Influences of climate, fire, grazing, and logging on woody species composition along an elevation gradient in the eastern Cascades, Washington

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ABSTRACT

Across western North America, current ecosystem structure has been determined by historical interactions between climate, fire, livestock grazing, and logging. Climate change could substantially alter species abundance and composition, but the relative weight of the legacy of historical factors and projected future conditions in informing management objectives remains unresolved. We integrated land use histories with broad scale climatic factors to better understand how inland Pacific Northwest ecosystems may develop under projected climates. We measured vegetation structure and age distributions in five vegetation types (shrub steppe to subalpine forest) along an elevation gradient in the eastern Cascades of Washington. We quantitatively assessed compositional changes, and qualitatively summarized the environmental history (climate, fire and fire suppression, grazing, and logging) of each site. Little change was evident in woody species composition at the shrub steppe site. At the shrub steppe/forest ecotone, densities of drought-tolerant *Artemisia tripartita* and *Pinus ponderosa* increased. In the dry conifer, montane, and subalpine forest sites, increases in *Pseudotsuga menziesii*, *Abies grandis*, and *Abies lasiocarpa*, respectively, and decreases in *Pinus ponderosa*, *Larix occidentalis*, and *Pinus contorta*, respectively, have shifted species composition from fire and drought-tolerant species to shade-tolerant species. Fire suppression, grazing, and logging explain changes in species composition more clearly than climate variation does, although the relative influence of these factors varies with elevation. Furthermore, some of the observed changes in composition are opposite what we expect would be most suited to projected future climates. Natural resource managers need to recognize that the current state of an ecosystem reflects historical land uses, and that contemporary management actions can have long-term effects on ecosystem structure. Understanding the processes that generated an ecosystem's current structure will lead to more informed management decisions to effectively respond to projected climate changes.

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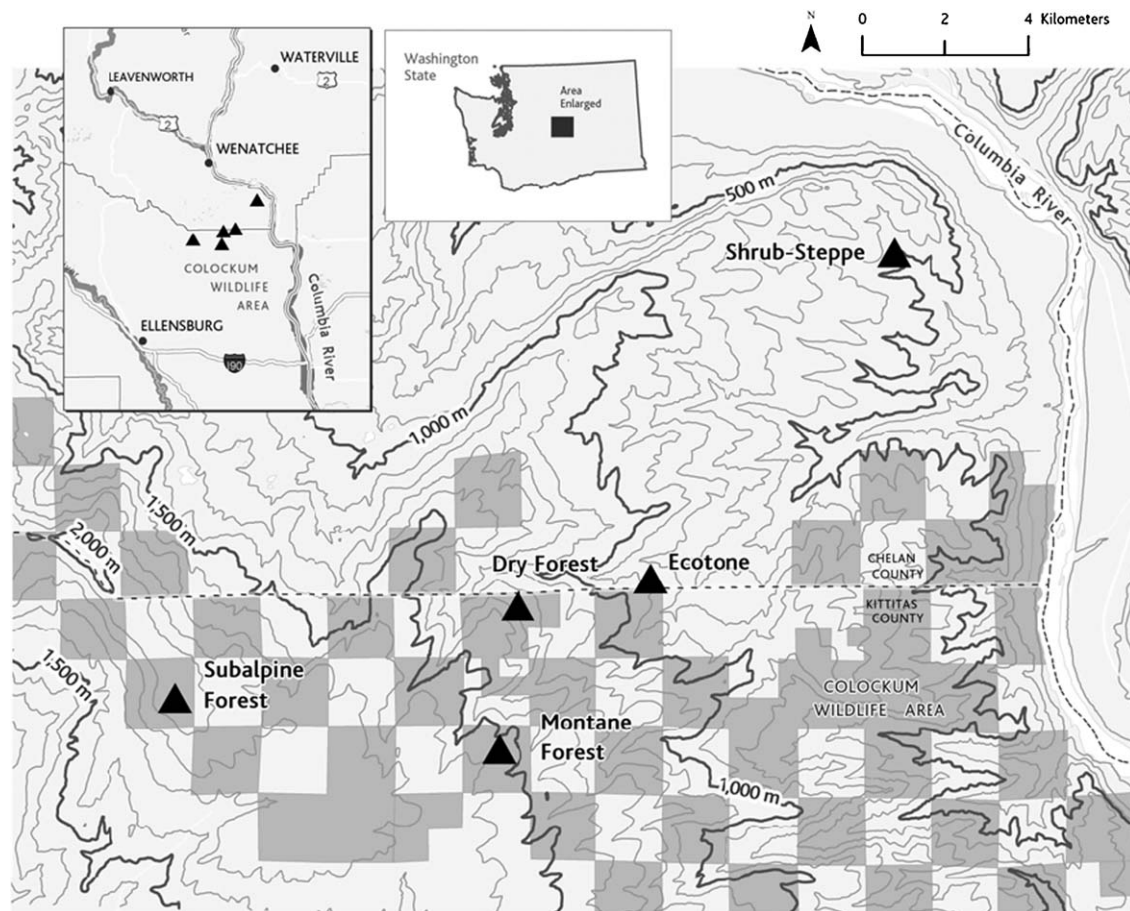
1. Introduction

Today's ecosystems are the product of long and complex interactions between environmental and human factors (Allen et al., 2002; Jackson and Hobbs, 2009). In North America's inland Pacific Northwest (inland PNW), European settlement starting in the 19th century substantially altered the processes affecting ecosystem structure and function. Numerous studies have examined how the historical structure and distribution of these ecosystems has been shaped by interactions between climate and fire (Hessl et al., 2004; Heyerdahl et al., 2006, 2008; Whitlock et al., 2003), and how 20th century wildfire suppression has affected the current

structure (Brown et al., 2004; Everett et al., 2007; Hessburg et al., 2005a). Other historical factors including logging and widespread (over)grazing by livestock have also significantly affected the trajectories of these ecosystems (Hessburg and Agee, 2003).

Climate change brings an added dimension to the complex influences on ecosystems. Upslope shifts of vegetation biomes attributable to 20th century climate change have already been documented (Danby and Hik, 2007; Gonzalez et al., 2010; Kelly and Goulden, 2008; Lenoir et al., 2008). Projections of 21st century vegetation indicate that the montane ecosystems common across the inland PNW are vulnerable to future biome shifts (Gonzalez et al., 2010; Littell et al., 2009). In the Cascades of Washington state, mean annual temperature significantly increased by 0.7 °C from 1901 to 2005 (IPCC, 2007). Although total annual precipitation shows no such trend, the fraction of precipitation falling as rain rather than snow increased significantly from 1949 to 2005 (Knowles et al.,

Fig. 1. Location of the Colockum Wildlife Area (gray shading), our research sites (triangles), and meteorological stations at Ellensburg, Wenatchee, and Waterville, in north-central Washington State.

2006). Future warming in the inland PNW could increase drought stress and tree mortality from fire and insects (Jenkins et al., 2008; Littell et al., 2009; Logan et al., 2003), suggesting that the interactions between environmental and human factors will not diminish in complexity.

Land managers frequently use pre-European settlement ecosystem structure and disturbance regimes to define management targets that promote ecosystem resilience and preserve biological diversity (Allen et al., 2002; Keane et al., 2009; Long, 2009). Under a changed climate, historical disturbance regimes may no longer have the desired effects, and historical structures may no longer provide the desired ecosystem goods and services (Davies et al., 2009; Harris et al., 2006; Lawler et al., 2010; Ravenscroft et al., 2010). This has opened a debate about whether historical conditions are an appropriate management target in light of climate change (Lawler, 2009; Wiens and Bachelet, 2010). Management decisions need to incorporate historical and projected future conditions, although the relative importance that natural resource managers should place on these two time periods in informing management objectives is an unresolved question. We suggest that understanding the processes that generated an ecosystem's current structure will lead to more informed management decisions in response to projected climates (e.g., Millar et al., 2007).

The goal of this study was to integrate land use histories with broad scale climatic factors and, by doing so, to better understand how ecosystems of the inland PNW may develop in the future under a changing climate. We examined ecosystem structure and environmental history along an elevational gradient that reflects conditions across much of the inland PNW. Our specific objectives were to: (1) characterize 19th and 20th century changes in the composition of woody species along the elevation gradient, and (2) investigate the causes of those changes, including climate, fire, livestock grazing, and logging.

2. Methods

2.1. Research area

The Colockum Wildlife Area (hereafter, 'Colockum') is on the north slopes of the Wenatchee Mountains in north central Washington State (Fig. 1). Elevation ranges from 500 to 2000 m a.s.l. Low elevations experience warm summers (average maximum 27.4 °C), cool winters (average minimum −4.7 °C), and low annual precipitation (250 mm y^{-1}) (Daly et al., 2008). Upper elevations are much cooler (average summer maximum 16.5 °C, average winter minimum −9.3 °C) and wetter (average precipitation 870 mm y^{-1}; Daly et al., 2008).

2.2. Field sampling and analysis

The vegetation in Colockum reflects elevational gradients across the inland PNW. We established five sites: (a) shrub steppe (550 m a.s.l); (b) shrub steppe/forest ecotone (900 m a.s.l.); (c) dry forest (1275 m a.s.l); (d) montane forest (1550 m a.s.l); and (e) subalpine forest (1950 m a.s.l) (Fig. 1). At each site, we established three 20 m × 50 m plots, approximately 50 m apart. In each plot, we tagged all live large trees (diameter at breast height (dbh) ≥ 19.5 cm) and measured the height (h) and dbh of each tree. All live shrubs and smaller conifers (<19.5 cm dbh) were tagged

Table 1
Best-fitting species-specific regression models to estimate tree age from morphological data. N = number of cross-dated ages used to build regression models. Height is measured in m and ground diameter in cm. Scatter plots of the data and models are in Appendix A.

Species	Model form	N	Predictor range	R^2	P	B_1	B_2
Abies grandis	a	26	0.3–23.8	0.833	<0.001	1.644	0.367
Abies lasiocarpa	a	27	0.5–25.7	0.905	<0.001	1.818	0.462
Artemisia tridentata	b	15	1.3–9.25	0.465	0.005	1.246	0.340
Artemisia tripartita	b	20	1.0–4.0	0.547	0.002	1.270	0.513
Pinus albicaulis	c	10	1.0–3.0	0.977	<0.001	−14.369	31.058
Pinus contorta	a	15	8.2–18.5	0.703	<0.001	0.957	1.182
Pinus ponderosa (dry forest)	a	20	1.0–28.0	0.792	<0.001	1.749	0.312
Pinus ponderosa (ecotone)	a	13	0.2–16.4	0.899	<0.001	1.257	0.582
Pseudotsuga menziesii	a	32	0.2–27.5	0.901	<0.001	1.606	0.451

Model forms:
a: $\log_{10}$ age = $B_1 + B_2 \times \log_{10}$ height.
b: $\log_{10}$ age = $B_1 + B_2 \times \log_{10}$ ground diameter.
c: age = $B_1 + B_2 \times$ ground diameter. Ages for trees with a ground diameter ≤ 0.25 cm was arbitrarily set to 2 years.

and measured for h and either dbh (where $h > 3$ m) or ground diameter (dg; where $h \leq 3$ m) within two 10 m × 10 m subplots per plot. Structural data (density, basal area, quadratic mean diameter (QMD)) were averaged across plots and subplots and adjusted to a per hectare basis. We obtained increment cores, taken as close to the ground as possible, from ~5 large trees per species per site. Trees were selected as close to the center of each plot as possible. We also took stem cross-sections from the bases of ~5 individuals per species of conifers <3 m height and of *Artemisia* spp. As this required destructive sampling of these individuals, we sampled trees and shrubs closest to the midpoint between plots (ensuring they were outside the plots themselves), up to a maximum of five samples per species per site. In some cases, this sampling was modified to capture the approximate range of sizes represented in the size measurements made at that site. All increment cores and cross-sections were prepared following standard dendrochronological methods (Stokes and Smiley, 1968), and ring widths were measured and cross-dated using COFECHA (Holmes, 1983). Corrections for age to core height were made based on species-specific simple regression models of the heights and ages of the basal cross-section samples.

Species-specific models were developed to predict ages from morphological data (h or dg); separate equations were developed for individual sites where necessary to improve overall model fit (Table 1; Appendix A). Low sample sizes prevented us from developing models for *Larix occidentalis* and *Picea engelmannii*, so we applied the equations for *Pseudotsuga menziesii* and *Abies lasiocarpa*, respectively, to calculate ages for these species. We applied the models to the stand structural data to obtain current age structures that reflect the net effect of historical regeneration and mortality patterns. Separating regeneration and mortality patterns would have required more comprehensive stand reconstructions (i.e. Bakker et al., 2008); the additional required data (size and identity of dead conifers, decay status, and decay rates) were beyond the scope of this study.

We used a functional trait approach (Violle et al., 2007) to examine shifts in species composition by comparing two time periods: 0-100 years ('young') and 100-200 years before present ('old'). We examined stand-level responses to climate and changes in shade, drought, and fire tolerance, defined as the ability to survive or vegetatively recover from shade, drought, or fire, respectively. We obtained tolerance rankings for each species from the USDA Forest Service's Fire Effects Information System (http://www.fs.fed.us/database/feis/) (Table 2). For conifers, we confirmed the tolerance rankings with information synthesized by Minore (1979). We calculated the proportion of trees with "low", "medium", or "high" tolerances, weighting species by their relative abundance (density). Proportions were calculated for each 25 year age bin and then averaged together for each time period ('young'

and 'old'). To investigate climate responses, we calculated temperature and precipitation trait values in the same fashion, assigning each species the median annual temperature and precipitation values for its' North American distribution (Table 2; Thompson et al., 1999).

2.3. Evaluation of influence of environmental factors on species composition

We evaluated changes in species composition along the elevational gradient in the context of four primary factors: climate, fire, livestock grazing, and logging. Using local meteorological records and regional climate reconstructions, we characterized past climatic variation for the Colockum. We reviewed the peer-reviewed and grey literature (e.g., local historical records) and interviewed local land managers for information about fire (including fire suppression), grazing, and logging in the Colockum. Finally, we assessed the expected compositional changes that each factor would produce at each site if it were a primary driver of species composition. For each factor, we qualitatively assigned a relative importance rating based on the degree of agreement between these expected changes in relative species composition and changes actually observed at our sites. This rating indicates the possibility that the factor was a primary driver:

- Yes: The rationale for the expected changes can fully explain the observed changes.
- Possible: There is no conflict between expected and observed changes, but there is uncertainty as to the weight of other drivers that could also explain the observed changes.
- Unlikely: It is not clear whether the factor occurred at a particular site, or some of the observed changes run counter to those expected.
- No: The factor is not relevant or did not occur at the particular site, or the direction of actual change is different and primarily opposite to what would be expected if this factor was the primary driver.

3. Results and discussion

3.1. Changes in species composition along the Colockum elevational gradient

Each study site contained a distinct species composition (Table 3). The shrub-steppe site is dominated by *Artemisia tridentata* with a minor component of *Artemisia tripartita*. The shrub steppe/forest ecotone site contains a diverse shrub layer primarily composed of *A. tripartita*, *Amelanchier alnifolia*, *Rosa woodsii*, and *Symphoricarpos albus*, with *A. tridentata* also present. *Pinus pon-*

Table 2
Functional characteristics of dominant tree and shrub species along the Colockum elevation gradient. Shade, drought, and fire tolerance are based on the USDA Forest Service Fire Effects Information System (http://www.fs.fed.us/database/feis/) and Minore (1979). Precipitation and temperature values are the annual medians for each species' North American distribution (Thompson et al., 1999). ND = no data.

	Shade tolerance	Drought tolerance	Fire tolerance	Precipitation ($mm\,y^{-1}$)	Mean annual temperature (°C)
Tree species					
Abies grandis	High	Medium	Medium	1260	6.6
Abies lasiocarpa	High	Low	Low	620	0.8
Larix occidentalis	Low	Medium	High	760	4.5
Picea engelmannii	Medium	Medium	Medium	720	2.1
Pinus albicaulis	Low	ND	ND	860	1.1
Pinus contorta	Low	High	Medium	620	1.2
Pinus ponderosa	Low	High	High	530	7.5
Pseudotsuga menziesii	Medium	High	High	740	4.1
Shrub species					
Amelanchier alnifolia	Medium	Medium	High	470	0.8
Artemisia tridentata	Low	High	Low	340	6.8
Artemisia tripartita	Low	High	High	ND	ND
Rosa woodsii	Medium	Medium	High	ND	ND
Sambucus cerulea	Medium	Medium	High	ND	ND
Symphoricarpos albus	Medium	Medium	High	ND	ND

derosa is the sole conifer at this site. The dry forest site has a much reduced shrub layer with only *A. alnifolia* and *Sambucus cerulea*. The overstory at this site contains *P. ponderosa*, *P. menziesii*, *Abies grandis*, and *L. occidentalis*. The montane forest site is dominated by *A. grandis* but also contains *P. ponderosa*, *L. occidentalis*, *Picea engelmannii*, and *A. lasiocarpa*. At the upper end of the elevation gradient, the subalpine forest site is dominated by *A. lasiocarpa* and *Pinus contorta*, with minor contributions from *Pinus albicaulis* and *P. engelmannii*.

Forest stand structure varied considerably across the elevational gradient (Table 3). On average, trees were largest within the dry forest, while density increased with elevation. Also notable were extremely dense but patchily distributed *A. lasiocarpa* seedlings and saplings at the subalpine site (e.g., >13,000 stems/ha for *A. lasiocarpa* < 1.4 m height).

In the shrub steppe site, species composition did not change substantially over time (Fig. 2). At all other elevations, we identified substantial changes in species composition during the 20th century (Fig. 3). At the shrub steppe/forest ecotone, there were young individuals of two drought-tolerant species, *A. tripartita* and *P. ponderosa*, but no old individuals (Figs. 2–4). In the dry, montane, and

subalpine forest sites, species composition shifted from fire and drought-tolerant species to shade-tolerant species (Fig. 4), showing increases in *P. menziesii*, *A. grandis*, and *A. lasiocarpa*, respectively, and decreases in *P. ponderosa*, *L. occidentalis*, and *P. contorta*, respectively (Fig. 3).

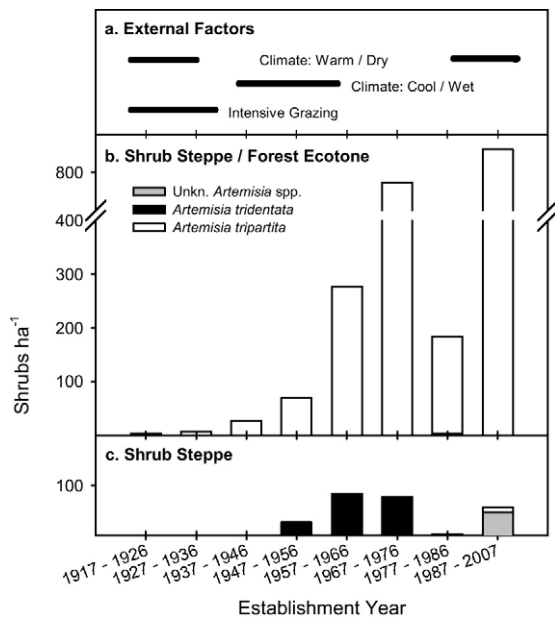### 3.2. Colockum environmental history

3.2.1. Climate

During the past 200 years, the inland PNW has experienced significant climatic variation at annual to decadal scales, due in part to the El Niño Southern Oscillation and the Pacific Decadal Oscillation. Tree-ring climate reconstructions and instrumental records identify region-wide periods of abnormally cool-wet conditions from the 1880s until the 1910s and abnormally warm-dry conditions during the 1920s and 1930s (Gedalof and Smith, 2001; Hessburg et al., 2005b). These trends are also evident from local meteorological records (Fig. 5). Local meteorological records also indicate a cooler period from the mid-1940s to late 1950s and a warmer period from the mid-1980s to present (Fig. 5). The Colockum area has experienced greater warming than the state as a whole. At Wenatchee,

Table 3
Stand composition and structural characteristics (mean ± SE) of the four forest sites. QMD = quadratic mean diameter. NA = species not present.

Site/species	Density (trees ha^{-1})		Basal area ($m^2\,ha^{-1}$)	QMD (cm)
	<1.4 m height	>1.4 m height		
Subalpine forest	13,489 ± 13,244	1302 ± 853	46 ± 4	24 ± 7
Abies lasiocarpa	13,387 ± 13,284	1059 ± 1005	24 ± 13	19 ± 5
Picea engelmannii	33 ± 58	10 ± 17	2 ± 3	15 ± 26
Pinus albicaulis	68 ± 76	18 ± 31	<1	<1
Pinus contorta	NA	212 ± 185	20 ± 12	37 ± 5
Pinus ponderosa	NA	3 ± 6	<1	18 ± 32
Montane forest	1667 ± 1557	1277 ± 376	30 ± 23	18 ± 9
Abies grandis	1533 ± 1427	1017 ± 431	16 ± 8	15 ± 8
Abies lasiocarpa	17 ± 29	NA	NA	NA
Larix occidentalis	NA	27 ± 25	2 ± 3	21 ± 19
Picea engelmannii	33 ± 29	NA	NA	NA
Pinus contorta	NA	3 ± 6	<1	10 ± 17
Pinus ponderosa	NA	7 ± 6	1 ± 1	31 ± 29
Pseudotsuga menziesii	83 ± 144	223 ± 65	10 ± 13	20 ± 12
Dry forest	400 ± 178	777 ± 180	43 ± 8	27 ± 1
Abies grandis	83 ± 118	33 ± 29	<1	10 ± 9
Larix occidentalis	NA	50 ± 36	2 ± 1	29 ± 17
Pinus ponderosa	17 ± 24	260 ± 156	28 ± 5	39 ± 8
Pseudotsuga menziesii	300 ± 178	433 ± 115	12 ± 5	19 ± 2
Shrub steppe/forest ecotone	67 ± 76	107 ± 119	4 ± 5	26 ± 13
Pinus ponderosa	67 ± 76	107 ± 119	4 ± 5	26 ± 13

Fig. 2. Age distributions for *Artemisia* species and key external factors in the Colockum Wildlife Area. Estimated time periods of key factors affecting abundance (a). Estimated age class distribution of *Artemisia spp.* in the shrub steppe/forest ecotone (b) and shrub steppe (c). Unknown *Artemisia* spp. were too small (seedlings) to identify to species.
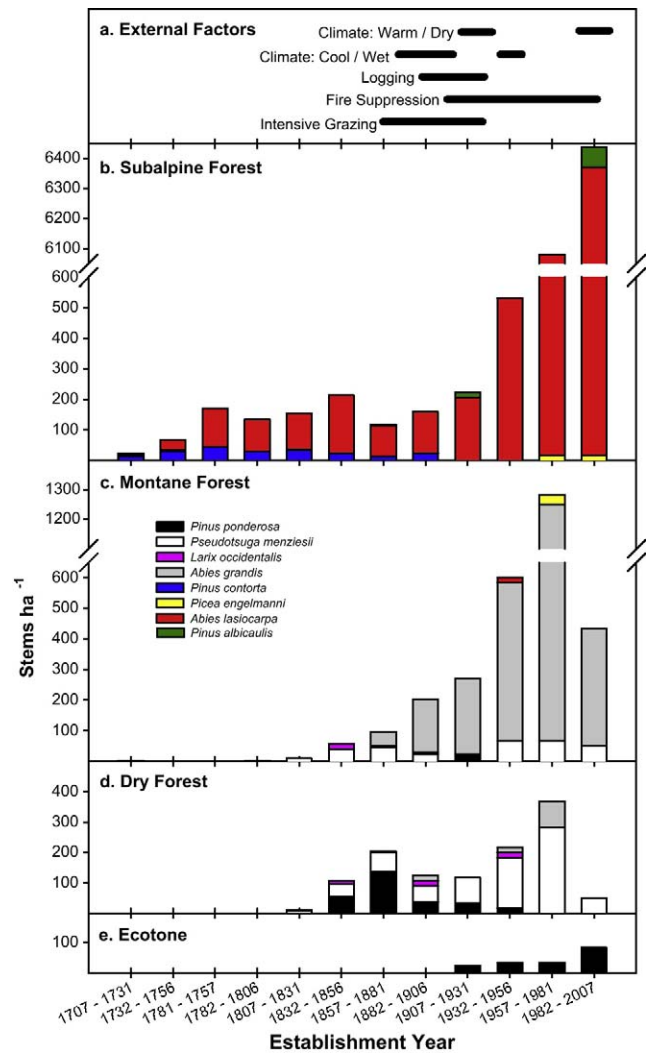
average annual temperature increased at a rate of 1.9 °C per century from 1931 to 2002 (NOAA, 2010). Mean annual precipitation, on the other hand, has not shown a significant trend over this period (NOAA, 2010).

3.2.2. Fire

Fire is one of the primary disturbance processes determining historical ecosystem structure and composition in the inland PNW (Hessburg and Agee, 2003). Historical fire extent was largely driven by climate variation at annual to decadal scales (Hessl et al., 2004; Heyerdahl et al., 2002, 2008). Native Americans almost certainly influenced fire regimes through the effects of their grazing animals on fine fuels and their intentional and unintentional ignitions (Boyd, 1999; Hessburg and Agee, 2003). The Wenatchee Mountains were inhabited and used by various tribes, including the Wenatchee, Rock Island, Yakima, Entiat and Chelan (Dow, 1963). Native American influences on the Colockum landscape dramatically declined with disease epidemics beginning in the 1840s and forced removal by the U.S. Army in the 1850s.

Formal fire suppression policies began in 1911, but fire exclusion began in the Colockum when large livestock herds were introduced in the 1870s and removed many of the fine fuels (Belsky and Blumenthal, 1997; Everett et al., 2000; Hessburg and Agee, 2003). At present, it is widely recognized that fire suppression in forests once characterized by low severity-high frequency fire regimes has promoted uncharacteristically high stand densities and fuel loadings (Agee and Skinner, 2005; Brown et al., 2004; Everett et al., 2000, 2007).
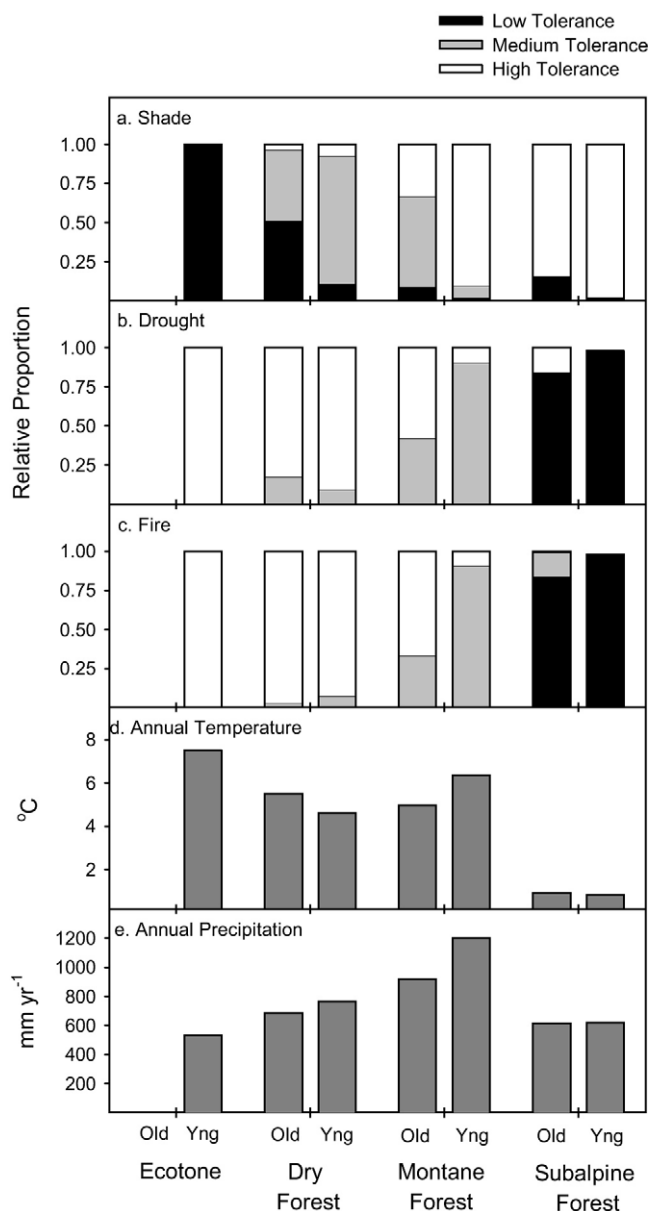
Historical fire regimes vary greatly along the Colockum elevation gradient. The historical fire frequency in sagebrush steppe ecosystems and the role of fire in these systems is currently a source of debate; estimates of fire return intervals in pre-settlement times range from 50 to 240 years (Baker, 2006; Mensing et al., 2006; Young and Evans, 1981). Fires in sagebrush steppe systems generally kill *A. tridentata*, though associated bunchgrasses tend to survive. Fire frequencies have increased significantly since European settlement, mainly associated with the expansion of exotic

Fig. 3. Age distributions of tree species and key external factors in the Colockum Wildlife Area. Estimated time periods of key factors affecting abundance (a). Estimated age class distribution of live trees in the four forest sites (b–e) ordered so that elevation decreases from (b) to (e).

annual grasses such as cheatgrass (*Bromus tectorum*; Mack, 1981). This highly flammable winter annual fuels larger and more frequent fires than these systems experienced historically, leading to the extirpation of sagebrush and reduced vigor and survival of the native bunchgrasses (D'Antonio and Vitousek, 1992).

For the forested sites, regional studies and the current vegetation indicate a geographic transition from historical low severity-high frequency fire regimes at lower elevations (shrub steppe/forest ecotone and dry forest) to a high severity-low frequency regime in the subalpine forest (Agee, 1993; Everett et al., 2000; Wright and Agee, 2004). In areas with historical low-severity fire regimes, the impacts of wildfire suppression, grazing and Native American burning on fire dynamics are substantial (Hessburg and Agee, 2003). Less is known about the historical dynamics of mixed- and high-severity fire regimes that characterize the upper Colockum elevations. At upper elevations, fine fuels play a smaller role in determining fire dynamics and thus the impacts of grazing and Native American use are less certain. Fire in these systems is more dependent upon favorable weather conditions and consequently climate variations play an increasingly important role in fire dynamics (Bessie and Johnson, 1995).

Fig. 4. Species composition of old (100–200 years) and young ('Yng'; 0–100 years) trees in the four forest sites, expressed as the relative proportion of trees with low, medium, or high tolerance for shade (a), drought (b), and fire (c) and as weighted average temperature (d) and precipitation (e) values based on the medians for each species (Table 2).

3.2.3. Livestock grazing

Although livestock grazing has not received the same attention within the ecological literature as fire, it has undoubtedly played a major role in shaping modern day ecosystems across the inland PNW. Grazing by Native American horses may have had localized impacts (Hessburg and Agee, 2003), but European settlement brought widespread grazing to the region (Galbraith and Anderson, 1991). Cattle were introduced to the Colockum around 1870 (Dow, 1963). Large herds were established quickly, and cattle grazed in nearly all habitats, from low-elevation shrub steppe to high-elevation subalpine meadows. By the 1890s, severe overgrazing was widely reported within the Colockum area and across the inland PNW (Bright, 1996; Dow, 1963; Galbraith and Anderson, 1991; Hessburg and Agee, 2003). Overgrazing often resulted in the near total elimination of native herbaceous vegetation cover, destruction of woody seedlings, widespread soil disturbance, and establishment of exotic annual weeds. Across large areas of shrub steppe in the inland PNW, overgrazing was closely followed by cheatgrass expansion during the late 19th and early 20th centuries (Mack, 1981).
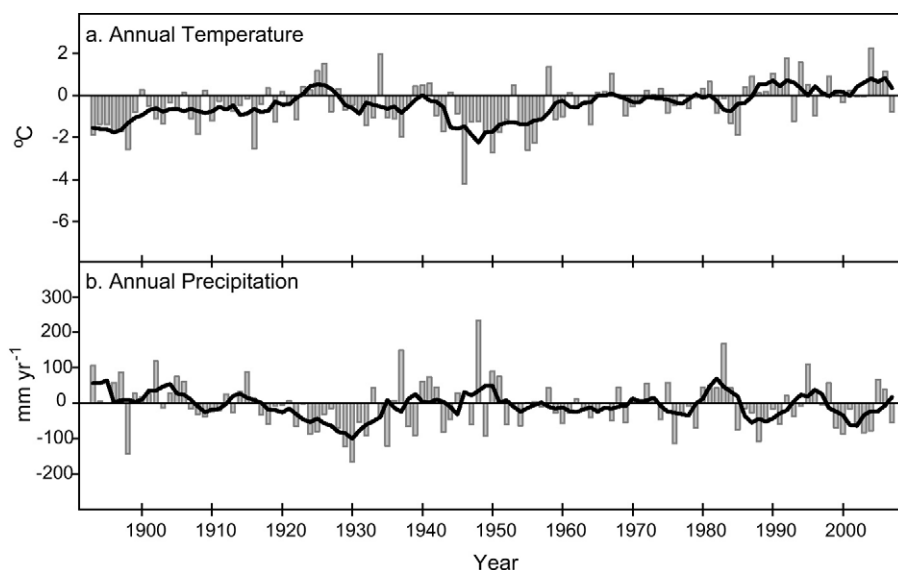
The degradation of range conditions promoted a widespread transition to sheep grazing during the 1890s. Sheep could more fully "utilize" the remaining vegetation on rangelands that could no longer support cattle (Bright, 1996). From the early 1900s onward, the Coffin family annually moved 60,000–100,000 sheep through the Colockum area (Bright, 1996; Dow, 1963). Washington Department of Fish and Wildlife records indicate that "no effective grazing management was ever used" within the Colockum, and that stock would follow the snowline up to the high elevation summer pastures of Colockum Pass (Pete Lopushinsky, WDFW, personal communication). The 1934 Taylor Grazing Act led to regulation of grazing on federal lands and reduced grazing intensities across the region. When grazing pressure was reduced in subsequent years, the reduction in herbaceous competition and exposed mineral soil often resulted in pulses of tree and shrub establishment (Bakker and Moore, 2007; Belsky and Blumenthal, 1997; Zimmerman and Neuenschwander, 1984). Colockum continues to be grazed by livestock each year (Tom Brannon, Washington State University, personal communication), though at much lower intensities than were experienced historically.

3.2.4. Logging

Logging occurred throughout the lower elevations of the eastern Cascades during the late 19th and early 20th centuries (Hessburg and Agee, 2003). In the Wenatchee Mountains, early logging targeted large *P. ponderosa* to supply the rapidly expanding apple industry with shipping boxes (Moltke, 1965). This high-grade logging removed the largest, oldest, and most fire resistant trees, and created substantial soil disturbances that promoted additional conifer establishment. As a result, high-grade logging exacerbated the effects of fire suppression in dry forests (Hessburg and Agee, 2003; Wright and Agee, 2004). Early logging in the Wenatchee Mountains focused on relatively flat areas, but by the 1930s logging operations had moved further into the mountains and harvested a wider variety of tree sizes and species (Moltke, 1965). Logging has not occurred on lands owned by the Washington Department of Fish and Wildlife in the Colockum since the 1950s, and precise harvest records from earlier dates are lacking (Tom Brannon, Washington State University, personal communication).

3.3. Relative influence of environmental factors along the elevational gradient

By juxtaposing the observed changes in species composition across our elevational gradient with the environmental histories of each site, we conclude that climate has been much less important than fire, livestock grazing, and logging in explaining the observed changes (summarized in Table 4). Below, we summarize our analysis for each site.

Table 4
Summary of the influences of climate, fire, livestock grazing, and logging on woody species composition along the Colockum elevational gradient, based on quantitative analyses of tree data and qualitative assessments of the environmental history of each site.

Site	Climate	Fire	Grazing	Logging
Subalpine forest	Possible	Unlikely	Unlikely	No
Montane forest	Possible	Possible	Possible	Unlikely
Dry forest	No	Yes	Possible	Yes
Shrub steppe/forest ecotone	Unlikely	Yes	Yes	Unlikely
Shrub steppe	Unlikely	Unlikely	Yes	No

Fig. 5. Annual mean temperature (a) and total precipitation (b) anomalies (from 1970 to 1999 means). Data are averaged from the Ellensburg, Waterville, and Wenatchee weather stations (see Fig. 1 for station locations in relation to study plots). Solid lines are 5-year running averages.

3.3.1. Shrub steppe

It is difficult to attribute the current ecological condition of the shrub steppe site to climate variation. Survival of *A. tridentata* seedlings is greatest in wetter than average periods (Cawker, 1980). The establishment during 1947–1956 occurred during a cooler period (Fig. 2b), but subsequent establishment pulses in 1957–1976 and 1987–2007 occurred during predominately warmer and drier conditions (Fig. 2c). The comparatively short life-span (compared to conifers) and fire intolerance of *A. tridentata* limits the temporal span of our inferences at this site. *A. tridentata's* sensitivity to fire (Table 2), however, suggests that this location has not burned since before the 1947–1956 period. This fire-free interval is arguably within the historical range of variability for shrub steppe ecosystems (Baker, 2006; Mensing et al., 2006). With its low elevation and gentle, easily accessible topography, the shrub steppe site likely received the greatest grazing pressure of all our sites (Rex Crawford, Washington Natural Heritage Program, Department of Natural Resources, personal communication). The most recent *Artemisia* establishment pulse (Fig. 2c) began after livestock were excluded following the designation of this location as a Washington State Natural Area Preserve in 1989.

3.3.2. Shrub steppe/forest ecotone

The shrub steppe/forest ecotone site is easily accessible and presumably received heavy grazing starting in the 1870s. In contrast to the shrub steppe site, the dominant shrubs here are sprouting species highly adapted to frequent fire (Table 2) and are perhaps a legacy of a pre-suppression low severity-high frequency fire regime. A reduction in fire frequency, initially due to cattle grazing and cessation of Native American ignition and later due to wildfire suppression, would promote *P. ponderosa* establishment (Heyerdahl et al., 2006) and explain the establishment pulse starting in the early 20th century (Fig. 3e). The lack of old trees suggests that the area was not treed before then: there is no direct evidence of logging (stumps, etc.) at the site, nor were any trees identified that established during the late 1800s (and which would have been too small for high-grade logging). At other ecotones in western North America, *P. ponderosa* establishment has been linked to the combination of sufficient seed rain and cooler and wetter climatic conditions (League and Veblen, 2006). However, initial *P. ponderosa* establishment at the Colockum ecotone site occurred during a relatively dry period (1907–1931), indicating that climate was not likely a direct driver of vegetation dynamics. It appears that cessation of low severity-high frequent fire, in part due to historical overgrazing, is the major driver of *P. ponderosa* expansion along the shrub steppe/forest ecotone.

3.3.3. Dry forest

Older trees (pre-1900 establishment) of fire tolerant species at the dry forest site indicate that it was historically characterized by a low severity-high frequency fire regime (Fig. 4c; Agee, 1993; Wright and Agee, 2004). Twentieth-century conifer establishment has produced a dramatic shift in species composition towards increased shade tolerance and decreased fire and drought tolerance (Fig. 4). This trend is also found in other dry forests across the interior U.S. that were once maintained by frequent fire, and indicates the importance of fire suppression for the Colockum dry forest (Agee, 1993; Everett et al., 2000; Harrod et al., 1999; Kennedy and Wimberly, 2009). There is also direct evidence of high-grade logging at this location. The loss of large, old *P. ponderosa* from the current stand due to logging amplifies the transition in stand trait characteristics towards increased shade and decreased fire and drought tolerance. As at the shrub steppe/forest ecotone, intense grazing in the late 19th century may have reduced fire frequency well before intentional fire suppression began in 1911 (Hessburg and Agee, 2003). It is unclear from the age structure, however, if or how grazing directly influenced conifer establishment and species composition. Climate variation does not explain patterns of conifer establishment in the dry forest. Furthermore, a comparison of the climate tolerances of individual conifer species indicates a shift during the past 100 years toward species more characteristic of cooler conditions (Fig. 4d), a trend that runs counter to the warming that has actually occurred in the Colockum area (Fig. 5).

3.3.4. Montane forest

During the 20th century, the montane forest site experienced a significant shift in species composition toward more shade tolerant and less drought and fire tolerant species (Fig. 4). This shift could have been promoted by fire suppression; grazing may have had an indirect fire exclusion effect. However, it is unclear whether the current structure and fire return interval is outside of its historical range of variability. The increasing dominance of *A. grandis* may simply represent the successional development of an *A. grandis* forest (Franklin and Dyrness, 1988). In the eastern Washington Cas-

cades, montane forests are generally classified as having a mixed severity fire regime, with characteristics of both low and high severity regimes (Agee, 1993). The very nature of a mixed severity regime makes it difficult to characterize the regime of a particular location. Direct physical evidence of logging was not found in the montane forest site. Climate variation does not explain the patterns and timing of conifer establishment. Unlike the dry forest, the montane forest is transitioning to marginally "warmer" species (Fig. 4d). However, the current trajectory of the stand was established well before significant 20th century warming, indicating that warming has not played a primary role in determining its current ecological condition.

3.3.5. Subalpine forest

The subalpine forest site is shifting from a stand co-dominated by *P. contorta* and *A. lasiocarpa* to nearly pure *A. lasiocarpa*. As at lower elevations, this is a transition towards increased shade tolerance and decreased fire and drought tolerance (Fig. 4a–c). However, *P. contorta* is recognized as a seral species within subalpine forests and replacement by *A. lasiocarpa* represents typical successional development (Agee, 1993). Subalpine forests are characterized by high-severity fires with very long (200–300+ years) return intervals, permitting long successional sequences. Generally, subalpine forests experienced grazing only if they served as driveways to higher elevation pastures (Bright, 1996). However, this grazing would not have had the same effects on the historical fire regime as at lower elevations due to the long fire return intervals. Similarly, while fire suppression may have reduced the prevalence of fires within the subalpine forest, this site is still within the historic range of variability (Agee, 1993). Compared to lower elevation sites, anthropogenic influences on the ecological condition of the subalpine forest are minimal.

3.4. Projected climate changes and land management implications

Projections of future climate in the inland PNW strongly point towards warmer, wetter winters and warmer, drier summers, though with little change in mean annual precipitation (Elsner et al., 2009; Mote and Salathe, 2009). IPCC (2007) projections, under the B_1 (lower), A_1B (medium), and A_2 (higher) emissions scenarios, project a $3.1 \pm 0.5\,^\circ$C increase in mean annual temperature and a $8 \pm 1\%$ increase of precipitation from 2000 to 2100 in the Colockum area (IPCC, 2007; Gonzalez et al., 2010).

Our elevational gradient illustrates the importance of integrating considerations of climate change with land use histories, which differ in relative importance among sites (Table 4). These differences must be recognized when managing sites for any objective, including adapting to current and future climate change.

At the lower end of the elevational gradient, the combined effects of high severity fire and invasion by exotic annual plants, particularly *Bromus tectorum*, present the greatest conservation threat for the shrub steppe and shrub steppe/forest ecotone. Forecasted climate change may strengthen the synergistic interaction between fire and exotic annuals (Ziska et al., 2005). Species with early and flexible phenologies (e.g., *B. tectorum*) may benefit from projected increases in winter precipitation and temperature while tolerating decreases in summer precipitation (Bradley, 2009). Enhanced growth of exotic annuals will in turn elevate fire risk due to increased fine fuel loads. Climate change will elevate the risk of the shrub steppe permanently shifting to exotic annual grassland through repeated, high intensity fires (West and Young, 2000). Despite the historical importance of frequent, low severity fire at the shrub steppe/forest ecotone (Everett et al., 2000), the re-occurrence of fire under future climate changes may have similar effects as in the shrub-steppe; the promotion of an exotic annual

grassland. Active management to limit the spread of exotic annuals will help maintain the ecological functioning and resilience of shrub steppe/forest ecotones.

Dry forests in the Colockum area have experienced substantial changes in composition and structure due mainly to the combined impacts of grazing, fire suppression and logging. These factors have left the dry forests particularly sensitive to the effects of projected future climate change. Despite the positive effects of increased carbon dioxide enrichment on water use efficiency (Latta et al., 2010), elevated summer and winter temperatures and decreased summer precipitation may increase drought stress during the growing season (Littell et al., 2009; Lutz et al., 2010). Recent stand conditions have promoted the establishment of conifer species that may not be able to tolerate the future climatic conditions at this elevation (e.g. *A. grandis* due to elevated drought stress and *P. menzesii* due to altered budburst timing; Harrington et al., 2010; Minore, 1979). Yet, Littell et al. (2009) argue that the greatest impacts of climate change will not be the direct physiological effects of climate on productivity and species distribution, but will instead be the indirect effects mediated through fire and insect attack (primarily mountain pine beetle, *Dendroctonus ponderosae*). *P. ponderosa* mortality due to the mountain pine beetle may increase due to climatic effects on the beetle life cycle and to conifer physiological stress (Kliejunas et al., 2009; Oneil, 2006). Elevated levels of drought and beetle mortality (and associated contributions to woody fuel) combined with an increased frequency of severe fire weather means that the dry forest will continue to be at risk of catastrophic disturbance. Active restoration, including thinning from below and re-establishment of frequent, low intensity fire, is necessary to sustain the structure and function of the dry forest, including its associated biological diversity (Agee and Skinner, 2005; Brown et al., 2004).

Montane forests may also be candidates for active management to create more fire resilient stands. The current stand condition is primed for high severity fire. As with the dry forest, projected climate changes will elevate the risks of both drought stress and insect attack, which in turn elevate fire risks. Fire risks in the montane forest may be even more closely tied to climate change than in the dry forest. At montane elevations, snowpack is a critical source of moisture for the growing season. Consequently, expected shifts in the form of winter precipitation from snow to rain (Elsner et al., 2009) may dramatically affect levels of summer drought stress and fuel moisture in montane forests (e.g. Littell et al., 2009; Lutz et al., 2010). However, the mixed severity fire regime of these forests, and the lack of clarity as to the main drivers of change in species composition, mean that there is still uncertainty as to what management actions would increase ecosystem resilience. Further research on these forest types is required to more confidently inform management decisions in light of future changes in climate.

To date, the subalpine forest has experienced the least change due to human influences. Direct management intervention in these stands is not currently required. Nonetheless, climate change may bring dramatic changes to the ecological structure of subalpine forests. As with the montane forest, the moisture balance of subalpine forests will be highly sensitive to the projected decreases in snowpack associated with climate change (Elsner et al., 2009). Increased temperatures and elevated moisture stress may in turn enhance the susceptibility of *A. lasiocarpa* to western spruce budworm (*Choristoneura occidentalis*) and *P. contorta* to mountain pine beetle attack and increase the likelihood of high severity fire (Edmonds et al., 2011; Littell et al., 2009).

4. Conclusions

We have shown that species composition in the Colockum has shifted away from fire and drought-tolerant species and toward

shade-tolerant species. To varying degrees along the elevational gradient, these changes are consistent with the history of human land use including fire suppression, logging and intensive livestock grazing. At times these changes are opposite those we expect would be most suited to projected future climates. Broad-scale climatic factors must be integrated with land use histories to understand how ecosystems have developed. Understanding this development is critical for deciding how ecosystems should be managed to achieve conservation goals, whether for resilience to future changes and disturbances or for biological diversity (Keane et al., 2009).

The environmental history of the Colockum area clearly demonstrates the extremely long-lasting effects of our actions on ecosystem properties (Lindenmayer et al., 2008). These consequences may be rapidly apparent (e.g., logging and intensive grazing), or may take decades to become evident (e.g., fire suppression). Natural resource managers should recognize that the current status of an ecosystem reflects historical land uses, and that contemporary management actions can have long term effects on ecosystem structure.

Studies of past ecosystem responses to climate variation are an important tool for projecting the effects of future climate change (Allen and Breshears, 1998; Gonzalez et al., 2010; Keane et al., 2009). However, these studies must also address environmental history to accurately identify climatic influences (Kelly and Goulden, 2008). To effectively manage the effects of climate change, natural resource managers must also explicitly incorporate environmental history in their management decisions. Understanding the processes that generated an ecosystem's current structure will lead to more informed management decisions to effectively respond to projected climate changes.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2010.09.021.

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