUT; inside upper terrace, UTIN; and outside upper terrace, UTOUT.

† Microplots classified as open vs. closed in 1982.

‡ Microplots with humus cover >50% in 1982.

§ Microplots with log cover >50% in 1982.

¶ Microplots having indications of standing water in 1982.

Live trees >5 cm dbh in associated tree plots in 1978 (Franklin et al. 2020).

the upper terrace (Table 1) may have created drier conditions there. Log cover was substantially higher in UTOUT than in other subplots, which may explain its slightly lower humus cover.

The four plant communities classified by TWINSPAN appeared to reflect environmental gradients of moisture and light (<https://doi.org/10.6084/m9.figshare.16563888>). The *Oxalis-Tiarella* community was associated with relatively drier conditions and a closed canopy. The *Poa-Athyrium* community occurred where evidence of standing water was absent, but where canopy cover was low. The *Maianthemum-Blechnum* community was associated with more open overstories and wetter sites than the *Oxalis-Tiarella* community. Standing water was most common in the *Lysichiton-Glyceria-Sphagnum* community and canopy conditions for this community appeared to be intermediate between open and closed.

Differences in light and water described for subplots (Table 1) were reflected in the abundance of plant community types (Table 2). The upper terrace was comprised mostly of microplots characteristic of the *Oxalis-Tiarella* community with microplots characteristic of *Maianthemum-Blechnum*. UTOUT also had some *Poa-Athyrium* microplots, corresponding to the higher “open canopy” in UTOUT vs. UTIN. The lower terrace was comprised of the most even distribution among microplots of all community types, including more of the wetter types, *Lysichiton-Glyceria-Sphagnum* and *Maianthemum-Blechnum*. The *Poa-Athyrium* community,

Table 2. Understory plant community distribution inside and outside of two ungulate exclosures in the south Fork Hoh Valley, Washington, June 1980, for exclosures established in 1979.

Subplot	Understory plant community (cover %)			
	<i>Maianthemum-Blechnum</i>	<i>Oxalis-Tiarella</i>	<i>Poa-Athyrium</i>	<i>Lysichiton-Glyceria-Sphagnum</i>
LTIN	34	23	24	18
LTOOUT	20	58	0	22
UTIN	17	83	0	0
UTOUT	10	63	27	0

Notes: Subplot abbreviations are as in Table 1. Plant communities are named by dominant species.

associated with lower canopy cover and less standing water, was only found in LTIN and UTOUT.

Tree regeneration

Abundance of the smallest height class of conifer seedlings (10–25 cm, Fig. 2c) declined in all plots during the study. Despite this apparent decline in seedbed availability across plots, *T. heterophylla* seedlings (>25 cm tall) increased numerically inside exclosures compared with outside (Fig. 2a), whereas *P. sitchensis* seedlings did not (Fig. 2b). High numbers for *T. heterophylla* persisted for most of the record. *P. sitchensis* increased and remained higher outside exclosures vs. inside. Regarding deciduous seedlings, a few *Malus fusca* (Raf.) C. K. Schneid. (Pacific crabapple) established inside of both exclosures by 1992. By 2016, three (LTIN) and

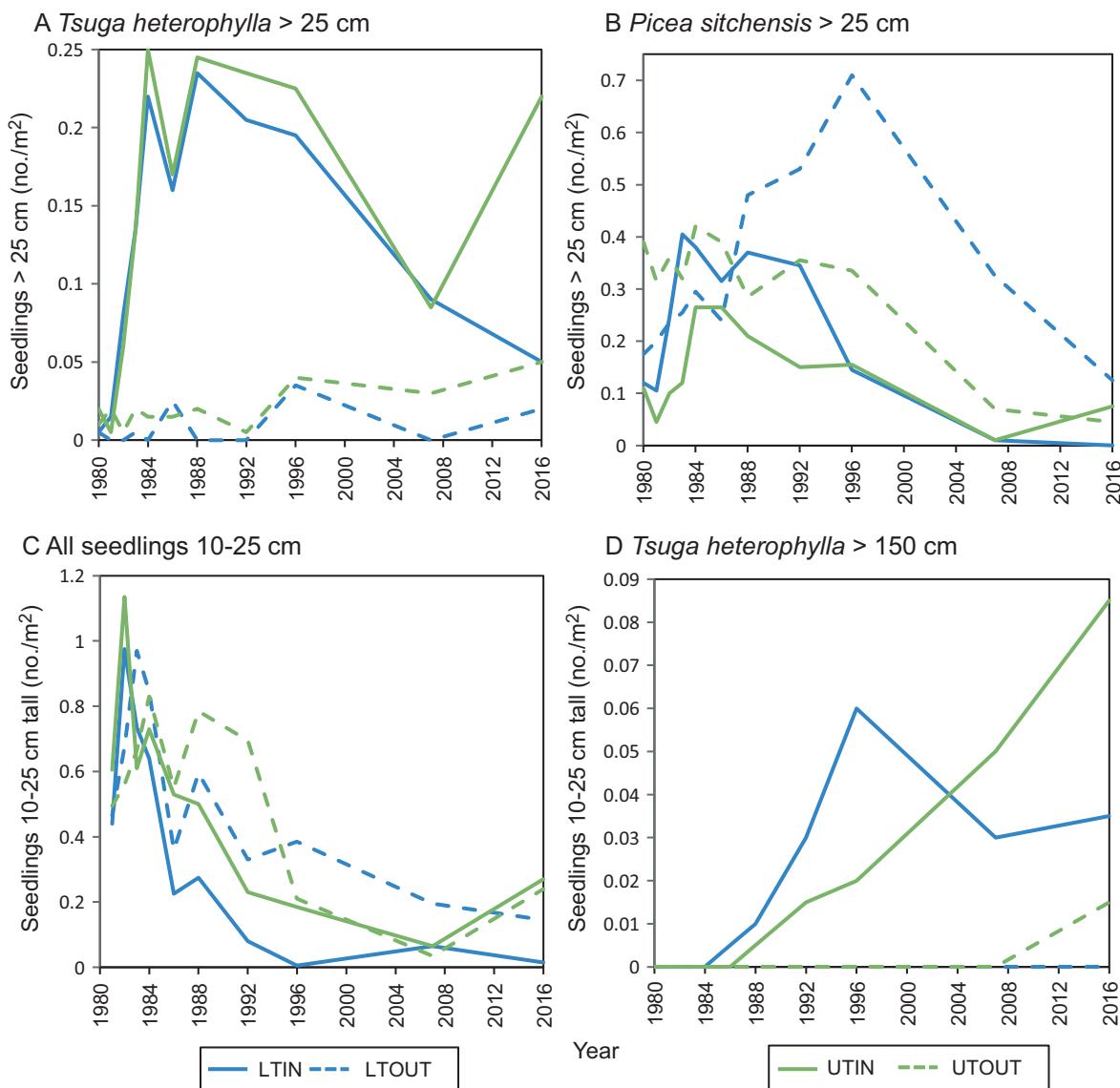


Fig. 2. Abundance of *Picea sitchensis* and *Tsuga heterophylla* seedlings in selected size classes over time since ungulate exclosure construction in South Fork Hoh valley, Washington. Abbreviations for subplots: LTIN, inside lower terrace exclosure; LTOU, outside lower terrace exclosure; UTIN, inside upper terrace exclosure; UTOU, outside upper terrace exclosure.

two (UTIN) individuals were greater than 150 cm tall.

Seedlings that exceed 150 cm in height are thought to be less vulnerable to mortality owing to elk browsing (Jacobs 1969, Ross et al. 1970) and therefore represent a long-term change in forest structure. Based on this metric, large *T. heterophylla* seedlings began to be abundant

enough to affect forest structure even if elk were allowed to return after approximately 15–20 yr (Fig. 2d).

Change in understory cover by plot

Cover of each vegetation layer (graminoids, herbs, ferns, and shrubs) initially increased inside both exclosures (Fig. 3). Shrub cover

(excluding *A. circinatum*) increased over 5-fold, reaching a peak approximately 15 yr following exclusion of ungulates and then stabilized after 1996. Cover of graminoids declined after 1983, whereas herb cover also declined after 1983, although more gradually than cover of

graminoids. Ferns also declined following elk exclusion but not noticeably until after 1988 (Fig. 3a, c). These patterns were somewhat obscured, however, by a good growing season in 1983 and an initial drop in cover of shrubs, graminoids, and herbs from 1980 to 1981 in LTIN.

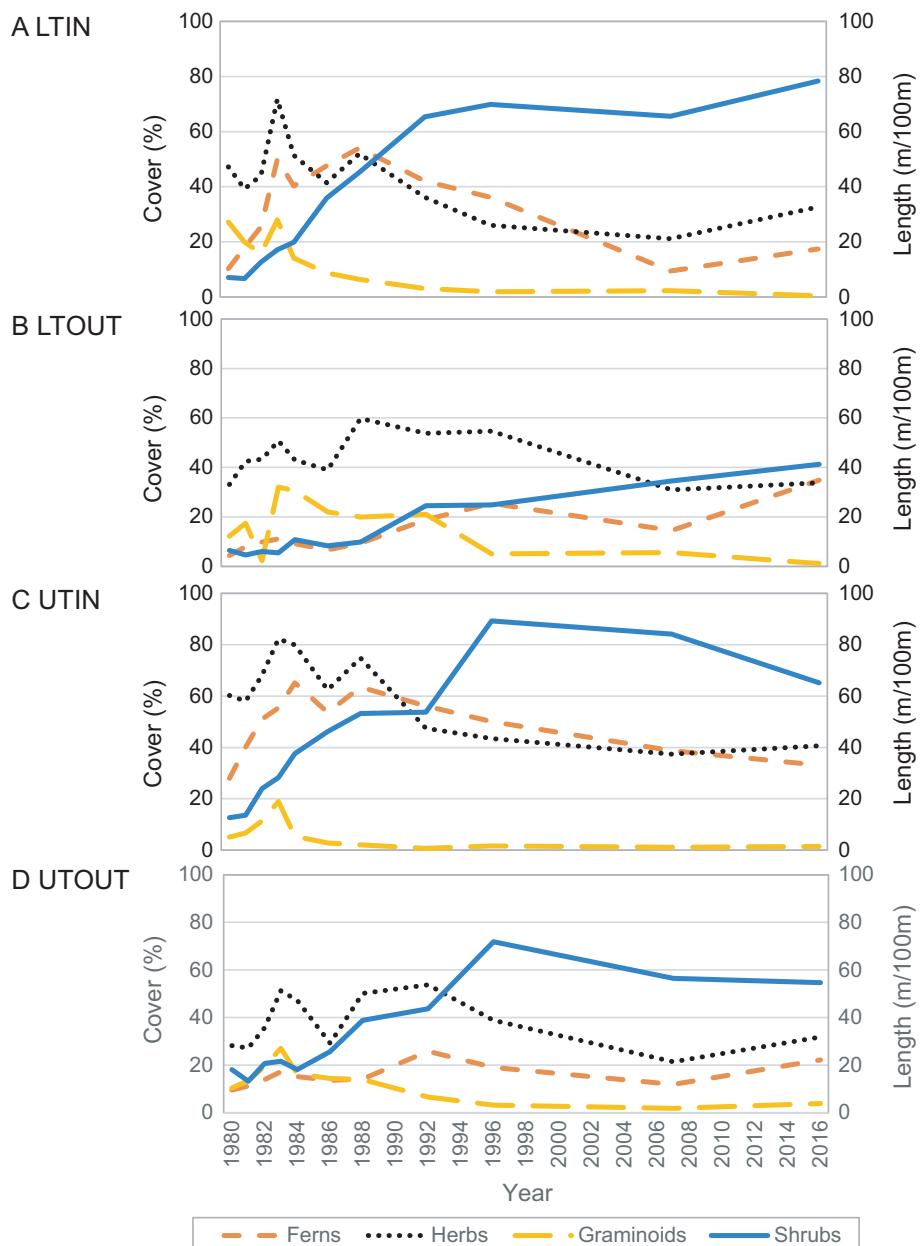


Fig. 3. Cover of vegetation layers by subplot inside and outside of two ungulate exclosures in the South Fork Hoh valley, Washington. Units for shrubs are m/100 m of line intercept transect length; all others are cover (%). Abbreviations for subplots: same as Fig. 2.

These irregular patterns of annual variation were possibly due to a combination of measurement error inherent in ocular estimates, variation among years due to phenologic differences at sampling, and possibly different levels of elk use before enclosure establishment.

In contrast to within the exclosures, vegetation cover classes remained relatively constant outside the exclosures from 1980 until 1988 (UTOUT) or 1992 (LTOUT). Beginning in 1988 or 1992, however, ferns and shrubs increased in cover while graminoids and herbs declined, similar to the trend seen inside the exclosures immediately following ungulate exclusion. Eventually, shrub cover stabilized in all plots, both inside and outside the exclosures, possibly depicting a new equilibrium.

Change in cover of plant species and vegetation layers

In the following, we present changes in cover relative to initial values for vegetation layers and example species within each layer. More results are available from Figshare (<https://doi.org/10.6084/m9.figshare.16563888>).

Shrubs.—*Rubus spectabilis* Pursh (salmonberry) had the greatest maximum absolute cover among shrub species at all sites. The dramatic response of *R. spectabilis* relative cover in LTOUT beginning in 1992, a change in absolute cover from 0.2% cover to 12.1% cover, dwarfed the results in the other plots (Fig. 4a). Generally, there was an increase in cover inside exclosures that eventually stabilized. There was also a slight increase in UTOUT beginning in 1996. In contrast, *Vaccinium* species showed a terrace effect, rather than an exclosure effect with relative cover increasing on the lower terrace more than the upper terrace despite being quite similar in 1980–1984 (Fig. 4b). Overall, shrubs showed an immediate increase inside the exclosures that stabilized in 1996 and an increase outside exclosures beginning in 1988 or 1992 (Fig. 4c). These conclusions did not differ whether *A. circinatum* was included or excluded from the analysis.

Ferns.—*Athyrium filix-femina* (L.) Roth (lady fern) had the greatest maximum absolute cover among fern species at all sites. *Athyrium filix-femina* increased inside exclosures until 1988 before declining to approximately initial levels (Fig. 5a). *Blechnum spicant* (L.) Sm. (deer fern,

Fig. 5b) and *Polystichum munitum* (Kaulf.) C. Presl (sword fern; Fig. 5c) also initially increased inside exclosures before declining, although the timing of the peak varied with exclosure and species. Total fern cover began to increase outside of exclosures in 1992, particularly in the lower terrace (Fig. 5d).

Herbs.—*Oxalis oregana* Nutt. (redwood sorrel, Fig. 6a) had the greatest maximum absolute cover among herb species at all sites. Both *O. oregana* and *Tiarella trifoliata* L. (foam flower, Fig. 6b) inhabit dry, closed-canopy areas; are abundant; and are consumed by elk (Jenkins and Starkey 1991, Happe 1993). However, *T. trifoliata* had an immediate response to elk removal while *O. oregana* did not.

Cover of *Maianthemum dilatatum* (false lily-of-the-valley) increased rapidly following ungulate exclusion on both terraces (Fig. 6c), but particularly on the lower terrace where the magnitude of increase was approximately double that of the upper terrace. Productivity of *M. dilatatum* has been shown to be greater in environments with higher light levels (Lezberg et al. 2001) as exemplified by lower terrace vs. upper terrace subplots (Table 1). Although *M. dilatatum* was identified in the diets of elk in the South Fork Hoh Valley, its proportional contribution could not be determined due to the large fraction of unidentifiable forb fragments found in the elk fecal samples (Happe 1993). The exclosure results corroborated that *M. dilatatum* was likely either highly sought as forage or highly susceptible to trampling.

Lysichiton americanus Hultén & H. St. John (skunk cabbage, Fig. 6d) grows in very wet areas, is consumed by elk (Jenkins and Starkey 1991), and was found primarily in the lower terrace subplots. Cover trends in *L. americanus* were inconsistent, first increasing for a brief period inside the lower terrace exclosure, then decreasing, and subsequently increasing again from 1986 through 2016. Outside this exclosure, *L. americanus* initially increased then gradually decreased. We speculate that some variation in measurement response of *L. americanus* may reflect inadequacies of the microplot sampling methods. The microplot size (0.20 × 0.50 m) is likely too small to describe changes in cover of leaves as large as those of *L. americanus*. Also, the observed difference in *L. americanus* inside and

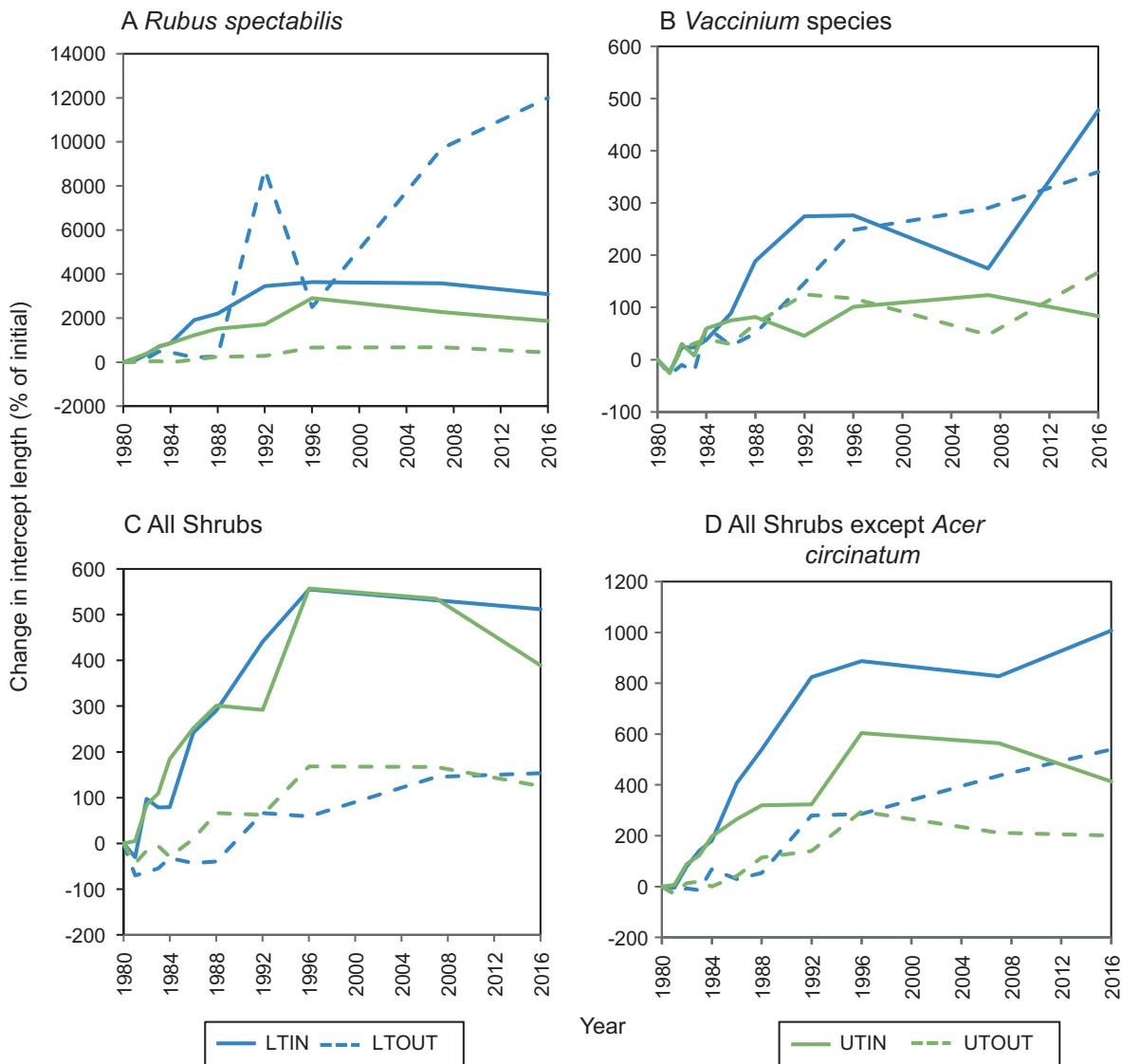


Fig. 4. Change in intercept length along line transect for selected shrub species inside and outside of two ungulate exclosures in the South Fork Hoh valley, Washington. Abbreviations for subplots: same as Fig. 2.

outside of the exclosures was one of morphology rather than cover. Plants not subject to herbivory were more erect in growth form with leaves typically growing at a 45° angle, whereas plants that were consumed had a more prostrate growth form.

Ranunculus repens L. (creeping buttercup, Fig. 6e) inhabits dry, open, disturbed areas; is consumed by elk (Jenkins and Starkey 1991, Happe 1993); and showed an initial strong and short-lived exclosure effect on the lower terrace.

Over the first few years after ungulate exclusion, *R. repens* declined inside exclosures and showed no change or an increase outside. Absolute cover of *R. repens* inside both exclosures was never >2.5% so small changes due to elk effects, phenology, and observer variation may be magnified when results are presented as relative cover. Absolute cover was as much as 6.4% (lower terrace) and 8.6% (upper terrace) outside exclosures.

Overall, cover of herbs species initially increased both inside and outside of exclosures,

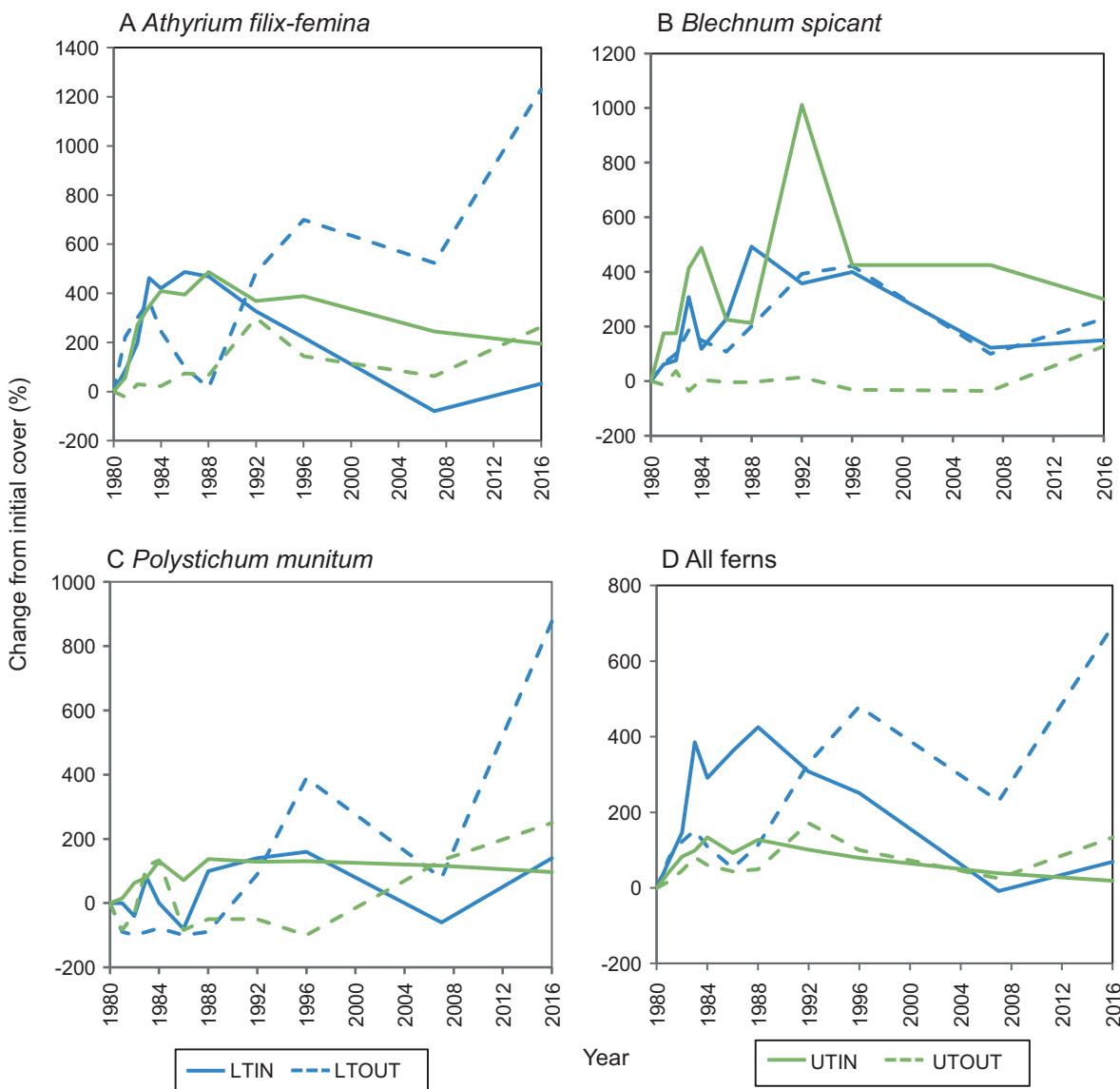


Fig. 5. Change in relative cover (% of initial cover) of selected fern species inside and outside of two ungulate exclosures in the South Fork Hoh valley, Washington. Abbreviations for subplots: same as Fig. 2.

and then, herb cover inside exclosures declined beginning in 1988 while cover outside exclosures remained high through 1996. Declines inside and outside coincide with increases in shrubs and ferns in the respective plots.

Graminoids.—*Poa trivialis* (Fig. 7a) had the greatest maximum absolute abundance among graminoids on all plots. *Poa trivialis* initially increased in all plots except LTIN, then declined

to lower than initial values by 1986 inside exclosures. Cover remained high outside exclosures until 1992 (UTOUT) or 1996 (LTOUT). The decline in cover of *P. trivialis* coincided with increases in shrub and fern cover.

Luzula parviflora (Ehrh.) Desv. (small-flowered wood rush, Fig. 7b) was fairly evenly distributed among all plots, where it initially increased inside both exclosures and outside the lower

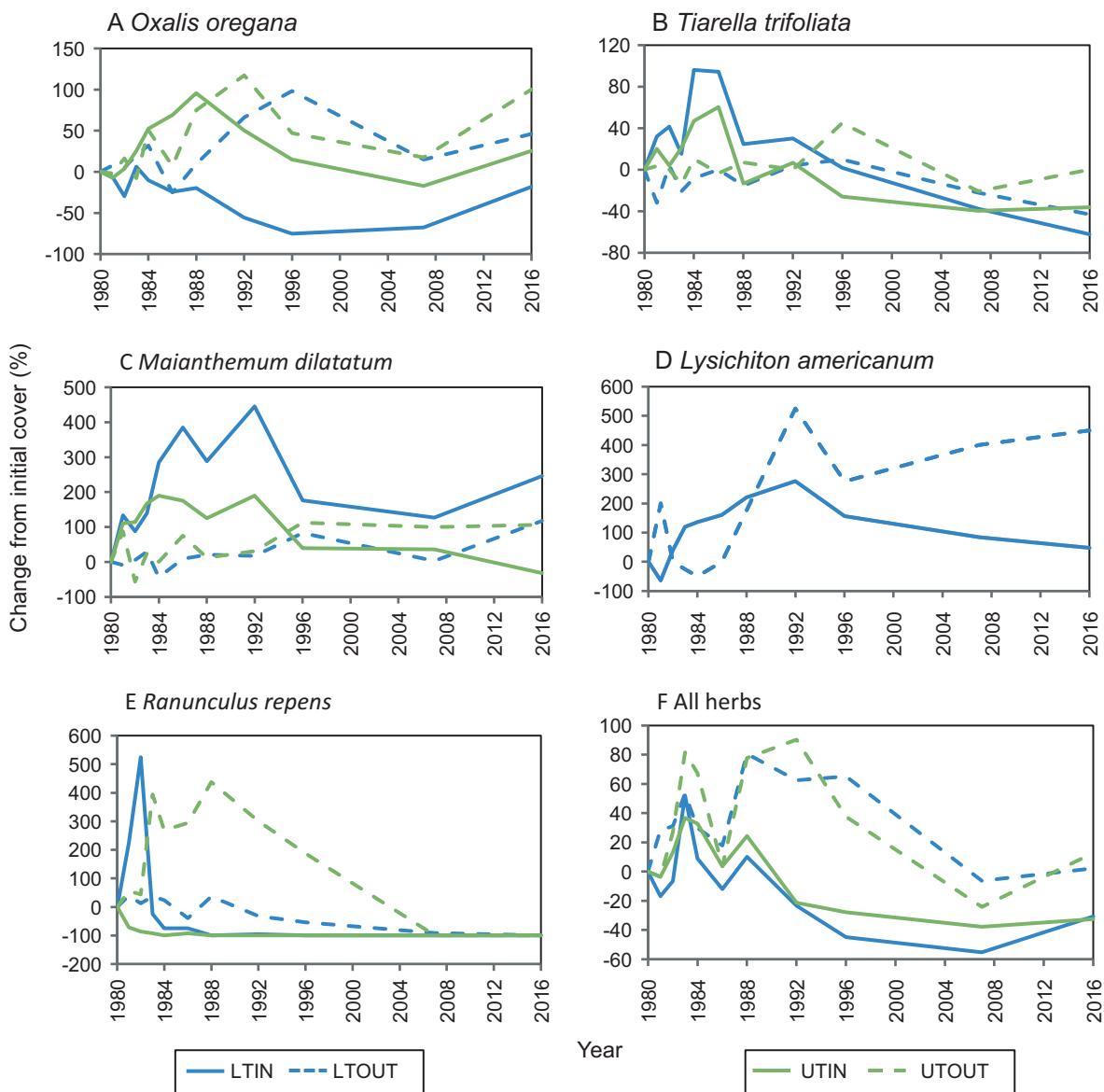


Fig. 6. Change in relative cover (% of initial cover) of selected herb species inside and outside of two ungulate exclosures in the South Fork Hoh valley, Washington. Abbreviations for subplots: same as Fig. 2.

terrace. *Luzula parviflora* subsequently declined rapidly, particularly inside the exclosures as shrubs and ferns increased.

Collectively, the sedges (*Carex deweyana* Schwein., *Carex mertensii* Prescott ex Bong., and *Carex obnupta* L.H. Bailey [Fig. 7c]) increased rapidly following ungulate exclusion in UTIN but they did not respond over time in the remaining subplots. Sedge species are consumed by elk (Jenkins and Starkey 1991, Happe 1993),

explaining the initial response until they were shaded by taller vegetation layers.

Total graminoid cover (Fig. 7d) increased sharply in all subplots in 1983, perhaps reflecting a particularly productive year, variation in sampling phenology, or observer variability. Higher cover values persisted outside of exclosures until 1996, while they declined beginning in 1984 inside exclosures. These changes coincide with increases in shrub and fern cover in respective plots.

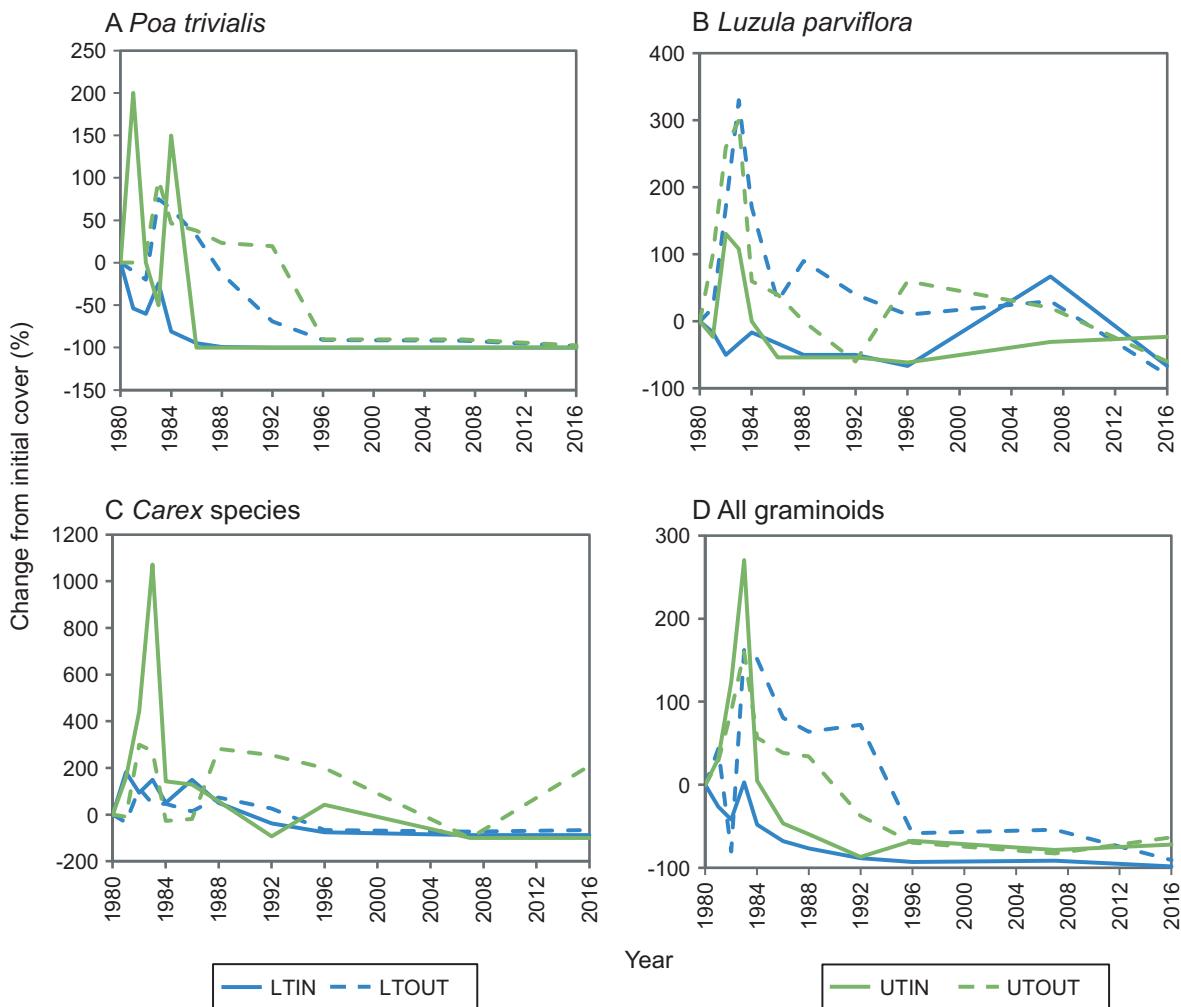


Fig. 7. Change in relative cover (% of initial cover) of selected graminoid species inside and outside of two ungulate exclosures in the South Fork Hoh valley, Washington. Abbreviations for subplots: same as Fig. 2.

Understory community change

Ordination.—Plant community ordination presents an integrated summary of the changes in species' abundances over time in each of the study plots (Fig. 8). Based on results from the first two ordination axes, communities inside and outside of exclosures and on different terraces were initially distinct, although the length of the axes is not large (<1 standard deviation unit) and plots on the same terrace were adjacent in ordination space. Initially, DCA2 explained more of the differences among plots as evidenced by greater distance among plots relative to DCA2 than DCA1. Following removal of elk, plots inside exclosures dramatically shifted in

ordination space parallel to DCA1. In contrast, community composition varied comparatively less with respect to DCA2. LTIN stabilized relative to DCA1 in 1992, while UTIN continued to the left before returning to approximately the 1992 value in 2016. Subplots outside of the exclosures were relatively stable in ordination space until 1992 when they also moved to the left and parallel relative to DCA1. By 2016, DCA1 values distinguished plots by treatment (in vs. out of exclosures), whereas DCA2 values distinguished plots by terrace.

Species diversity.—Species richness, the simplest measure of species diversity, showed a steady decline over time inside of elk exclosures for

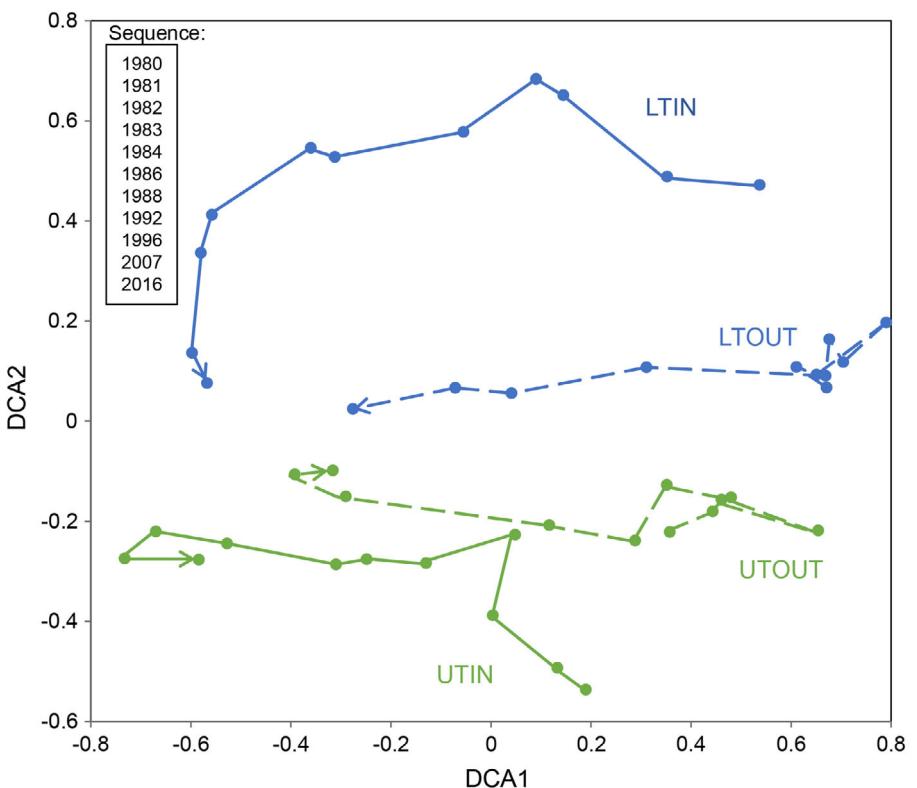


Fig. 8. Detrended correspondence analysis (DECORANA) ordination of understory plant communities inside and outside two ungulate exclosures in the South Fork Hoh valley, Washington showing first two axes (DCA1 and 2). Points represent the time sequence shown on chart. Abbreviations for subplots: same as Fig. 2.

understory vegetation (Fig. 9). The change amounted to a loss of 44% and 48% of initial species in LTIN and UTIN, respectively, primarily due to the loss of herb and graminoid species (only 3 of 12 graminoid species and 12 of 48 herb species remained inside exclosures in 2016). In contrast, there was in no change in the number of shrub species (7 species across both exclosures) and a small change in the number of fern species (1 of 7 species lost across both exclosures) by 2016. Species richness remained steady outside of exclosures until 1988 but subsequently declined, amounting to a loss of 18% and 32% of initial species in LTOUT and UTOOUT, respectively (Fig. 9). These changes again corresponded to a loss of graminoids and herbs and an increase in shrub and fern cover.

Association of ordination with community change.—Ordination scores along DCA1 were positively correlated with graminoid cover and

negatively correlated with shrub cover (Tables 3 and 4). Of all the graminoids examined, cover of *Luzula parvifolium* and *Carex* species tended to be least associated with changes in DCA1 scores, perhaps because these taxa were scarce relative to other graminoids. Ferns did not show a consistent relationship with DCA1 (Table 5), collectively or by species. Among herb species, *M. dilatatum* and *Lysichitum americanum* showed negative correlations with DCA1 (Table 6).

Drivers of vegetation change

Changes in elk abundance, climate, and over-story vegetation are all potential drivers of vegetation change. The comparison of plots inside with outside of exclosures clearly contrasts the natural abundance of ungulates at the time the exclosures were installed with an abrupt presumed change to zero ungulates. However, the number of elk outside of exclosures also declined

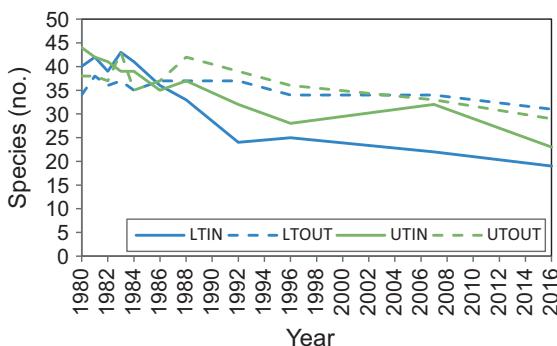


Fig. 9. Species diversity through time inside and outside of ungulate exclosures in the South Fork Hoh valley, Washington. Abbreviations for subplots: same as Fig. 2.

gradually as the study progressed (Fig. 10a), providing opportunity to observe whether the effects of a gradual decline in elk were similar to those observed following complete exclusion. Temperature and precipitation data show the range of annual variation in annual averages of climate variables, but no appreciable trend during the study period (Fig. 10b). Canopy cover may also influence vegetation structure by mediating competitive interactions among species relative to shade tolerance (Fig. 10c). Tree density increased until 2007 when it stabilized on both terraces. However, continued growth of trees established since 1978 likely provided increasing shade throughout the study.

Subplot values for DCA1 were positively correlated with elk counts outside of exclosures and negatively correlated with tree density, though not significantly at UTIN (Table 7). Weather variables were not associated with DCA1. Consequently, the right end of DCA1 is associated with the lowest tree density, highest elk count, highest

grass cover, and lowest shrub cover. Because changes in plant cover associated with higher DCA1 values (higher graminoid, lower shrub) are better explained by higher elk numbers rather than lower tree cover, we conclude that elk numbers rather than tree cover and weather is most strongly associated with DCA1.

DISCUSSION

Exclosure studies are naturally limited in scope and replication and individually can only

Table 4. Pearson correlation coefficient of ordination axis DCA1 values with cover of selected shrubs inside and outside of two ungulate exclosures in the South Fork Hoh Valley, Washington.

Subplot	Shrubs		
	<i>Rubus spectabilis</i>	<i>Vaccinium</i> spp.	All shrubs
LTIN	-0.965***	-0.824**	-0.953***
LTOOUT	-0.878***	-0.972***	-0.969***
UTIN	-0.962***	-0.866***	-0.972***
UTOOUT	-0.944***	-0.684*	-0.894***

Notes: Subplot abbreviations are as in Table 1.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 5. Pearson correlation coefficients of ordination axis DCA1 values with cover of selected ferns inside and outside of two ungulate exclosures in the South Fork Hoh Valley, Washington.

Subplot	Ferns			
	<i>Athyrium filix-femina</i>	<i>Blechnum spicant</i>	<i>Polystichum munitum</i>	All ferns
LTIN	-0.083	-0.592	-0.418	-0.235
LTOOUT	-0.867***	-0.430	-0.857***	-0.869***
UTIN	-0.416	-0.521	-0.753**	-0.034
UTOOUT	-0.590	-0.235	-0.257	-0.336

Notes: Subplot abbreviations are as in Table 1.

* $P < 0.01$, *** $P < 0.001$.

Table 3. Pearson correlation coefficients of ordination axis DCA1 values with cover of selected graminoids inside and outside of two ungulate exclosures in the South Fork Hoh Valley, Washington.

Subplot	Graminoids				
	<i>Carex</i> species	<i>Luzula parvifolia</i>	<i>Poa trivialis</i>	<i>Trisetum cernuum</i>	All graminoids
LTIN	0.628*	0.147	0.900***	0.866***	0.930***
LTOOUT	0.765**	0.637*	0.887***	0.525	0.689*
UTIN	0.536	0.562	0.653*	0.694*	0.670*
UTOOUT	0.093	0.583	0.930***	0.813**	0.912***

Notes: Subplot abbreviations are as in Table 1.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 6. Pearson correlation coefficients of ordination axis DCA1 values with cover of selected herbs inside and outside of two ungulate exclosures in the South Fork Hoh Valley, Washington.

Subplot	Herbs				
	<i>Lysichitum americanum</i>	<i>Maianthemum dilatatum</i>	<i>Oxalis oregana</i>	<i>Tiarella trifoliata</i>	All herbs
LTIN	-0.649	-0.612*	0.739**	0.286	0.552
LTOUT	-0.822**	-0.700*	-0.571	0.311	0.282
UTIN	...	0.264	-0.103	0.591	0.708*
UTOUT	...	-0.697*	-0.449	-0.199	0.363

Notes: Subplot abbreviations are as in Table 1.

* $P < 0.05$, ** $P < 0.01$.

add incremental evidence to support or refute hypotheses regarding the interactions of herbivores, plant species, and plant communities. Below, we put our results in the context of extant concepts regarding herbivory.

Plant community composition

We examined the effects of complete ungulate removal within exclosures and gradually declining elk numbers outside exclosures on plant community composition in an old-growth temperate rainforest following construction of two exclosures in 1979. Ordination results from inside exclosures, which synthesize multivariate changes in plant community structure through time, show immediate, dramatic, and parallel changes in ordination space that tended to stabilize after 12–16 yr. After exploring possible effects of other ecosystem drivers, we attribute these results to ungulate removal. Meanwhile, the ordination results describing plant communities outside of exclosures showed little variation until 1992 when plots began changing in magnitude and direction similar to changes seen inside exclosures immediately following elk removal. This change coincided with a decline in elk abundance monitored in the South Fork Hoh Valley and is an example of the natural variation in system drivers anticipated in our third hypothesis. We conclude that changes in plant communities were initiated by total elk removal inside exclosures in 1980 and gradual elk population decline outside of exclosures beginning in the 1990s. Plant community change in ordination space due to a gradual decline in elk numbers was of similar magnitude as that following total elk removal and may be an example of threshold dynamics in herbivore effects (reviewed in Hester et al. 2000, Putnam et al. 2011).

Closer examination of plant community changes following ungulate exclusion shows immediate changes in all vegetation layers. These results concur with observations that Roosevelt elk are generalist foragers with a high degree of dietary plasticity (Jenkins and Starkey 1991). Studies of elk feeding behavior conducted on the Olympic Peninsula indicate that conifers and ferns are most important when other choices are limited (fall, winter, and spring); shrubs are primarily consumed in summer and fall; and forbs and graminoids are most important in spring, summer, and fall when they are most available (Schwartz and Mitchell 1945, Leslie et al. 1984, Happe 1993). On an annual basis, Leslie et al. (1984) found a fairly even distribution of the diet among vegetation layers, whereas Happe (1993) found forbs to be most important (34% of diet) and ferns least important (8% of diet) with conifers, shrubs, and graminoids each comprising approximately 20% of the diet.

In our first hypothesis, we predicted that short-term outcomes would vary among species within vegetation layers because plant characteristics mediate species responses to ungulate herbivory. Specifically, plant morphology and physiology confer browsing tolerance (species avoided and/or able to compensate) vs. intolerance (species selected and/or unable to compensate) on plant species (Augustine and McNaughton 1998). Understanding plant response is complicated by the dependence of preference on accessibility of plant species and relative preference of alternatives (Ellis et al. 1976). Moreover, ungulate effects may include trampling and other physical damage (Gill 1992, Hobbs 1996, Pastor et al. 1997). Although the response of individual plant species to herbivory may be the complex product of multiple factors

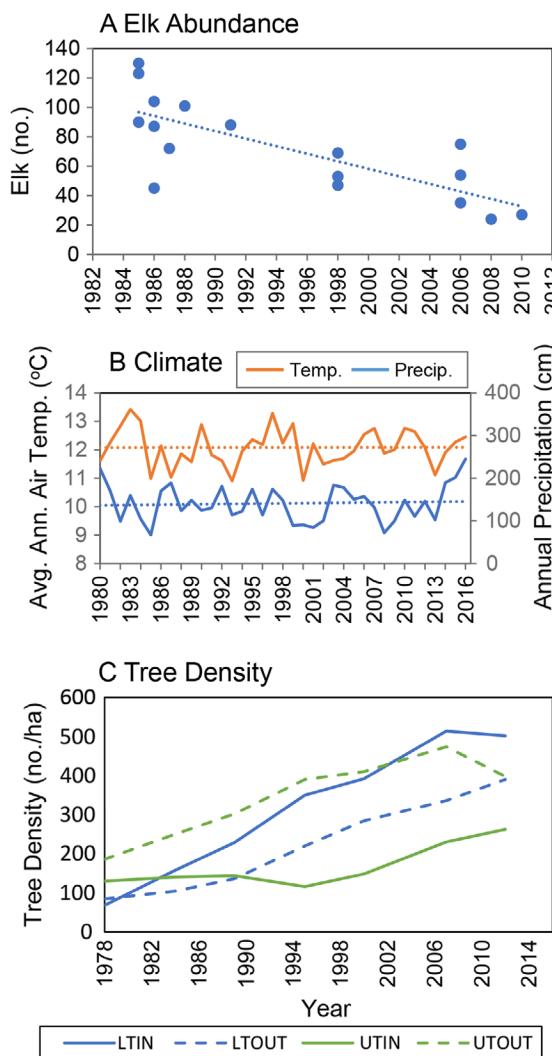


Fig. 10. Trends in potential drivers of vegetation change 1978–2012, South Fork Hoh valley, Washington, including elk abundance (Jenkins and Happe 2018), climate (Clearwater weather station), and tree density (Franklin et al. 2020). Abbreviations: LT, lower terrace; UT upper terrace. Abbreviations for subplots: same as Fig. 2; Temp., temperature; Precip., precipitation.

and adaptations, in the following we examine selectivity of herbivores and ability of plants to tolerate herbivory as the primary drivers of plant species responses.

Palatability is a complex interaction among plants, animals, and environmental conditions that influences forage selection by herbivores

Table 7. Pearson correlation coefficients of ordination axis DCA1 values with potential drivers of vegetation change inside and outside of two ungulate exclosures in the South Fork Hoh Valley, Washington.

Subplot	Drivers			
	Elk count (no.)	Tree density (trees/ha)	Annual precipitation (cm)	Average annual temperature (°C)
LTIN	...	-0.830***	0.084	0.097
LTOUT	0.938***	-0.951***	0.086	-0.272
UTIN	...	-0.449	0.123	0.064
UTOOUT	0.898***	-0.935***	0.206	-0.157

Notes: Subplot abbreviations are as in Table 1. Ellipses indicate that correlation is not meaningful.

*** $P < 0.001$.

and, consequently, vulnerability to herbivory. We cannot specifically rate palatability among plant species, but based on studies of elk diets in the western Olympics (Leslie et al. 1984, Jenkins and Starkey 1991, Happe 1993), we can compare responses of some species with disparities in observed use by ungulates. In general, removal of ungulates favored species that comprised significant components of ungulate diets and inhibited or had no effect on species less used. Among trees, we saw a substantial increase inside exclosures of the more consumed tree species, *T. heterophylla*, compared with little change in *P. sitchensis* abundance. Among ferns, *A. filix-femina* use was much greater than that of *P. munitum* (Happe 1993), which was consumed primarily when little else was available or in early spring when new fronds emerge. Our results (Fig. 5) and those of others (Schwartz and Mitchell 1945, Newman 1958) showed a dramatic response of *A. filix-femina* to ungulate exclosures compared with *P. munitum*. The response of *A. filix-femina* was likely magnified by its occurrence in more open areas with higher light levels and greater potential productivity than the habitat of *P. munitum* and the insensitivity of *P. munitum* cover due to sampling methodology (plant size greatly exceeds that of the microplot). Among herbs, *R. repens* is a minor component of elk diets (Jenkins and Starkey 1991, Happe 1993). *Ranunculus* species contain a glycoside toxin, protoanemonin, that causes irritation to the mucous membranes (Burrill 1996) and likely

renders it less palatable than other common herbs. In addition, because *R. repens* is ruderal, it may benefit from physical ground disturbance by elk. *R. repens* showed an immediate (UTIN) or almost immediate (LTIN) decline following exclosure, while most other herbs showed increases.

Ability to avoid or compensate for biomass removal enables plant species to tolerate ungulate herbivory (Augustine and McNaughton 1998). Avoidance of critical biomass removal is exemplified by graminoid species, which have basal meristems and below-ground nutrient reserves that enable regrowth and confer high tolerance to grazing (McNaughton 1979, Stebbins 1981, Coughenour 1985). In our study, initial variability was followed by increased cover outside of exclosures and an immediate (LTIN) or slightly delayed (UTIN) decrease inside exclosures as graminoids lost their competitive advantage over other herbaceous species when grazing ceased. Several herbs also protect much of their biomass below ground. *Maianthemum dilatatum* and *O. oregana* each have at least 80% of plant biomass as roots and rhizomes (Lezberg et al. 1999, 2001) compared with 45–50% for *T. trifoliata* (Six and Halpern 2008). This explains the strong response of *M. dilatatum* (>400% increase) to elk removal and the weaker response of *T. trifoliata* (<100% increase). However, *O. oregana* showed only a weak response (100% increase) and only in one exclosure (UTIN), indicating that other factors are also important.

Plants may also compensate for biomass loss through rapid growth, a functional trait that has been associated with herbivory-tolerant plant species (Diaz et al. 2001, Laliberte et al. 2012, Disbrow 2018). Plants with fast growth also tend to have low leaf nutrient content, short leaf lifespan, low dry-matter investment per leaf area and other traits associated with a “resource acquisitive” ecological strategy (Wright et al. 2004, Reich 2014). The “resource acquisitive” to “resource conservative” continuum is recognized as a global organizing construct of plant communities, which describes investment in growth vs. defense and storage. Although it has been difficult to find a simple relationship between plant tolerance to herbivory and ecological strategy (Peco et al. 2012), understanding the relationship would increase understanding of how herbivores

structure plant communities (Westoby 1998, Diaz et al. 2001, 2007, Peco et al. 2012, Disbrow 2018). We do not have detailed descriptions of functional traits for all species in our study, but we did see that *R. spectabilis*, *A. filix-femina*, and *M. dilatatum* showed the greatest response to elk removal in their respective vegetation layers. The dramatic response of *R. spectabilis* compared with *Vaccinium* species may be due to its ability to vigorously grow aerial stems and rhizomes (Tappeiner et al. 1991) and its tendency to grow in more open, well-lit conditions with higher potential productivity than *Vaccinium* species (Kennedy and Quinn 2001). *Rubus spectabilis* also showed relatively high specific leaf area among plants measured in coastal forests of Oregon (Burton et al. 2020), which is an indicator of high growth rate. This vigorous growth also seems to overcome loss of brittle *R. spectabilis* stems due to trampling. In contrast, *Vaccinium alaskense*, in particular, forms compact clones and appears to depend on seedling production more than vegetative expansion for spread (Tappeiner and Alaback 1989). The deciduous leaves of *A. filix-femina* vs. evergreen leaves of *P. munitum* and *B. spicant* exemplify a resource acquisitive trait that supports the strategy of maximizing growth rather than persistence of tissues. In contrast, *M. dilatatum* regrows and spreads quickly owing to below-ground resources, which is representative of the resource conservative strategy and avoidance of biomass loss, showing that both compensation and avoidance confer effective tolerance of herbivory.

Our second hypothesis predicted that over the longer term, the effects of ecosystem dynamics other than the direct effects of herbivory would become apparent in plant community structure. Most obviously, the dramatic increase in shrubs and ferns following exclosure construction appears to have altered plant competitive interactions such that cover of herbs and graminoids inside exclosures eventually fell below initial values owing to shading by taller vegetative layers. Besides interactions among plants, other ecosystem dynamics eventually played a role in determining plant community structure. By the end of the study, the number of *T. heterophylla* seedlings inside exclosures was greater than pre-exclosure but had declined from the initial peak in the first few years. The decreasing abundance of both

T. heterophylla and *P. sitchensis* seedlings 10–25 cm tall suggests a reduction in seed bed availability provided primarily by logs in decay class 3, which have enough moss cover to trap seeds but not so much as to out-compete them (>5 cm depth; Harmon and Franklin 1989). Habitat abundance also appeared to affect long-term plant species responses as seen, for example, with *M. dilatatum* and *O. oregana*. Both increased in cover inside exclosures but *M. dilatatum* responded more strongly in the lower terrace exclosure, which was dominated by comparatively wetter, more open conditions where *M. dilatatum* is most productive (Lezberg et al. 2001); *O. oregana* responded more strongly in the upper terrace exclosure, which had a greater abundance of comparatively drier, more closed habitat to which *O. oregana* is adapted (Bjorkman and Powles 1981). Meanwhile, conditions independent of exclosures appear to have favored the growth of *Vaccinium* species in all plots as growth was continuously positive in all subplots with rate dependent on terrace.

In aggregate, vegetation composition shifted after 36 yr from a system dominated by herbaceous cover and having a major graminoid component to one dominated by shrubs (5–6-fold increase) and ferns (5–7% increase in absolute cover), a decrease in absolute herb cover (15–20% loss) and an almost total loss of graminoids (<1.5% cover remaining in any plot) after release from selective feeding and subsequent effects of other drivers. Because species richness of the herb and graminoid layers was much higher than the shrub and fern layers in this and other studies (reviewed in Gilliam 2007), a by-product of plant community changes was an overall loss of plant diversity. The association of elk herbivory with lower cover of shrubs and higher forb cover, thus higher diversity, has been observed in other coniferous forest ecosystems (Hester et al. 2000, Diaz et al. 2007, Hegland et al. 2013).

Exclosure studies

Our study addressed many weaknesses of ungulate exclosure studies (Sarr 2002, Bergstrom and Edenius 2003, Hobbs 2003) in that the exclosures were relatively large (0.5 ha) and were measured for a long period (over three decades), the elk population (i.e., treatment) was quantitatively characterized, and initial plant cover values were determined for all plots. Moreover, the exclosures

were sited in areas originally chosen to be representative of old-growth temperate rainforest structure rather than in areas heavily used by ungulates where results may exaggerate forest-wide effects of herbivores. These study characteristics facilitate interpretation of results and enhance confidence that results have minimal bias.

Our study was initiated when study designs were normally based on analysis of variance and illustrates why this approach would not be recommended today (Hobbs 2003). First, spatial variation in natural environments meant that even these proximal pairs of plots representing the same forest type and as similar as one might expect were not exact replicates as evidenced by the initial differences in ordination space. The greatest variation was along DCA2, which likely reflects environmental variation (e.g., canopy cover, soil moisture); the higher initial values for DCA1 on the lower terrace may indicate higher elk use in that area. Second, the experimental conditions were not static because elk numbers, and therefore treatment level, changed over time. Also, although the exclosures represent great investment of effort and expense, the sample size of two sites is insufficient to describe the natural range of variation in elk use and environmental conditions existing in even a small area of the forest. Finally, many relationships between herbivory intensity and response variables are non-linear (Rooney and Waller 2003, Putnam et al. 2011, Hegland et al. 2013) and therefore cannot be detected with an experimental design having only one treatment level. More recently, it has been recognized that in a spatially and temporally heterogeneous world, the ability to extend results across scales is as important as statistical power and freedom from bias, which are the goals of traditional plot designs (Hobbs 2003). Given the infeasibility of having enough plots to describe large spatial scales, it is suggested that exclosure studies be coupled with remotely sensed data, be arrayed in scale-sensitive experimental and sampling designs, be used to test among competing models rather than hypotheses, be used to investigate gradients in animal use and environmental conditions, and otherwise enabled to describe a larger context than captured by individual plots (Hester et al. 2000, Sarr 2002, Bergstrom and Edenius 2003, Hobbs 2003, Rooney and Waller 2003).

Previous assessments of exclosure studies have pointed out that for exclosure studies to be most revealing, exclosures should be sufficiently large to minimize the effects of fencelines and to encompass dynamic processes that affect plant communities (Anderson and Loucks 1979, Reimoser and Suchant 1992, Sarr 2002). Determination of an adequate size can be guided by the spatial dimensions of heterogeneity in forest structure, often described as canopy patches and gaps (Franklin and Van Pelt 2004) as this pattern relates to the scale of processes determining stand development and ecosystem function (McIntire and Fajardo 2009). Old-growth *P. menziesii* stands of Western Washington are extremely complex both vertically and horizontally with pattern having grain variously observed as 5–30 m (Bradshaw and Spies 1992) or 10–15 m (Kane et al. 2011). These results suggest that for old-growth coniferous forests, our 0.5-ha exclosures were large enough to include patch dynamics and consequent changes in microclimate and habitat for plants and other biota. Perhaps the clearest manifestation of the effects of gap dynamics in our results is the observation that substrate for seedling establishment appeared to vary over the study period. This substrate is created when fallen trees reach the appropriate stage of decomposition and colonization by mosses (Harmon 1987, 1989a, 1989b).

Exclosure studies have also been criticized for often having too short duration (Sarr 2002, Wisdom et al. 2006, Bernes et al. 2018). While direct effects of ungulate herbivory may be observed in a few years, indirect effects of ungulates on plant competitive interactions and nutrient cycles take longer to manifest in plant community composition. Our 36-yr study was long enough to determine that after 8 yr, 50 (UTIN) to 100 (LTIN) *T. heterophylla* trees/ha grew tall enough to be largely invulnerable to elk (>150 cm, Jacobs 1969) with potential to become trees (>5 cm dbh). If they survive, they would substantially add to the 1.3 (UTIN and UTOUT) and 2.7 (LTIN and LTOUT) *T. heterophylla* trees·ha⁻¹·yr⁻¹ that grew large enough to be counted in tree surveys during 1978–2012. In addition, we saw a stabilization in community structure relative to the ordination axis associated with ungulate effects (DCA1) after 12–16 yr when ungulates were completely removed. The long time period of this study also

allowed us to observe changes outside of exclosures resulting from a decline in elk numbers. These results quantify the time course of herbivory dynamics for comparison with the rate of ecological processes driving forest composition and structure such as succession (Van Pelt et al. 2006), catastrophic disturbance (Franklin and Dyrness 1973, Henderson et al. 1989), and gap dynamics (Taylor 1990).

Effects of ungulates on forest succession

Ungulates have the potential to influence forest succession by selectively consuming tree regeneration. Our data show that elk inhibit *T. heterophylla* establishment compared with *P. sitchensis*. This suggests that without elk present *T. heterophylla* should replace *P. sitchensis* because *T. heterophylla* is more shade tolerant and outcompetes *P. sitchensis* under a forest canopy (Krajina 1969, Hines 1971, Franklin and Dyrness 1973). Even with ungulates present, exclusion of *T. heterophylla* is not complete because it can establish and survive in ungulate refugia such as tip-up mounds (Schreiner et al. 1996). This may partially explain the lack of correspondence between tree establishment patterns and elk abundance observed by others in the vicinity of our plots (Harmon and Franklin 1983). Given that other factors (e.g., substrate, light) also influence tree species regeneration, the effects of elk exclusion on forest succession appears more complex than simple replacement of *P. sitchensis* by *T. heterophylla*.

A critical limiting factor for establishment of both dominant tree species in these forests is the availability of downed logs at the appropriate stage of decomposition (McKee et al. 1982, Harmon and Franklin 1989). In 1978, such logs covered only 9.25% (UT) and 5.15% (LT) of our plots (Graham and Cromack 1982). By the end of the study, the low number of 10–25 cm tall seedlings of either species suggests a lack of suitable substrate for establishment. However, this decline may be temporary as the supply of substrate is periodically renewed by tree mortality. In general, the magnitude of herbivory effects on tree establishment observed inside ungulate exclosures is limited by the availability of establishment substrate at the required stage of decay and may not be apparent if refugia initially happen to be present due to the arrangement of fallen logs.

The amount of light reaching the forest floor is also an important factor regulating the response of tree regeneration to elk removal. In closed forests, the regeneration of *P. sitchensis* can be light limited (Krajina 1969, Hines 1971, Franklin and Dyrness 1973). Hence, the removal of elk in closed forest might lead to an increase in *T. heterophylla*, but not a change in the dominance of *T. heterophylla*. In contrast, *P. sitchensis* seedlings are abundant in western Olympic Peninsula forests, which are open and have plentiful downed logs. Hence, despite the increase in our study of taller seedlings of *T. heterophylla* caused by elk removal, *P. sitchensis* seedlings >25 cm tall greatly outnumbered *T. heterophylla* seedlings after 8–16 yr of ungulate exclusion. It will likely take many more years before shade from the current pulse of reproduction will hamper the establishment of *P. sitchensis* seedlings. Thus, our study was not long enough to describe the eventual relationship between *T. heterophylla* and *P. sitchensis* regeneration in the absence of ungulates.

Effects of ungulates on plant community biodiversity

Species diversity is an attribute of plant communities thought to be associated with community stability through enabling productivity, resilience to disturbance, and resistance to invasive species (Cardinale et al. 2011, Standish et al. 2014, Lefcheck et al. 2015, Smith-Ramesh et al. 2017). The intermediate disturbance hypothesis (IDH) holds that species diversity is related to disturbance intensity by a hump-shaped inverse quadratic function such that greatest diversity occurs at intermediate intensity or frequency of disturbance (Grime 1973, Connell 1978). While there is uncertainty and controversy regarding the mechanisms supporting IDH (Dornelas 2010, Fox 2013), studies have shown that the IDH generally holds for ungulate herbivory as a disturbance (Svensson et al. 2012, Yeboah and Chen 2016). However, because many studies have relied on extant gradients of ungulate herbivory rather than experimental contrasts, few studies in forested ecosystems have included a wide enough range of intensity to describe the entire curve (but see Hegland et al. 2013). Consequently, studies must be interpreted relative to whether they describe low to intermediate

intensity (Hegland et al. 2013) or intermediate to high intensity (e.g., Rooney and Waller 2003). In forests, the mechanism for the IDH is hypothesized to be a reduction in woody vegetation by ungulate herbivores that leads to greater resources and substrate for lower-growing species (Hegland et al. 2013, Pekin et al. 2015). Because species richness is greatest in the herb layer (reviewed in Gilliam 2007), ungulate herbivory that causes a reduction in woody vegetation also results in greater species diversity.

Our study supports the IDH mechanism described for forests because the removal of ungulate herbivores resulted in no change in the number of shrub species and a small change in the number of fern species by 2016. In contrast, only 3 of 12 graminoid species and 12 of 48 herb species remained inside exclosures in 2016, presumably due to increased cover of shrubs and ferns and other competitive interactions. Graminoid species are known to be adapted to survive the presence of ungulate herbivores (McNaughton 1979, Stebbins 1981, Coughenour 1985) but compete poorly in shade and in competition with other non-woody species. Four of the remaining herb species were prominent in elk diets (*Lysichiton americanum*, *M. dilatatum*, *O. oregana*, and *T. trifoliata*; Happe 1993, Jenkins and Starkey 1991, Leslie et al. 1984) and likely benefited when protected from herbivory. We have no clear explanation for the identity of the other eight remaining species, but we suspect they are more shade tolerant, more competitive for other resources and/or less susceptible to trampling than those that were lost. Assuming the IDH holds for our sites, our observation that decreasing herbivory is associated with decreasing diversity suggests that our sites were on the ascending limb of the intensity-diversity curve and perhaps more diversity would result from higher elk density than that existing at the beginning of the study.

Ungulate–forest relationships: information needs and uses

Ecologists have long understood that characteristics of herbivore populations and vegetation communities are inextricably linked whereby ungulates influence vegetation and vice versa (McNaughton 1978, Hobbs 1996). These relationships also have a spatial dimension in

heterogeneous forested landscapes such as the temperate rainforest of the Pacific Northwest where vegetation patch types are associated with differing levels of ungulate use (Fig. 11). Forest patch heterogeneity reflects the extent of disturbance and successional processes at multiple spatial scales. Resulting patches are defined by tree density, distance from the river, terrace level, and other factors that determine availability of light and moisture, density of downed logs, and distribution of animal species. Elk frequent patches depending on ungulate-relevant

characteristics such as forage quality, ease of movement, and exposure to pests and predators. The resulting mosaic describes areas having variable forest structure and composition plus intensity of ungulate herbivory where ungulates and vegetation each influence the condition of the other. The size and distribution of elk populations are also determined by changes in predation and hunting pressures, disease spread, and changes in life stage rates, and constitutes another dimension of the ungulate–forest relationship.

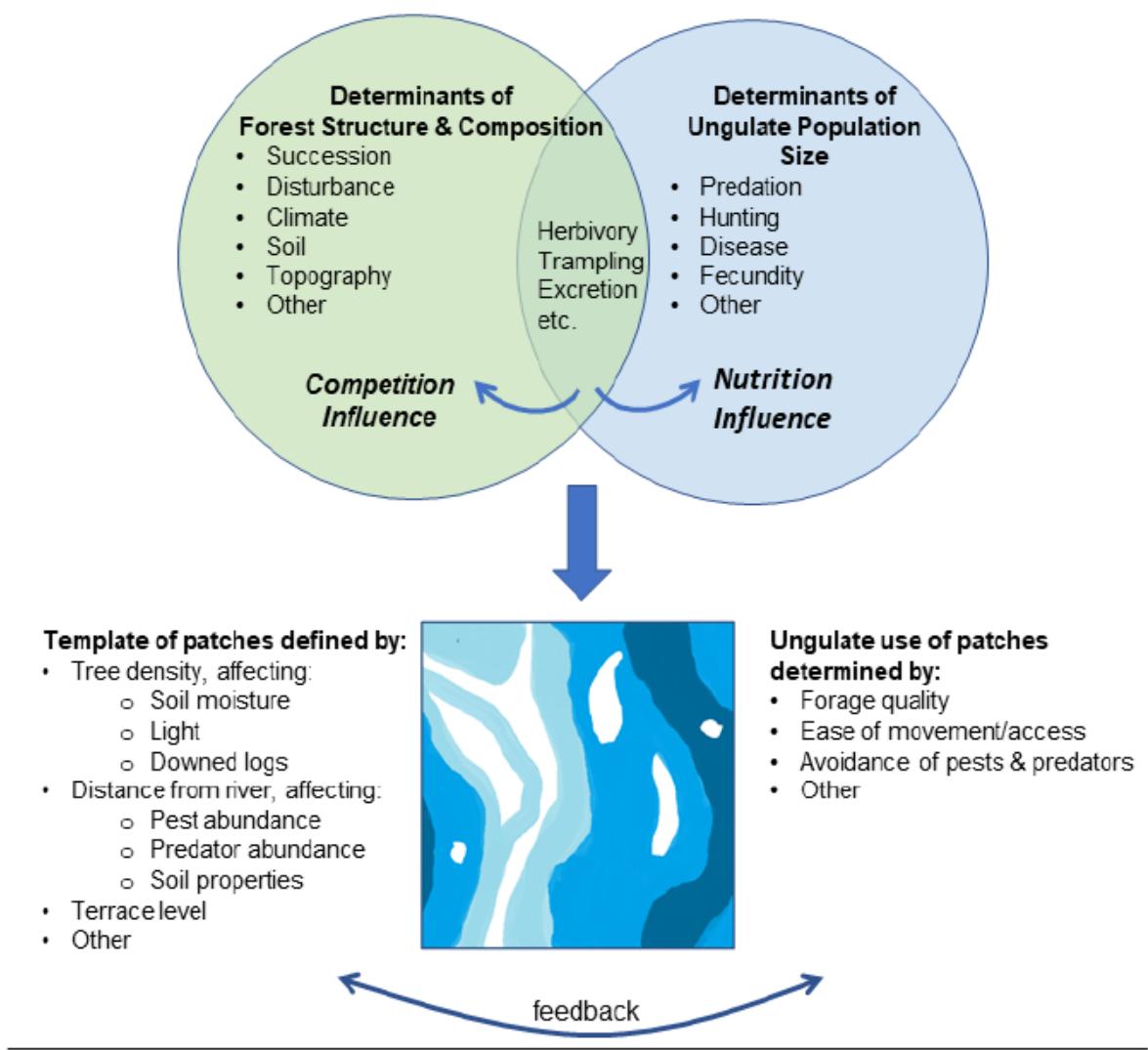


Fig. 11. Conceptual model showing that variation in forest structure is reflected in attractiveness to ungulates and therefore intensity of herbivory. Shades of color indicate variation in intensity of herbivory.

Current understanding of ungulate–forest relationships on the Olympic Peninsula is limited by the inability to extrapolate from detailed, spatially limited studies, such as exclosure studies, to the entire forest. Several lines of research could be used to address this need. For example, by identifying diagnostic characteristics of vegetation patch types associated with different levels of elk use that can be remotely sensed it would be possible to map ungulate-relevant vegetation patches and extend patch-level understanding of ungulate effects to a larger area. This map would become more meaningful with intensive evaluation of ungulate effects on a more inclusive list of patch types than previously studied, such as including gravel bars, lower terraces, and alder flats. By evaluating the effect of a range of elk numbers, rather than simple exclusion, one could determine, for example, whether cottonwood usage is high across a range of elk numbers as found by Endress et al. (2016). If the effect of elk on cottonwood recruitment is insensitive to variation in elk abundance (except at very low abundances), riparian forest succession may not have been influenced by the historical range in elk numbers to the extent previously suggested (Beschta and Ripple 2008). Additionally, a fuller understanding of how ungulates use habitat depends on knowing how patches are used both daily and seasonally. Among other uses, this information collectively will make it possible to identify bottlenecks in availability of patch types that might control ungulate success. While it would also be desirable to quantify the natural range of variation of the ungulate population, this is likely impossible given that changes in human hunting and predation patterns over time have obscured the range of variability in herbivore–vegetation equilibria that existed before EuroAmerican settlement. An objective analysis of historical accounts may inform our understanding of historic variation in elk numbers, however, and would inform our understanding of the natural range of vegetation condition.

Although new approaches are needed to extrapolate exclosure studies, continued maintenance of the South Fork Hoh exclosures and monitoring of elk populations could yield further understanding of ungulate–forest relationships from the long time series of data at these sites. Comparing vegetation inside exclosures with

vegetation changes in response to changing elk numbers outside has already suggested that there may be threshold dynamics at play. We also have the chance to look at natural fluctuations in elk numbers rather than merely total removal. Finally, even if the exclosures are not maintained we could observe the effects of returning elk and compare restoration dynamics with those of removal.

The ungulate–forest relationship and consequences for both forest vegetation and animal populations are concerns for agencies charged with managing them. At various times throughout the historical record, pioneers, park biologists, settlers, and other observers of forest structure on the Olympic Peninsula have offered qualitative opinions on the appropriateness of the existing vegetation and herbivore densities. Over time, perspectives have ranged from considering vegetation to be severely damaged and elk to be overabundant (Schwartz and Mitchell 1945), to viewing vegetation and herbivores as reflecting an acceptable ecological balance (Newman 1958, Jenkins 1981), to perceptions that ungulate grazing actually optimizes ecological carrying capacity for large ungulates (Happe 1993), and to the growing acknowledgment today that loss of a top predator may have impacted tree recruitment along riparian zones (Beschta and Ripple 2008). Each of these perspectives likely reflects actual changes in ungulate densities and vegetation communities over time, but the accompanying interpretations may also have been colored by underlying management or ecological perspectives, for example, those having to do with restoring or curtailing hunting, livestock grazing, or predator populations (Jenkins and Happe 2018). The first pioneers to describe vegetation conditions in the lowland rainforest valleys in the western Olympics provided limited reference perspectives on the range of vegetation conditions encountered before these ecosystems were affected by settlement patterns, including predator removal, livestock grazing, and market or subsistence hunting. These ranged from descriptions of the first explorers battling their way through “underbrush so dense as to be almost impenetrable” (Meany 1890) and through “veritable pastures” maintained by herbivores (Barnes 1890). Clearly, the early explorers encountered multiple patch

types, demonstrating that dramatic heterogeneity in forest structure is likely the norm. Achieving a desired balance between ungulate numbers and vegetation condition is a legitimate management goal, but science alone cannot determine which management values to emphasize or the desired distribution of vegetation patches each of which reflect the joint expressions of herbivory, forest disturbances, and site factors. However, answers to scientific questions can inform the means to achieve specific goals based on those values and potential consequences of management actions.

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DATA AVAILABILITY

Data summarized by subplot and year are available from Figshare: <https://doi.org/10.6084/m9.figshare.16563888>. Raw data are available at Franklin et al. (2020).