ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE

Socio-Ecological Systems

Fire severity drives understory community dynamics and the recovery of culturally significant plants

Sarah Dickson-Hoyle[1] | **Sƛ̓uxwtéws (Bonaparte First Nation)**[2] |
Skeetchestn Natural Resources Corporation[3] | **Arial Eatherton**[1] |
Jennifer N. Baron[1] | **Florencia Tiribelli**[1] | **Lori D. Daniels**[1]

[1]Department of Forest and Conservation Sciences, University of British Columbia, Vancouver, British Columbia, Canada

[2]Sƛ̓uxwtéws (Bonaparte First Nation), Cache Creek, British Columbia, Canada

[3]Skeetchestn Indian Band, Savona, British Columbia, Canada

Correspondence
Sarah Dickson-Hoyle
Email: sarah.dickson-hoyle@ubc.ca

Abstract

Anthropogenic influences are altering fire regimes worldwide, resulting in an increase in the size and severity of wildfires. Simultaneously, throughout western North America, there is increasing recognition of the important role of Indigenous fire stewardship in shaping historical fire regimes and fire-adapted ecosystems. However, there is limited understanding of how ecosystems are affected by or recover from contemporary "megafires," particularly in terms of understory plant communities that are critical to both biodiversity and Indigenous cultures. To address this gap, our collaborative study, in partnership with Secwépemc First Nations, examined understory community recovery following a large, mixed-severity wildfire that burned in the dry and mesic conifer forests of British Columbia, Canada, with a focus on plants of high cultural significance to Secwépemc communities. To measure the effect of a continuous gradient of fire severity across forest types, we conducted field assessments of fire severity and sampled understory plants 4 years postfire. We found that native species richness and richness of species of high cultural significance were lowest in areas that burned at high severity, with distinct compositional differences between unburned areas and those that burned at high severity. These findings were consistent across forest types characterized by distinct historical fire regimes. In contrast, richness of exotic species increased with increasing fire severity in the dominant montane interior Douglas-fir forests, with exotic species closely associated with areas that burned at high severity. Our study indicates that recent megafires may be pushing ecosystems outside their historical range of variability, with negative implications for ecosystem recovery and cultural use across these fire-affected landscapes. We also found consistently higher plant diversity, and both native and cultural species richness, in subalpine forests. Collectively, our results provide strong evidence of the ecological and cultural significance of low- to moderate-severity fire and subalpine forests, and the longstanding and ongoing role of Indigenous peoples in

shaping these landscapes. As wildfires continue to impact ecosystems and human communities, this study offers novel insights into the recovery of important ecological and cultural values, while highlighting the need to support ethical research collaborations with Indigenous communities and Indigenous-led revitalization of fire and plant stewardship.

INTRODUCTION

Fire is a key disturbance agent in many ecosystems worldwide, shaping the global distribution of vegetation and biodiversity, and ecosystem heterogeneity across a range of spatiotemporal scales (Bond et al., 2005; Hoffman et al., 2021; McLauchlan et al., 2020). In fire-prone ecosystems, such as the dry and mixed conifer forests of western North America, including British Columbia (BC), Canada, vegetation structure, composition, and diversity are strongly influenced by patterns of fire frequency, size, seasonality and severity, collectively referred to as the fire regime (Daniels et al., 2017; Turner, 2010). While humans have long influenced fire regimes (Bowman et al., 2011), recent and rapid anthropogenic impacts are altering fire regimes worldwide, resulting in an increase in size and severity of wildfires (Bowman et al., 2020; Coops et al., 2018; Hanes et al., 2019); a trend that is only expected to increase (United Nations Environment Programme [UNEP], 2022). Western North America is a global hotspot for these "megafires," defined as spatially and temporally continuous fires exceeding 10,000 ha in area (Linley et al., 2022), which pose increasing risks to people and ecosystems alike (UNEP, 2022). Conservation scientists and land managers now highlight concerns that the scale and severity of these megafires may lead to "catastrophic" vegetation degradation or ecosystem conversion (Coop et al., 2020; Falk et al., 2022; Seidl & Turner, 2022; Stephens et al., 2014). As such, there is a critical need to better understand how ecosystems are affected by and recover from megafires (Nimmo et al., 2022), including fine-scale vegetation responses (Donovan et al., 2020).

These challenges are particularly prevalent throughout western North America, where increasing evidence points to the role of over a century of fire suppression, exclusion of Indigenous peoples and their fire stewardship practices, and timber-oriented forest management in disrupting historical fire regimes (Hagmann et al., 2013, 2021; Knight et al., 2022; Levine et al., 2022). In BC, these impacts followed European colonization from the mid-1800s and have resulted in widespread fire deficits across many forest ecosystems (Baron et al., 2022; Hagmann et al., 2021; Parisien et al., 2020). Many fire scientists and land managers are now advocating the need to "restore fire-resilient landscapes" (Hessburg et al., 2015), including through the restoration of historical fire regimes (Hagmann et al., 2021). Simultaneously, western-trained scientists are increasingly recognizing the role of Indigenous cultural burning in shaping historical fire regimes (Copes-Gerbitz et al., 2023) and associated biodiversity and ecosystem structure (Fletcher et al., 2021; Hoffman et al., 2021; Mariani et al., 2022).

Improved understanding of understory plant community responses to fire is particularly important given the critical contribution of understory plants to biodiversity and ecosystem functioning. In temperate and boreal forest ecosystems, understory plants contribute the majority of vascular plant diversity (Halpern & Spies, 1995; Hart & Chen, 2006; Kerns et al., 2006) and regulate a wide range of ecosystem processes such as nutrient cycling, soil fertility and retention, and energy flow (Gilliam, 2007). Understory plants are also critical to many Indigenous cultures as a source of food and medicines and supporting cultural practices and connections to the land (Deur & Turner, 2005; Ignace & Ignace, 2017; Kuhnlein & Turner, 1991; Turner et al., 2013) and have long been managed and maintained by Indigenous peoples through frequent, low-severity burning (Anderson, 2005; Dickson-Hoyle et al., 2022; Gottersfeld, 1994; Turner, 1999). However, there have been relatively few studies in western North America of understory plant community responses to wildfire, with most studies occurring in the southwestern United States, the Californian Sierra Nevada, or, to a lesser extent, in Canadian boreal forests. Further, while recent collaborative studies have examined the responses of single species to prescribed or cultural fire or other restoration treatments (see for e.g., Halpern, 2016; Hart-Fredeluces et al., 2021; Marks-Block et al., 2019), to our knowledge, none have examined the responses of a diversity of culturally significant species to wildfire.

Understory plants exhibit diverse responses to fire, with community-level responses shaped by both the characteristics of the fire, such as duration or severity, and the attributes of species growing in and near the burn area (Fornwalt & Kaufmann, 2014; Kerns et al., 2006). Following a fire, recovery can follow three pathways. In situ recovery is driven by individuals that survive within the burned area; ex situ recovery is driven by off-site colonization from outside the fire footprint; and nucleated recovery is driven by survivors in fire refugia that remained unburned or burned less severely (Downing et al., 2020; Nimmo et al., 2022). These three pathways are facilitated by a range of plant fire-adaptive traits, such as the capacity to resprout (e.g., from underground structures such as large taproots, corms, or rhizomes), fire-cued seed germination or seed dispersal capacity, and availability of and distance to propagule source (Clarke et al., 2013; Morgan et al., 2015; Nolan et al., 2021; Roberts, 2004; Stark et al., 2006).

Regeneration traits and associated plant community responses are tightly linked to fire regime attributes. For example, fire-resilient traits such as the ability to resprout from below ground organs may provide an advantage in low- to moderate-severity fire regimes, but not protect against damage from high-severity crown fire that results in high soil temperatures and consumes structures located in organic layers (Midgley et al., 2011; Miller & Safford, 2020; Nolan et al., 2021; Stephan et al., 2010). In contrast, high-severity wildfire can facilitate the establishment and spread of exotic species (Crawford et al., 2001; Fornwalt et al., 2010; Freeman et al., 2007), which are often seral opportunists that can colonize open, disturbed habitats and dominate immediate postfire environments (Halpern, 1989).

Fire severity, defined as the immediate and direct effect of fire on an ecosystem through loss or decomposition of organic matter (Keeley, 2009), is an important driver of understory plant composition and structure (Abella & Fornwalt, 2015; Burkle et al., 2015; Huisinga et al., 2005; Morgan et al., 2015). However, the effects of fire severity on understory plant communities are not consistent across ecosystems and are generally poorly understood (Abella & Springer, 2015). Studies across temperate and boreal mixed conifer forests in western North America variably found that species diversity increased (Huisinga et al., 2005, 6 years postfire) or decreased (Halpern & Antos, 2022, 2 years postfire; Richter et al., 2019, 5–14 years postfire) with high-severity fire; that species richness peaked in low- to moderate-severity burns (Richter et al., 2019, 5–14 years postfire); or that communities in unburned areas either differed (Burkle et al., 2015, 6–12 years postfire) or were not compositionally distinct (Day et al., 2017, 10 years postfire) from burned areas. While understory species richness has been shown to plateau as early as 3–4 years postfire (Day et al., 2017; Wang & Kemball, 2005), other studies highlight the effect of time since fire on species richness or composition, with evidence of ongoing differentiation or declines in diversity up to 10–15 years postfire (Abella & Fornwalt, 2015; Abella & Springer, 2015). For example, recent research found that following moderate- and high-severity fires in ponderosa pine and mixed conifer forests in California, alpha diversity significantly declined and community divergence between fire severity classes increased with time, up to 9 years after fire (Weeks et al., 2023).

In their review of different understory community responses to wildfire across the Western United States, Miller and Safford (2020) found that understory recovery is contingent upon the historical fire regime. Specifically, they hypothesized that postfire understory plant richness would be maximized under the disturbance severity historically associated with the given ecosystem. For example, in ecosystems historically characterized by a frequent, low-severity fire regime, such as low-elevation dry ponderosa pine forests, high-severity fire would have a negative effect on plant richness, relative to low- or moderate-severity fire (Miller & Safford, 2020). Brodie et al. (2021) further demonstrated that productivity mediates the effect of fire severity on understory plants. They found that higher productivity stands were associated with greater postfire colonization by far-dispersing species due to greater competitive release, through greater changes in light and bare soil availability.

However, the lack of either experimental or observational studies examining continuous fire severity gradients, the limited studies on the effects of wildfire on understory plants across ecosystem types, and the variable findings described above mean that no conclusive trends can be identified (Abella & Springer, 2015; Miller & Safford, 2020). Understanding how the full spectrum of fire severity affects ecosystem responses is critical for postfire ecosystem management (UNEP, 2022), biodiversity conservation, and the restoration of fire-adapted and fire-prone forest ecosystems (Hart & Chen, 2008; Keeley, 2009).

In this study, we examined the effects of fire severity on understory plant community dynamics, with a focus on plants of high cultural significance to the Indigenous people of the Secwépemc Nation. To do so, we sampled understory plant communities across a fire severity gradient four years after the 2017 "Elephant Hill" wildfire that burned throughout Secwépemc territory (Secwepemcúlecw). Specifically, we aimed to determine: (1) how fire severity affected understory species richness, diversity, and

composition; and (2) whether effects varied across eco-systems with distinct historical fire regimes. We hypothesized the following:

1. Richness of native understory plant species and species diversity are maximized when fire severity emulates the historical fire regime, following Miller and Safford (2020).
2. Richness of exotic species is greatest following high-severity fire, particularly in subalpine closed-canopy forests where prefire resources are most limited.
3. Across all ecosystems, richness of species of high cultural significance is greatest following low- to moderate-severity fire, reflecting the role of Indigenous fire stewardship practices.

METHODS

Study area and context

The study area is the mixed-severity "Elephant Hill" wildfire, which burned 192,000 ha after igniting in the southern interior of BC, near the Village of Ashcroft (Figure 1). This wildfire—a human-caused wildfire ignited by discarded smoking materials, likely a cigarette—was the third-largest fire of the record-breaking 2017 fire season in BC, which burned 1.2 million ha throughout the province. The Elephant Hill wildfire burned across an elevational gradient (500–1700 m above sea level [asl]) spanning ponderosa pine, interior Douglas-fir, and higher elevation mixed conifer forests, each characterized by distinct historical fire regimes (Hagmann et al., 2021; Marcoux et al., 2013; Pogue, 2017). The study area experiences a temperate continental climate, strongly influenced by the rain shadow of the Coast Mountains. Climate normals (1981–2010) for Red Lake (50.94° N, 120.8° W, 1162 m asl) and Bridge Lake (51.5° N, 120.79° W, 1155 m asl) located southeast and north of study area, respectively, had mean annual temperatures of 3.7 and 4.3°C, respectively (mean monthly temperature of 14.3 and 15.5°C in the warmest month of July) and mean annual precipitation of 505 and 595 mm (303 and 380 mm as rainfall) (Government of Canada, 2023).

The Elephant Hill wildfire impacted the traditional and unceded territory of the Secwépemc Nation, Secwepemcúlecw, a vast, ecologically and culturally diverse territory that extends over 150,000 km² throughout the southern and central interiors of BC. The wildfire directly affected the land under the caretakership of eight Secwépemc communities (First Nations), centered on the territory of Sťuxwtéws (Bonaparte First Nation). In response to these impacts and concerns over understory plant recovery, these Secwépemc communities issued a *Declaration on the Understory in the Forests of Secwepemcúlecw*, asserting Secwépemc jurisdiction over the understory and the importance of understory plants to Secwépemc people, economies, and culture (Dickson-Hoyle & John, 2021). Our collaborative study
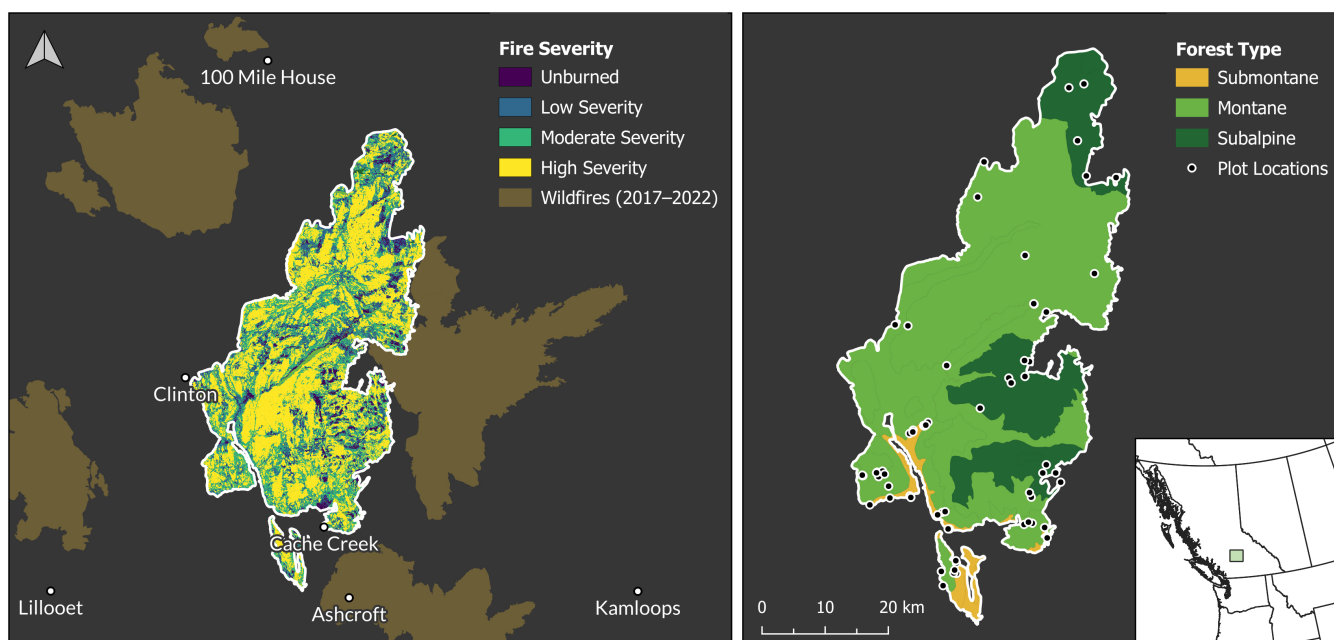

FIGURE 1   Study area map. Left: The Elephant Hill wildfire and surrounding wildfires (2017–2022). Fire severity classes for the Elephant Hill wildfire are shown based on modelled Composite Burn Index. Right: The distribution of forest types within the Elephant Hill wildfire perimeter and the location of understory plant plots ($n = 66$).

with St̓uxwtéws was initiated by former Kukpi7 (Chief) Ryan Day, who invited us to partner with them to help understand the impacts of this fire on these important ecocultural values, and trajectories of ecosystem recovery.

The study area has a long history of both human and natural disturbance. Secwépemc people have lived in and actively managed this landscape for over 10,000 years (Ignace & Ignace, 2017) including through regular, intentional burning to manage understory plant resources (Dickson-Hoyle et al., 2022; Peacock et al., 2016). Historical reconstructions indicate diverse fire regimes across ecosystem types prior to colonial fire exclusion and fire suppression policies introduced in the late 1800s (Christianson, 2015; Copes-Gerbitz et al., 2023) and the increased effectiveness of fire suppression from the early to mid-1900s (Copes-Gerbitz et al., 2022). In the southern interior of BC, mean fire return intervals derived from fire scars and forest demographics range from 10 to 20 years in low-elevation dry forests (Harvey et al., 2017; Heyerdahl et al., 2007) and 20 to 50 years in mid-elevation montane forests (Brookes et al., 2021; Chavardès et al., 2022; Copes-Gerbitz et al., 2023). In high-elevation subalpine forests that lack fire scars, contemporary fire-free intervals range from 100 to 350 years (Marcoux et al., 2013, 2015). Across this elevational gradient, multiple studies highlight the influence of low- and mixed-severity fire regimes throughout dry forest ecosystems and the important contribution of Indigenous cultural burning (Copes-Gerbitz et al., 2023; Hessburg et al., 2019). Since the early 20th century, a provincial government focus on fire suppression and managing forests for timber values has led to a disruption of these historical fire regimes (Copes-Gerbitz et al., 2022). Extensive logging and cattle grazing have also impacted, and continue to impact, the composition and configuration of forests and understory plant communities.

Field sampling

In 2018, the first growing season after the Elephant Hill wildfire, we selected and established plots throughout the burned area using a stratified random sampling design (Figure 1). We stratified the study area based on forest type (submontane, montane, and subalpine) along elevation and temperature-moisture gradients, and fire severity class (unburned, low, moderate, and high), based on differenced normalized burn ratio (dNBR) (Key & Benson, 2006) derived from 30-m multispectral Landsat Collection 2—Landsat 8 Operational Land Imager (US Geological Survey, 2018) taken before (July 5, 2017) and after (August 22, 2017) the fire. Due to the lack of prefire vegetation data, the unburned plots served as control treatment plots. We updated this preliminary fire severity map using images taken on clear days one year later (August 9, 2018), as the previous imagery was taken approximately two weeks before the fire was fully suppressed.

Submontane forests comprised low-elevation (475–900 m asl) sites in hot-dry climates, with open-canopy forests dominated by *Pinus ponderosa* (ponderosa pine) or *Pseudotsuga menziesii* var. *glauca* (interior Douglas-fir), corresponding to the Ponderosa Pine Biogeoclimatic Ecosystem Classification (BEC) zone. Montane forests comprised mid-elevation (800–1200 m asl) sites in warm-dry to mesic climates, with closed-canopy forests dominated by interior Douglas-fir, corresponding to the Interior Douglas-fir BEC zone. Montane forests were the dominant ecosystem across the study area (Figures 1 and 2).

F I G U R E 2 Plots in the montane forest type, dominated by *Pseudotsuga menziesii* var. *glauca* (interior Douglas-fir). Left: Unburned plot. Right: Plot that burned at high severity, one year postfire (2018). Photo credit: UBC Tree-Ring Lab.

Subalpine forests comprised high-elevation (1000–1700 m) plateaus with cool-mesic climates and closed-canopy forests dominated by *Pinus contorta* var. *latifolia* (lodgepole pine) or *Picea engelmannii × glauca* (hybrid white spruce), with *Abies lasiocarpa* (subalpine fir) codominant at the highest elevations. Subalpine forests corresponded to the Montane Spruce, Sub-Boreal Pine Spruce, and Engelmann Spruce—Subalpine Fir BEC zones. Due to extensive logging and historic wildfires across the high-elevation plateaus, subalpine forests also included areas of planted and naturally regenerating lodgepole pine. At the northern extent of the study area, montane and subalpine forest types also included stands dominated by the deciduous species *Populus tremuloides* (trembling aspen). Across interior BC, these three forest types (submontane, montane, and subalpine) were historically characterized by frequent, low-severity fire regimes, mixed-severity fire regimes, and infrequent, high-severity fire regimes, respectively (Hessburg et al., 2019; Marcoux et al., 2013).

Plot centers were randomly generated between 50 and 500 m from roads to minimize road edge effects while optimizing accessibility. We surveyed a total of 64 plots and departed from a fully balanced design due to the dominance of montane forests and the classification of fire severity class based on Composite Burn Index (CBI) following field verification (see below).

To assess fire severity one-year post-fire (in 2018), we used nested circular plots around plot centre to sample fire impacts on five strata: A) ground (substrates and woody debris); B) herbs, ferns, mosses and bryophytes; C) shrubs; D) sub-canopy trees; and E) canopy trees. Within a 5.64-m radius plot, we recorded the percent of ground that was scorched with exposed mineral soil and measured the depth of burn class (Ryan, 1982). Woody debris, including stems and branches with diameter >1 cm, were sampled along two perpendicular 30-m transects crossing at plot center. For each plot, we recorded the percent of wood pieces that were charred. We also assessed three understory plant strata (mosses and bryophytes; herbs and ferns; and shrubs) in the 5.64-m radius plot. For each plant stratum, we estimated the percent of plants that were discolored, damaged, or killed by fire. A 11.28-m radius plot was used to assess large trees (dbh > 12.5 cm). To sample 15–20 small trees (5 cm < dbh ≤ 12.5 cm), we used a plot radius of either 5.64 or 3.99 m, depending on tree density. For each live tree or snag with intact branches or bark (decay classes 3 or 4 in Thomas, 1979), which were assumed to have been killed by the fire, we recorded the following three attributes: bark char height (in meters); percent crown scorch (to nearest 10%, based on estimate of percentage space occupied by prefire crown); and crown scorch using a qualitative scale assessed in terms of crown discoloration as follows: 0: unaffected, green; 1: very light, green/yellow; 2: light, yellow; 3: medium, orange/red; 4: severe, brown/black; 5: no foliage, dead prior to fire.

Four years postfire (between June and August 2021), we sampled understory plant composition and abundance in the 64 existing plots, plus in two additional unburned plots established in the montane forest type, as this class was underrepresented ($n = 66$ plots). Based on previous studies in similar ecosystems, this period since fire was determined to be sufficient to identify trajectories of species recovery and compositional gradients associated with fire severity (Abella & Fornwalt, 2015; Day et al., 2017). At each plot, species and abundances were recorded in four 1.128-m radius subplots, each located at one end of the two 30-m transects crossing at plot center. We visually estimated percent canopy cover for each live vascular species, excluding tree species, rooted in the subplots. Species with less than 1% cover were recorded as 0.5% cover. If a plant could not be identified to species level in the field, a specimen of the same species was collected and later identified. All vascular plants were recorded to the species level except for a small number of species including *Salix* spp., five *Carex* spp., and a number of plants in the Poaceae family ($n = 4$) or *Hieracium* genus ($n = 2$), for which there was insufficient vegetative or reproductive material. Nomenclature followed, and nativity was determined using, E-Flora BC—electronic atlas of the flora of British Columbia (E-Flora BC, n.d., https://linnet.geog.ubc.ca/biodiversity/eflora/index.html [accessed February 2022]).

Each species was categorized into one of three functional groups—forbs, graminoids, and woody plants—and classified as either native or exotic. We further categorized all plants according to their level of "cultural significance" by cross-referencing our species list with a database of culturally significant plant species provided under a data-sharing agreement by Skeetchestn Indian Band, a Secwépemc community. This database includes uses of plants (e.g., medicinal, food, and technological) and levels of "significance" (high, medium, or low) to Skeetchestn community members.

Understory species total richness was calculated as the number of species recorded within the four 1.128-m radius subplots at each plot (combined total for each plot, 16 m² total area). For each plot, we also calculated the richness of the subsets of native, exotic, and high cultural significance species. Alpha diversity of all species was calculated for each plot using the Shannon–Weiner diversity index (Shannon diversity), calculated as

$$H^{\mathrm{I}} = - \sum (p_i)(\ln p_i),$$

where H^{I} is the Shannon–Weiner index number measuring uncertainty/unpredictability and p_i is the proportion of all individuals that belong to species i.

Composite burn index calculation and fire severity classification

The CBI (Key & Benson, 2006) represents the variable effects of fire across forest strata, encompassing multiple potential drivers of understory plant community response, such as bare ground or reduction in canopy cover. We modified the methods developed by Key and Benson (2006) to minimize assumptions of prefire vegetation abundance and condition. We then used our field data to calculate CBI scores (continuous scale of 0–3) for the ground, herb, shrub, sub-canopy tree, and canopy tree strata (Appendix S1: Table S1) and mean CBI across these strata for each plot. To distinguish the effects of surface fire from crown fire, we also calculated "understory CBI" as the average of CBI components A–C (fire impacts on the ground layer, herbs, ferns, mosses and bryophytes, and shrubs) and "overstory CBI" as the average of components D–E (fire impacts on the sub-canopy and canopy).

Plots were classified based on CBI values as follows: unburned ≤0.50; low severity 0.50 < CBI ≤ 1.50; moderate severity 1.50 < CBI ≤ 2.50; high severity >2.50. Based on this classification, there were 17 unburned plots, 5 plots burned at low severity, 10 plots burned at moderate severity, and 34 plots burned at high severity. Due to the low number of low-severity plots, a combined "low–moderate" severity class was used ($n = 15$) for linear regression modelling; separate low- and moderate-severity classes were retained for indicator species analysis and ordination analysis.

Statistical analyses

All statistical analyses were conducted in R version 4.1.2 (R Core Team, 2022) with α = 0.05. Understory species richness (total, native, exotic, and high cultural significance) and diversity (total) were modelled as functions of CBI, forest type, and their interaction, with understory and overstory CBI fit separately due to collinearity. For total, native, exotic, and high cultural significance species richness, we fit Poisson-distributed generalized linear models; we tested for overdispersion and used a quasi-Poisson distribution in the case of overdispersion.

For species diversity, we fit multiple linear regression models. All models were then fit with fire severity classes in place of understory or overstory CBI to explore any differential effects compared with the continuous CBI variables. Model assumptions were verified by testing for normality and heteroscedasticity of residuals. Backward stepwise selection was conducted to remove interactions terms where doing so improved model fit, using p-values (F-test or Chi-squared test) as a selection criterion (Appendix S1: Table S2). We then conducted post hoc Tukey's tests to determine differences in model predictions using "emmeans" package (Lenth et al., 2023).

We conducted indicator species analysis to test the strength of correlations between the abundance of understory vascular plant species at the plot scale and fire severity classes using the "indicspecies" package (De Cáceres et al., 2022). Indicator species for each fire severity class, defined as those that are found mostly within a defined severity class and present in the majority of plots within that severity class (Dufrêne & Legendre, 1997), were identified by calculating an indicator value index.

We performed non-metric multidimensional scaling (NMDS) to assess differences in community composition, using species abundance data for each plot using the vegan package (Oksanen et al., 2022). A three-dimensional solution was selected by plotting stress against the number of dimensions to optimize dimensionality and model fit (McCune et al., 2002); stress for the three-dimensional solution was 0.14. Data values were transformed using a Wisconsin double standardization and square root transformation. Distance was calculated using the Bray–Curtis dissimilarity metric for species abundance (cover) data from 66 plots; rare species were not removed (Poos & Jackson, 2012). A single ordination, with a maximum of 100 iterations, was performed and converged after 20 iterations. Result scaling was standardized to facilitate interpretation by centering, applying principal components rotation, and half-change scaling. Species scores were added to the final solution as weighted averages. We added covariance ellipses to visualize plot groupings by fire severity class. We compared community composition among fire severity classes (unburned, low, moderate, and high) using an analysis of similarities (ANOSIM) test with Bray–Curtis distance and 9999 permutations.

RESULTS

We recorded 196 understory plant species across the 66 plots, comprising 128 forb species, 40 graminoids and 28 woody species (shrubs and subshrubs). Of the 196 species,

155 (79%) were native, 33 (17%) were exotic, and 8 species (4%) could only be identified to family or genus level and could not be confirmed as native or exotic. Three species—*Centaurea stoebe* subsp. *micranthos* (spotted knapweed), *Cirsium arvense* (Canada thistle), and *Sonchus arvensis* (perennial sowthistle)—are classified as noxious weeds in the Province of BC, and an additional two species—*Cirsium vulgare* (bull thistle) and *Tragopogon dubius* (yellow salsify)—are identified as invasive plants of concern in BC (Invasive Species Council of BC, 2021). Of the 196 species, 98 (50%) have a documented and ongoing cultural use by Secwépemc people, including for food, medicinal, or technological purposes, and 31 species (16%) are identified by Skeetchestn as being of *high* cultural significance. Of these 31 species, 13 (42%) are perennial forbs and 18 (58%) are shrubs; 8 (26%) were recorded in only one plot.

Across all plots, the most frequently recorded species were *Achillea millefolium* (yarrow, 75% of plots), *Epilobium angustifolium* (fireweed, 74%), *Taraxacum officinale* (common dandelion, 73%; an exotic species), *Calamagrostis rubescens* (pinegrass, 68%), and *Rosa acicularis* (prickly rose, 62%). The most frequent species of high cultural significance were prickly rose, *Fragaria virginiana* (wild strawberry, 48% of plots), *Eurybia conspicua* (showy aster, 41%), *Arctostaphylos uva-ursi* (kinnikinnick, 35%), and *Salix* spp. (willows, 29%). A large proportion of species ($n = 112$, 57%) were rare, being recorded in three plots or fewer; 65 species (33%) were recorded in only one plot.

Species richness and diversity

Model results show that species richness and diversity were significantly affected by fire severity (see Appendix S1: Table S2), although the magnitude and direction of CBI effects varied among native, culturally significant, and exotic species (Figure 3).

Across all forest types, richness of both native species and species of high cultural significance decreased significantly with increasing CBI, with similar magnitudes of effect for understory (Figure 3; $p < 0.001$ and <0.002, respectively) and overstory (data not shown; $p < 0.001$ for both native and culturally significant species) CBI. These richness values were significantly related to fire severity class ($p = 0.008$ and $p = 0.018$, respectively): despite no significant pairwise contrasts, model-derived mean richness of native species (14, 95% CI = 12, 16) and richness of species of high cultural significance (3, 95% CI = 3, 4) were lowest in plots that burned at high severity (Figure 4). While native species richness was greatest in unburned plots (17, 95%

CI = 15, 20), richness of species of high cultural significance was greatest in plots that burned at low to moderate severity (5, 95% CI = 4, 6). Richness of both native species (21, 95% CI = 18, 24) and species of high cultural significance (6, 95% CI 5, 7) was significantly greater in subalpine forests than in montane ($p = 0.001$, $p = 0.008$, respectively) or submontane forests ($p < 0.001$).

In contrast, the effects of fire severity on the richness of exotic species significantly interacted with forest type (Figure 3). The strongest effects of CBI were observed in montane forests, in which richness of exotic species showed significant increases with increasing understory and overstory CBI; the magnitude of the effect on richness of exotic species was approximately 10% greater for overstory CBI than for understory CBI. Richness of exotic species in montane forests was significantly greater in plots that burned at low to moderate severity (4, 95% CI = 3, 5; $p = 0.003$) and high severity (3, 95% CI = 2, 4; $p = 0.006$), compared with unburned plots (1, 95% CI = <1, 2) (Figure 4). The 95% CIs for the slope coefficients for understory and overstory CBI in submontane and subalpine forests indicated uncertainty as to the effect on richness of exotic species.

Shannon diversity for all species was significantly affected by understory CBI, but not by overstory CBI or fire severity class. Understory CBI interacted with forest type to affect species diversity (Figure 3; $p = 0.042$). Shannon diversity decreased with increasing understory CBI in montane and subalpine forests. However, the 95% CIs for the slope coefficient for understory CBI in submontane forests indicate uncertainty as to its effect.

Indicator species

Ten indicator species were identified that distinguished fire severity classes (Table 1). Nine of the fire severity indicator species are forbs, and one is a woody species. Three of the indicator species are of high cultural significance, all of which indicated relatively low-severity fire (i.e., two indicated only low severity and one indicated unburned to moderate-severity fire). In addition, *Epilobium angustifolium* (fireweed) was identified as an indicator of burned sites. While this species is listed as being of "medium" cultural significance and was not included in our analyses of species of high cultural significance, some Secwépemc people consider it an important medicinal plant (M. Ignace, personal communication, 2022). Two indicator species are exotic, one of which indicated high-severity fire.
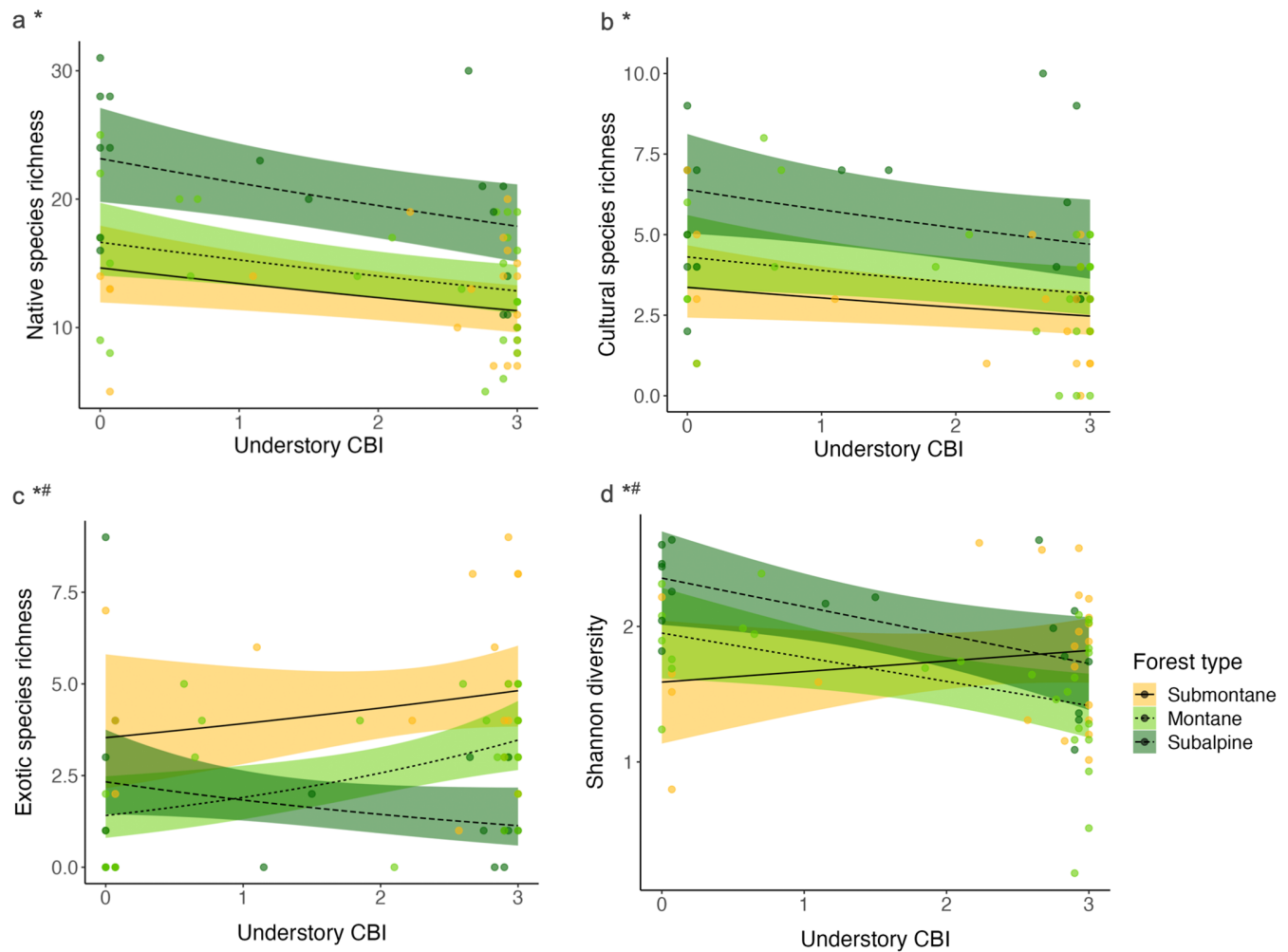
FIGURE 3 (a–c) Significant but differential effects of plot understory Composite Burn Index (CBI), as a metric of fire severity, on species richness (a, native species; b, species of high cultural significance; c, exotic species) and (d) Shannon diversity. Dashed and solid lines show the modelled effect of understory CBI on richness and diversity for each forest type; colored bands represent the 95% CIs. * indicates significant effects of both understory CBI and forest type on species richness. *# indicates significant interaction effect between understory CBI and forest type. Raw data are overlaid as points.

Community composition

NMDS revealed distinct differences in understory plant community composition between unburned and high-severity classes (Figure 5). While low- and moderate-severity plots showed a high degree of similarity in community composition, there was a degree of separation from the unburned and high-severity classes. ANOSIM found a significant effect of fire severity class ($R = 0.146$, $p = 0.008$) on understory plant community composition, corroborating the differences between unburned and high-severity classes. Further, across all fire severity classes, subalpine plots tended to cluster along axis 1 of the NMDS, separated from plots in submontane or montane ecosystems (Figure 5).

Of the 196 species considered in the ordination, 54 contributed significantly to differences in community composition: 49 of these are native and 5 are exotic species. Thirteen species are of high cultural significance, 9 (69%) of which are shrubs and the majority of which are closely associated with unburned plots or low-severity plots. All exotic species are associated with plots that burned at moderate to high severity; these include annual hawksbeard and common dandelion, identified above as indicators of high-severity fire and burned plots, respectively.

DISCUSSION

Fire severity, measured by CBI, was a significant driver of species richness and diversity across all forest types, with both native species richness and richness of species of high cultural significance negatively affected by increasing severity, and Shannon diversity negatively affected by understory
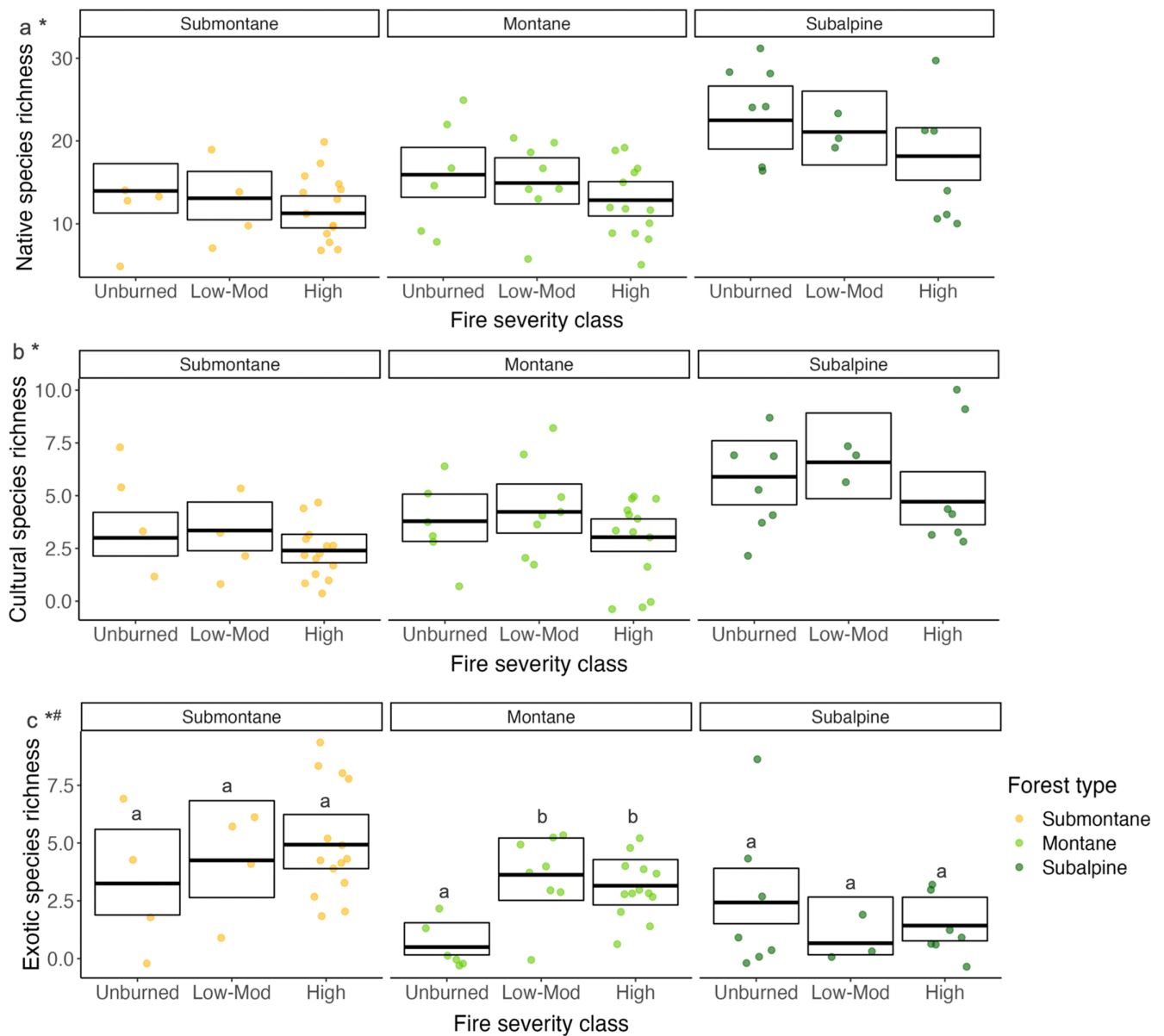
FIGURE 4 (a–c) Effects of fire severity class and forest type on species richness (a, native species; b, species of high cultural significance; c, exotic species). Boxplot midlines show model-derived means, and upper and lower limits of boxes correspond to 95% CIs. * indicates significant effects of both fire severity class and forest type on species richness. *# indicates significant interaction effect between fire severity and forest type. For panel c, letters compare model-estimated means within each forest type; no significant pairwise contrasts were found for a or b, despite significant effects of fire severity and forest type. Raw data are overlaid as points.

fire severity in both montane and subalpine forests. These findings, which are consistent across different forest types each characterized by a distinct historical fire regime, contrast with previous studies and ecological theory that predict that understory plant response to fire is contingent on the historical disturbance regime that shaped the respective ecosystem (Miller & Safford, 2020).

Specifically, we found that:

1. High-severity fire negatively impacted native species richness and species composition across all forest types, and Shannon diversity in both montane and subalpine forests, each characterized by distinct historical fire regimes; these results contrast with hypothesis 1.

2. In montane forests, richness of exotic species increased with increasing fire severity and was greatest in burned than in unburned plots, providing support for hypothesis 2. However, fire severity negatively affected richness of exotic species in subalpine forests, with high uncertainty, contrasting with the second component of hypothesis 2.

TABLE 1 Indicator species of fire severity classes.

Species' scientific name (common name)	Specificity	Fidelity	Indicator value	p
Unburned				
Lathyrus nevadensis (purple peavine)	1.0	0.24	0.24	0.042
Low severity				
Balsamorhiza sagittata + (arrow-leaved balsamroot)	0.84	0.60	0.50	0.004
Penstemon fruticosus + (shrubby penstemon)	0.76	0.40	0.30	0.026
Sedum lanceolatum (lance-leaved stonecrop)	0.87	0.40	0.35	0.017
High severity				
*Crepis tectorum** (annual hawksbeard)	0.90	0.41	0.37	0.05
Unburned, low, and moderate severity				
Fragaria virginiana + (wild strawberry)	0.86	0.63	0.54	0.044
Symphyotrichum foliaceum (leafy aster)	0.94	0.47	0.44	0.019
Burned: Low, moderate, and high severity				
Epilobium angustifolium (fireweed)	0.98	0.86	0.84	0.001
Epilobium brachycarpum (tall annual willowherb)	1.0	0.43	0.43	0.040
*Taraxacum officinale** (common dandelion)	0.91	0.84	0.76	0.011

Note: Species of high cultural significance are indicated by +; exotic species are indicated by *. Specificity is the probability that the plot belongs to the fire severity class, given that the species has been found. Fidelity is the probability of finding the species in plots belonging to the particular fire severity class. Species with values of "1" are considered to have complete specificity or fidelity. The indicator value is the product of these two components.
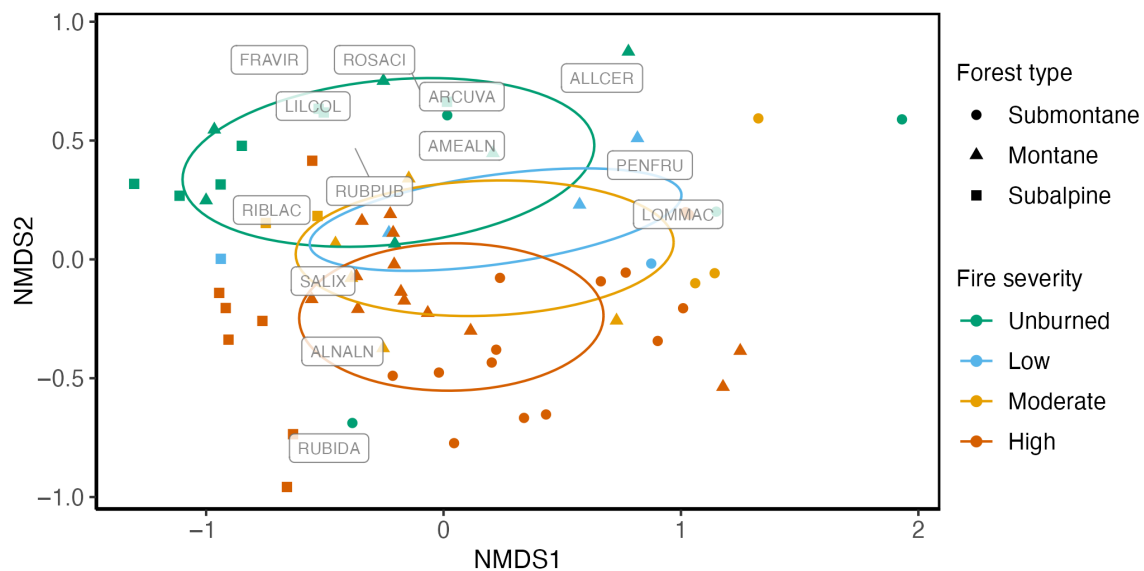

FIGURE 5 Nonmetric multidimensional scaling (NMDS) bi-plot of plant community composition data across all plots. Each point represents a single plot ($n = 66$) in community composition space. Points closer to each other have more similar understory species composition than points farther apart. Ellipses visualize clustering of plots within each fire severity class. Species labels for species of high cultural significance are overlaid. Points closer to a species label have a relatively higher proportion of that species than points further away. Species corresponding to abbreviated species codes can be found in Appendix S1: Table S3.

3. Richness of species of high cultural significance was greatest in areas that burned at low to moderate severity, and species of high cultural significance were more closely associated with plots that burned at low to moderate severity, reflecting the role of Indigenous fire stewardship practices and supporting hypothesis 3.

High-severity fire negatively impacts native species across forest types

We found little support for hypothesis 1, that the effect of fire severity on native understory plant richness is contingent upon the historical fire regime that shaped plant evolutionary processes (Brodie et al., 2021; Miller & Safford, 2020; Richter et al., 2019). In contrast, across all forest types and historical fire regimes, richness of native species declined with increasing fire severity. Further, total species diversity declined with increasing understory fire severity in montane and subalpine forests.

Native species richness was lowest in plots that burned at high severity, compared with unburned or low-moderate fire severity plots. Contrary to our expectations, this remained true in the subalpine forests that are characterized by an infrequent, high-severity fire regime, and should be adapted to this disturbance severity. These results contrast with previous studies in forests historically characterized by infrequent, high-severity fire that found a positive relationship between species richness and fire severity (Brodie et al., 2021; Miller & Safford, 2020). The negative effects of fire severity on richness of native species and diversity of all species were reflected in the NMDS analysis, which showed a lack of similarity in species composition between unburned and high-severity plots across all forest types, four years after fire. Across all forest types in our study area, our findings of lower richness of native species associated with high-severity fire, and the compositional dissimilarity between unburned plots and those that burned at high severity, demonstrate low resilience to and limited short-term (and potentially longer term) understory recovery following high-severity fire.

Hypothesis 1, that historical fire regimes mediate the effect of fire on native understory species richness and diversity, is contingent on contemporary disturbances being within the historical range of variability (Brodie et al., 2021; Stephens et al., 2014). The negative effects of increasing fire severity on richness of native plants and diversity of all species in subalpine forests in our study area may be due to the extensive, contiguous patches that burned at high severity, which characterized this megafire. The extent of these patches increased the distance to off-site seed source, potentially beyond the dispersal capacity of species that would otherwise drive recolonization in these forest types (Nolan et al., 2021). Pre- and postfire disturbances, including clear-cut harvesting and salvage logging, may have further contributed to slower postfire recovery by altering understory species composition and propagule availability in both burned and unburned stands.

Exotic species richness increases postfire in montane forests

Following the first component of hypothesis 2—that predicted richness of exotic species would be greatest following high-severity fire—we found a strong positive relationship between fire severity and richness of exotic species in montane forests. This finding is consistent with previous studies in dry mixed conifer forests in the western United States that reported an increase in exotic species following fire (Abella & Fornwalt, 2015; Fornwalt et al., 2010) or higher richness of exotic species in areas that burned at high severity compared with unburned areas (Crawford et al., 2001; Freeman et al., 2007). Increases in exotic species, particularly those that are short-lived and far-dispersing, can be facilitated by the postfire increase in the availability of light and bare mineral soil, and microsite conditions conducive to their establishment (Brodie et al., 2021; Roberts, 2004). The strong effect of overstory CBI on richness of exotic species suggests that reduced canopy cover and associated microsite changes, such as increased surface microtopography from tip-up mounds or increased coarse woody debris (Roberts, 2004), facilitated establishment of exotic species postfire in our study area.

Fire severity had a negative effect on richness of exotic species in subalpine forests, with high uncertainty. This finding is contrary to the second component of hypothesis 2, that severe fire in light-limited closed-canopy subalpine forests would facilitate exotic species. Hypothesis 2 was supported by Brodie et al. (2021), whose study of understory plant community response in California's subalpine forests found that short-lived and far-dispersing colonizer species showed a greater increase with increasing fire severity than long-lived and near-dispersing species. They found that this pattern was more pronounced in higher productivity stands, with evidence of competitive release as a key mechanism for this increased richness. In contrast, in the subalpine forests in our study area, exotic species richness was potentially negatively affected by fire severity. As was the case with native species, this is potentially due to the extensive, contiguous patches that burned at high severity, limiting off-site seed dispersal, although further monitoring and research on fire effects in subalpine ecosystems is needed.

The lack of a clear effect of fire severity on exotic species in the submontane forests in our study area also contrasts with previous research. Crawford et al. (2001), Dodson and Fiedler (2006), and Freeman et al. (2007) all demonstrated a significant increase in the richness or abundance of exotic species following wildfire or prescribed burning in dry ponderosa pine forests. While the effect of fire severity was not apparent in our study, overall exotic

species richness was higher throughout the submontane (ponderosa pine-dominated) forest type. Presence of exotic species is likely the result of interacting disturbances at lower elevations, including cattle grazing, rangeland seeding with pasture grasses, and proximity to roads, all of which can facilitate spread of exotic species (Christen & Matlack, 2009; Lozon & MacIsaac, 1997; Meunier & Lavoie, 2012; Peppin et al., 2010; Pyke et al., 2013).

Postfire conditions favor colonizer species that rapidly establish following disturbance and take advantage of reduced competition (Brodie et al., 2021; Freeman et al., 2007; Morgan et al., 2015). While we did not explicitly test for the effect of fire severity on colonizer-type species—those with short lifespans and long-distance dispersal capabilities—approximately 50% of the 33 exotic species we recorded were short-lived (annual or biennial) forbs or graminoids. For example, *Crepis tectorum* (annual hawksbeard) was recorded in 16 plots, was indicative of high-severity fire (Table 1), and was strongly associated with plots that burned at high severity (Figure 5). The invasive annual graminoid *Bromus tectorum* (cheatgrass) was also recorded in 14 plots. While Strand et al. (2019) found that cheatgrass was more likely to occur in areas that burned at low or moderate severity, we recorded this species in seven plots (50%) that burned at high severity, while the remaining seven plots were unburned or burned at low or moderate severity. Cheatgrass can also be introduced through postfire rehabilitation of fireguards and infrastructure reconstruction (Fornwalt et al., 2010), which were extensive in this study area. This invasive species rapidly establishes and spreads following fire and can create positive feedbacks, with even a low cover of cheatgrass increasing fire potential (Balch et al., 2013; Bradley et al., 2018; Peeler & Smithwick, 2018). This ability of non-native invasives to persist and potentially increase following high-severity fire (Abella & Fornwalt, 2015; Dodson et al., 2008; Fornwalt et al., 2010) and to alter fire regimes—for example, through altered burn probabilities and mean fire size (Tortorelli et al., 2023)—is significant given concerns about potential climate and disturbance-driven range expansions of exotic species throughout western North America. Further, the positive relationship between high-severity fire and exotic species raises concerns regarding the loss of cultural values in post-wildfire landscapes, given that the majority of exotic plant species in the region are not identified by Secwépemc people as being of cultural significance.

The ecological and cultural significance of low-severity fire and subalpine forests

Richness of species of high cultural significance was greatest in areas that burned at low–moderate severity and lowest in areas that burned at high severity, supporting our hypothesis 3 that richness of species of high cultural significance would reflect the role of Indigenous fire stewardship in actively managing numerous plant species. This practice of frequent, low-severity burning was, and in many places continues to be, a common form of vegetation management by Secwépemc people and other Indigenous peoples throughout western North America, used to promote berry production (Lepofsky et al., 2005; Turner, 1999), increase the quality of construction and basketry materials (Anderson, 2005; Marks-Block et al., 2019), and promote regeneration of herbaceous food and medicine plants (Dickson-Hoyle et al., 2022; Stewart, 2009). Our results support the role of low- to moderate-severity fire in stimulating the regeneration of such species and the need to support Indigenous peoples in revitalizing their traditional roles and practices of fire stewardship (Hoffman et al., 2022), including to restore traditional plant resources.

Three indicator species of high cultural significance were also associated with either low-severity fire or a combination of unburned, low- and moderate-severity fires (Table 1). One of these species, *Balsamorhiza sagittata* (arrow-leaved balsamroot), provided a significant food source for Secwépemc people (Peacock et al., 2016). In addition, the cultural keystone species *Lomatium macrocarpum* (large-fruited desert parsley) was also associated with plots that burned at low and moderate severities, based on NMDS compositional analysis. Both of these species have the capacity to resprout from large taproots and were historically managed through frequent burning at approximately 5- to 10-year intervals (Peacock et al., 2016). Members of the Skeetchestn Secwépemc community continue to burn to promote *L. macrocarpum*, among other cultural keystone species (Dickson-Hoyle et al., 2022).

While richness was significantly affected by fire severity class, the absence of statistically significant contrasts may have arisen from merging low- and moderate-severity classes due to the limited low-severity fire, and the unbalanced sampling design across fire severity classes. However, we found a clear negative effect of high-severity fire on culturally significant plants in our study area. This pattern is of concern given the large extent of high-severity effects within the fire perimeter and subsequent high-severity megafires burning near our study area and throughout Secwépemc territory in 2018, 2021, and 2023 (BC Wildfire Service, 2023). In addition to the direct negative impacts of high-severity fire on cultural plant resources, representatives from Skeetchestn and other Secwépemc communities have expressed concern that the extensive area burned at high severity by wildfires in their territory is limiting the potential for

reintroducing cultural or prescribed burning, and therefore restoration (S. Freeman, personal communication, 2022).

It is noteworthy that high cultural significance species richness was greatest in the subalpine forests. This finding reinforces both the ecological and cultural importance of high-elevation landscapes for the Secwépemc and other Indigenous peoples in interior BC (Lepofsky et al., 2005; Reimer, 2000; Turner et al., 2011; Tyhurst, 1992). Existing research on Indigenous stewardship of cultural plants in interior BC has often focused on riverine valleys and low- to mid-elevation grasslands and dry forests, yielding rich archaeological and ethnobotanical records for these ecosystems. Our research complements these studies and provides new insights into the contemporary availability of culturally important plants in subalpine ecosystems.

For example, the three plots with the greatest richness of high cultural significance species were all in subalpine forests. Most high cultural significance species in these plots were woody species, including *Alnus alnobetula* subsp. *sinuata* (sitka alder) and berry-producing shrubs such as *Rubus idaeus* (red raspberry), *Rubus parviflorus* (thimbleberry), and *Ribes lacustre* (black gooseberry). These species are all relatively resistant to fire kill and are able to resprout from surviving rhizomes and root crowns (Haeussler et al., 1990; US Forest Service, 2022). Studies have shown significant increases in the cover of these species even following severe fire and germination from both in situ seed beds and off-site colonization through avian-mediated seed dispersal (Haeussler et al., 1990). The resilience of these shrubs to high-severity fire is reflected in our results, whereby the two plots with highest richness of high cultural significance species burned at high severity. However, it should be noted that one of these plots was in a riparian area and therefore likely had higher prefire cultural species richness, and potentially faster recovery.

Early successional postfire communities can provide important habitat structures and resources for culturally important animals, such as shrub browse for native ungulates. While we observed vigorous resprouting of sitka alder and willows in subalpine forests, many of the culturally significant shrubs recorded in plots that burned at high severity were seedlings, immature plants, or plants that were resprouting but had relatively low vegetative cover. As such, at four years postfire, high species richness does not necessarily correspond to high use value such as berry production or for construction materials. However, anecdotal reports from Secwépemc community members in the summer of 2023 (6 years postfire) indicated high production of sxúsem (*Shepherdia canadensis*, soapberry) berries within the Elephant Hill

wildfire area. As such, longer term monitoring will be important to better understand the relationship between time since fire and the recovery of these cultural values.

This diversity of plant resources in subalpine forests adds support, in the form of contemporary ecological evidence, to the importance and practice of a "seasonal round," where Indigenous stewardship practices create "patches of resources distributed over both time and space" (Peacock et al., 2016, p. 196). Turner et al. (2016, p. 9) describe how, as part of this seasonal round in Secwepemcúlecw, "families traveled around their territories in a patterned seasonal round, stopping and camping, sometimes for weeks at a time ... to harvest and preserve the meat, roots, berries, and other resources they needed for year round living." The Secwépemc seasonal round and calendar (Ignace, 2014) traces these plant resources throughout the year, from *Pesll7éwten*, the "melting month" (April), when the first plant shoots come out and early root plants are dug, through *Pelltqelqél'tkemc*, "getting ripe month" (July to early August), when numerous berries ripen and people harvest medicines in the high plateau, to *Pesqelqlélten*, the "many salmon month" (August to early September), when berries are harvested at higher elevations. However, as indicated above, the quantitative metrics of species richness, cover, or diversity do not indicate quality or condition, as defined by resource users (e.g., medicinal properties, suitability as construction material, and berry production and taste), of these plants following fire.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Our study offers novel and salient insights into the recovery of understory plant communities following a mixed-severity megafire in British Columbia, Canada, with a focus on plants of high cultural significance to local Indigenous people. In doing so, this study responds to recent calls for a new "megafire ecology" that better understands the effects of exceptionally large fires on species, communities, and ecosystems (Nimmo et al., 2022). The negative relationship between fire severity and species richness and diversity, even in the subalpine forests in our study area that were historically characterized by infrequent, high-severity fire, highlights how recent megafires may be pushing these ecosystems outside of the historical range of variability, with negative implications for ecosystem recovery. Ongoing monitoring, including of exotic species, is required to understand longer term trends such as further community differentiation or homogenization and to assess ecosystem resilience to high-severity megafires.

Improved understanding of the response of culturally significant plants to fire also requires adapting monitoring approaches to better capture variables of interest to Indigenous community members and resource users. This study only examined the response of a subset of species with identified medicinal, food, technological, or other uses by Secwépemc people; that is, plants identified by one Secwépemc community as being of "high" cultural significance, that could be integrated into the existing study design. Our ongoing collaborative research with Secwépemc communities is prioritizing the development of culturally relevant monitoring protocols and deeper community engagement to better assess the impact of recent megafires on culturally significant plants and other ecocultural values throughout Secwepemcúlecw. This research, grounded in Secwépemc priorities for restoration and knowledges of plant uses and stewardship practices, aims to address the limitations of dominant science approaches to answering these questions. As megafires continue to impact ecosystems and human communities alike, collaborative monitoring and research approaches that deploy a new form of "transdisciplinary fire ecology" (Coughlan & Petty, 2012) and ethically draw on both western and Indigenous sciences are needed to better understand human-fire-landscape interactions and support Indigenous-led revitalization of fire and plant stewardship.

These results also have implications for the management and restoration of fire-prone ecosystems throughout western North America, including the restoration of historical fire regimes and systems of Indigenous fire stewardship that shaped these landscapes. Due to the dominance of moderate- and high-severity fires across our study area, we were unable to quantify the effect of low-severity fire on species richness or diversity. However, given the important role of frequent, low-severity Indigenous burning in managing plant resources, there is a critical need for research examining plant responses to low-severity fire, including to cultural and prescribed burning. Further collaborative fire history studies in subalpine forests, conventionally considered to be characterized by infrequent, high-severity fire regimes, are needed to better understand the role of cultural burning in these systems. Given the richness of culturally significant plants in the subalpine forests, which have been subject to compounding disturbances of high-severity wildfire, clearcut logging, and insect outbreaks, there is a critical need to protect and restore these high-elevation ecosystems and acknowledge the longstanding and ongoing Indigenous use across these landscapes.

As stated in the Secwépemc *Declaration on Understory Within the Forests of Secwepemcúlecw*:

Yeri7 re spellqwlút.s-kucw re syecwmíns xwexwéytes k stemi te kwelkúltes ne t7íweltks re Secwepemcúlecw.

Te m-sq̓7es re Secwépemc yecwmíns xwexwéyt re tsreprép ell xwexwéytes k stem̓i w7ec te kwelkúltes ne lluqwlecw, i̓ri7 tšilem ell re syecwmíns re séwllkwe ne Secwepemcúlecw.

(The people of the Secwépemc Nation have been managing and utilizing the forests including their understory, and have looked after the water within Secwepemcúlecw since time immemorial.)

AUTHOR CONTRIBUTIONS

Lori D. Daniels and Sṫuxwtéws initiated the collaborative study. Sarah Dickson-Hoyle, Arial Eatherton, and Sṫuxwtéws conducted field sampling. Skeetchestn Natural Resources Corporation contributed cultural plant information. Sarah Dickson-Hoyle conducted statistical analyses and wrote the manuscript. Jennifer N. Baron and Florencia Tiribelli contributed to statistical analyses. All authors reviewed and edited the manuscript.

ACKNOWLEDGMENTS

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Dickson-Hoyle, 2023) are available from the Open Science Framework: https://osf.io/4kvn2/.

ORCID

Sarah Dickson-Hoyle https://orcid.org/0000-0001-8710-2832

Jennifer N. Baron https://orcid.org/0000-0003-0351-0930

Florencia Tiribelli https://orcid.org/0000-0003-4746-1704

Lori D. Daniels https://orcid.org/0000-0002-5015-8311

REFERENCES

Abella, S. R., and P. J. Fornwalt. 2015. "Ten Years of Vegetation Assembly after a North American Mega Fire." *Global Change Biology* 21: 789–802. https://doi.org/10.1111/gcb.12722.

Abella, S. R., and J. D. Springer. 2015. "Effects of Tree Cutting and Fire on Understory Vegetation in Mixed Conifer Forests." *Forest Ecology and Management* 335: 281–299. https://doi.org/10.1016/j.foreco.2014.09.009.

Anderson, K. M. 2005. *Tending the Wild: Native American Knowledge and the Management of California's Natural Resources*. Berkeley, CA: University of California Press.

Balch, J. K., B. A. Bradley, C. M. D'Antonio, and J. Gómez-Dans. 2013. "Introduced Annual Grass Increases Regional Fire Activity across the Arid Western USA (1980-2009)." *Global Change Biology* 19(1): 173–183. https://doi.org/10.1111/gcb.12046.

Baron, J. N., S. E. Gergel, P. F. Hessburg, and L. D. Daniels. 2022. "A Century of Transformation: Fire Regime Transitions from 1919 to 2019 in Southeastern British Columbia, Canada." *Landscape Ecology* 37: 2707–27. https://doi.org/10.1007/s10980-022-01506-9.

BC Wildfire Service. 2023. "Wildfire Season Summary." https://www2.gov.bc.ca/gov/content/safety/wildfire-status/about-bcws/wildfire-history/wildfire-season-summary.

Bond, W. J., F. I. Woodward, and G. F. Midgley. 2005. "The Global Distribution of Ecosystems in a World without Fire." *New Phytologist* 165(2): 525–538. https://doi.org/10.1111/j.1469-8137.2004.01252.x.

Bowman, D. M. J. S., J. Balch, P. Artaxo, W. J. Bond, M. A. Cochrane, C. M. D'Antonio, R. DeFries, et al. 2011. "The Human Dimension of Fire Regimes on Earth." *Journal of Biogeography* 38(12): 2223–36. https://doi.org/10.1111/j.1365-2699.2011.02595.x.

Bowman, D. M. J. S., C. A. Kolden, J. T. Abatzoglou, F. H. Johnston, G. R. van der Werf, and M. Flannigan. 2020. "Vegetation Fires in the Anthropocene." *Nature Reviews Earth and Environment* 1(10): 500–515. https://doi.org/10.1038/s43017-020-0085-3.

Bradley, B. A., C. A. Curtis, E. J. Fusco, J. T. Abatzoglou, J. K. Balch, S. Dadashi, and M. N. Tuanmu. 2018. "Cheatgrass (*Bromus tectorum*) Distribution in the Intermountain Western United States and Its Relationship to Fire Frequency, Seasonality, and Ignitions." *Biological Invasions* 20(6): 1493–1506. https://doi.org/10.1007/s10530-017-1641-8.

Brodie, E. G., J. E. D. Miller, and H. D. Safford. 2021. "Productivity Modifies the Effects of Fire Severity on Understory Diversity." *Ecology* 102(11): 1–9. https://doi.org/10.1002/ecy.3514.

Brookes, W., L. D. Daniels, K. Copes-Gerbitz, J. N. Baron, and A. L. Carroll. 2021. "A Disrupted Historical Fire Regime in Central British Columbia." *Frontiers in Ecology and Evolution* 9(June): 1–14. https://doi.org/10.3389/fevo.2021.676961.

Burkle, L., J. A. Myers, and R. T. Belote. 2015. "Wildfire Disturbance and Productivity as Drivers of Plant Species Diversity across Spatial Scales." *Ecosphere* 6(10): 202–214.

Chavardès, R. D., L. D. Daniels, J. E. Harvey, G. A. Greene, H. Marcoux, B. N. I. Eskelson, Z. E. Gedalof, et al. 2022. "Regional Drought Synchronised Historical Fires in Dry Forests of the Montane Cordillera Ecozone, Canada." *International Journal of Wildland Fire* 31(1): 67–80. https://doi.org/10.1071/WF21035.

Christen, D. C., and G. R. Matlack. 2009. "The Habitat and Conduit Functions of Roads in the Spread of Three Invasive Plant Species." *Biological Invasions* 11(2): 453–465. https://doi.org/10.1007/s10530-008-9262-x.

Christianson, A. C. 2015. "Social Science Research on Indigenous Wildfire Management in the 21st Century and Future Research Needs." *International Journal of Wildland Fire* 24(2): 190–200. https://doi.org/10.1071/WF13048.

Clarke, P. J., M. J. Lawes, J. J. Midgley, B. B. Lamont, F. Ojeda, G. E. Burrows, N. J. Enright, and K. J. E. Knox. 2013. "Resprouting as a Key Functional Trait: How Buds, Protection and Resources Drive Persistence after Fire." *New Phytologist* 197(1): 19–35. https://doi.org/10.1111/nph.12001.

Coop, J. D., S. A. Parks, C. S. Stevens-Rumann, S. D. Crausbay, P. E. Higuera, M. D. Hurteau, A. Tepley, et al. 2020. "Wildfire-Driven Forest Conversion in Western North American Landscapes." *BioScience* 70(8): 659–673. https://doi.org/10.1093/biosci/biaa061.

Coops, N. C., T. Hermosilla, M. A. Wulder, J. C. White, and D. K. Bolton. 2018. "A Thirty Year, Fine-Scale, Characterization of Area Burned in Canadian Forests Shows Evidence of Regionally Increasing Trends in the Last Decade." *PLoS One* 13(5): 1–19. https://doi.org/10.1371/journal.pone.0197218.

Copes-Gerbitz, K., L. D. Daniels, and S. M. Hagerman. 2023. "The Contribution of Indigenous Stewardship to an Historical Mixed-Severity Fire Regime in British Columbia, Canada." *Ecological Applications* 33: e2736. https://doi.org/10.1002/eap.2736.

Copes-Gerbitz, K., S. M. Hagerman, and L. D. Daniels. 2022. "Transforming Fire Governance in British Columbia, Canada: An Emerging Vision for Coexisting with Fire." *Regional Environmental Change* 22(48): 1–15. https://doi.org/10.1007/s10113-022-01895-2.

Coughlan, M. R., and A. M. Petty. 2012. "Linking Humans and Fire: A Proposal for a Transdisciplinary Fire Ecology." *International Journal of Wildland Fire* 21(5): 477–487. https://doi.org/10.1071/WF11048.

Crawford, J. A., C.-H. A. Wahren, S. Kyle, and W. H. Moir. 2001. "Responses of Exotic Plant Species to Fires in *Pinus ponderosa* Forests in Northern Arizona." *Journal of Vegetation Science* 12(2): 261–68. https://doi.org/10.2307/3236610.

Daniels, L. D., L. L. Yocom Kent, R. L. Sherriff, and E. K. Heyerdahl. 2017. "Deciphering the Complexity of Historical Fire Regimes: Diversity among Forests of Western North America." In *Dendroecology: Tree-Ring Analyses Applied to Ecological Studies*, edited by M. M. Amoroso, L. D. Daniels,

J. J. Carnerero, and P. J. Baker, 185–210. Cham: Springer Nature. https://doi.org/10.1007/978-3-319-61669-8.

Day, N. J., S. Carrière, and J. L. Baltzer. 2017. "Annual Dynamics and Resilience in Post-Fire Boreal Understory Vascular Plant Communities." *Forest Ecology and Management* 401: 264–272. https://doi.org/10.1016/j.foreco.2017.06.062.

De Cáceres, M., F. Jansen, and N. Dell. 2022. "Package 'indicspecies': Relationship between Species and Groups of Sites (Vol. Version 1)." CRAN. https://doi.org/10.1890/08-1823.1.

Deur, D. E., and N. Turner. 2005. *Keeping It Living: Traditions of Plant Use and Cultivation on the Northwest Coast of North America*. Seattle, WA: University of Washington Press.

Dickson-Hoyle, S. 2023. "Fire Severity Drives Understory Community Dynamics and the Recovery of Culturally Significant Plants." Data. Open Science Framework. https://osf.io/4kvn2.

Dickson-Hoyle, S., R. E. Ignace, M. B. Ignace, S. M. Hagerman, L. D. Daniels, and K. Copes-Gerbitz. 2022. "Walking on Two Legs: A Pathway of Indigenous Restoration and Reconciliation in Fire-Adapted Landscapes." *Restoration Ecology* 30(4): 1–9. https://doi.org/10.1111/rec.13566.

Dickson-Hoyle, S., and C. John. 2021. *Elephant Hill: Secwépemc Leadership and Lessons Learned from the Collective Story of Wildfire Recovery*. Kamloops: Secwepemcúl'ecw Restoration and Stewardship Society.

Dodson, E. K., and C. E. Fiedler. 2006. "Impacts of Restoration Treatments on Alien Plant Invasion in *Pinus ponderosa* Forest, Montana, USA." *Journal of Applied Ecology* 43: 887–897.

Dodson, E. K., D. W. Peterson, and R. J. Harrod. 2008. "Understory Vegetation Response to Thinning and Burning Restoration Treatments in Dry Conifer Forests of the Eastern Cascades, USA." *Forest Ecology and Management* 255: 3130–40. https://doi.org/10.1016/j.foreco.2008.01.026.

Donovan, V. M., D. Twidwell, D. R. Uden, T. Tadesse, B. D. Wardlow, C. H. Bielski, M. O. Jones, B. W. Allred, D. E. Naugle, and C. R. Allen. 2020. "Resilience to Large, "Catastrophic" Wildfires in North America's Grassland Biome." *Earth's Future* 8(7): 1–16. https://doi.org/10.1029/2020EF001487.

Downing, W. M., M. A. Krawchuk, J. D. Coop, G. W. Meigs, S. L. Haire, R. B. Walker, E. Whitman, G. Chong, C. Miller, and C. Tortorelli. 2020. "How Do Plant Communities Differ between Fire Refugia and Fire-Generated Early-Seral Vegetation?" *Journal of Vegetation Science* 31(1): 26–39. https://doi.org/10.1111/jvs.12814.

Dufrêne, M., and P. Legendre. 1997. "Species Assemblages and Indicator Species: The Need for a Flexible Asymmetrical Approach." *Ecological Monographs* 67(3): 345–366. https://doi.org/10.2307/2963459.

E-Flora BC: Electronic Atlas of the Flora of British Columbia. n.d. https://ibis.geog.ubc.ca/biodiversity/eflora/. [Accessed February 2022].

Falk, D. A., P. J. van Mantgem, J. E. Keeley, R. M. Gregg, C. H. Guiterman, A. J. Tepley, D. J. N. Young, and L. A. Marshall. 2022. "Mechanisms of Forest Resilience." *Forest Ecology and Management* 521: 120129.

Fletcher, M. S., T. Hall, and A. N. Alexandra. 2021. "The Loss of an Indigenous Constructed Landscape following British Invasion of Australia: An Insight into the Deep Human Imprint on the Australian Landscape." *Ambio* 50(1): 138–149. https://doi.org/10.1007/s13280-020-01339-3.

Fornwalt, P. J., and M. R. Kaufmann. 2014. "Understorey Plant Community Dynamics Following a Large, Mixed Severity Wildfire in a *Pinus ponderosa-Pseudotsuga menziesii* Forest, Colorado, USA." *Journal of Vegetation Science* 25(3): 805–818. https://doi.org/10.1111/jvs.12128.

Fornwalt, P. J., M. R. Kaufmann, and T. J. Stohlgren. 2010. "Impacts of Mixed Severity Wildfire on Exotic Plants in a Colorado Ponderosa Pine-Douglas-Fir Forest." *Biological Invasions* 12(8): 2683–95. https://doi.org/10.1007/s10530-009-9674-2.

Freeman, J. P., T. J. Stohlgren, M. E. Hunter, P. N. Omi, E. J. Martinson, G. W. Chong, and C. S. Brown. 2007. "Rapid Assessment of Postfire Plant Invasions in Coniferous Forests of the Western United States." *Ecological Applications* 17(6): 1656–65. https://doi.org/10.1890/06-1859.1.

Gilliam, F. S. 2007. "The Ecological Significance of the Herbaceous Layer in Temperate Forest Ecosystems." *BioScience* 57(10): 845–858. https://doi.org/10.1641/B571007.

Gottersfeld, L. M. 1994. "Aboriginal Burning for Vegetation Management in Northwest British Columbia." *Human Ecology* 22(2): 171–188.

Government of Canada. 2023. "Canadian Climate Normals." https://climate.weather.gc.ca/climate_normals/index_e.html.

Haeussler, S., D. W. Coates, and J. Mather. 1990. *Autecology of Common Plants in British Columbia: A Literature Review*. Victoria: Canada/BC Economic & Regional Development Agreement.

Hagmann, R. K., J. F. Franklin, and K. N. Johnson. 2013. "Historical Structure and Composition of Ponderosa Pine and Mixed-Conifer Forests in South-Central Oregon." *Forest Ecology and Management* 304: 492–504. https://doi.org/10.1016/j.foreco.2013.04.005.

Hagmann, R. K., P. F. Hessburg, S. J. Prichard, N. A. Povak, P. M. Brown, P. Z. Fulé, R. E. Keane, et al. 2021. "Evidence for Widespread Changes in the Structure, Composition, and Fire Regimes of Western North American Forests." *Ecological Applications* 31(8): e02431. https://doi.org/10.1002/eap.2431.

Halpern, A. 2016. "Prescribed Fire and Tanoak (*Notholithocarpus densiflorus*) Associated Cultural Plant Resources of the Karuk and Yurok Peoples of California." PhD thesis, University of California. https://escholarship.org/uc/item/98384265.

Halpern, C. B. 1989. "Early Successional Patterns of Forest Species: Interactions of Life History Traits and Disturbance." *Ecology* 70(3): 704–720. https://doi.org/10.2307/1940221.

Halpern, C. B., and T. A. Spies. 1995. "Plant Species Diversity in Natural and Managed Forests of the Pacific Northwest." *Ecological Applications* 5(4): 913–934.

Halpern, C. B., and J. A. Antos. 2022. "Burn Severity and Pre-Fire Seral State Interact to Shape Vegetation Responses to Fire in a Young, Western Cascade Range forest." *Forest Ecology and Management* 507(January): 120028. https://doi.org/10.1016/j.foreco.2022.120028.

Hanes, C. C., X. Wang, P. Jain, M. A. Parisien, J. M. Little, and M. D. Flannigan. 2019. "Fire-Regime Changes in Canada over the Last Half Century." *Canadian Journal of Forest Research* 49(3): 256–269. https://doi.org/10.1139/cjfr-2018-0293.

Hart, S. A., and H. Y. H. Chen. 2006. "Understory Vegetation Dynamics of North American Boreal Forests." *Critical Reviews in Plant Sciences ISSN* 25: 381–397. https://doi.org/10.1080/07352680600819286.

Hart, S. A., and H. Y. H. Chen. 2008. "Fire, Logging, and Overstory Affect Understory Abundance, Diversity, and Composition in Boreal Forest." *Ecological Monographs* 78(1): 123–140. https://doi.org/10.1890/06-2140.1.

Hart-Fredeluces, G. M., T. Ticktin, and F. K. Lake. 2021. "Simulated Indigenous Fire Stewardship Increases the Population Growth Rate of an Understorey Herb." *Journal of Ecology* 109(3): 1133–47. https://doi.org/10.1111/1365-2745.13542.

Harvey, J. E., D. J. Smith, and T. T. Veblen. 2017. "Mixed-Severity Fire History at a Forest-Grassland Ecotone in West Central British Columbia, Canada." *Ecological Applications* 27(6): 1746–60. https://doi.org/10.1002/eap.1563.

Hessburg, P. F., D. J. Churchill, A. J. Larson, R. D. Haugo, C. Miller, T. A. Spies, M. A. North, et al. 2015. "Restoring Fire-Prone Inland Pacific Landscapes: Seven Core Principles." *Landscape Ecology* 30(10): 1809–39. https://doi.org/10.1007/s10980-015-0218-0.

Hessburg, P. F., C. L. Miller, S. A. Parks, N. A. Povak, A. H. Taylor, P. E. Higuera, S. J. Prichard, et al. 2019. "Climate, Environment, and Disturbance History Govern Resilience of Western North American Forests." *Frontiers in Ecology and Evolution* 7. https://doi.org/10.3389/fevo.2019.00239.

Heyerdahl, E. K., K. Lertzman, and S. Karpuk. 2007. "Local-Scale Controls of a Low-Severity Fire Regime (1750–1950), Southern British Columbia, Canada Emily." *Ecoscience* 14(1): 40–47.

Hoffman, K. M., A. Christianson, S. Dickson-Hoyle, K. Copes-Gerbitz, W. Nikolakis, D. A. Diabo, R. Mcleod, et al. 2022. "The Right to Burn: Barriers and Opportunities for Indigenous-Led Fire Stewardship in Canada." *FACETS* 7: 464–481. https://doi.org/10.1139/facets-2021-0062.

Hoffman, K. M., E. L. Davis, S. B. Wickham, K. Schang, A. Johnson, T. Larking, P. N. Lauriault, N. Q. Le, E. Swerdfager, and A. Trant. 2021. "Conservation of Earth's Biodiversity Is Embedded in Indigenous Fire Stewardship." *Proceedings of the National Academy of Sciences of the United States of America* 118(32): 1–6. https://doi.org/10.1073/pnas.2105073118.

Huisinga, K. D., D. C. Laughlin, P. Z. Fulé, J. D. Springer, and C. M. Mcglone. 2005. "Effects of an Intense Prescribed Fire on Understory Vegetation in a Mixed Conifer Forest." *The Journal of the Torrey Botanical Society* 132(4): 590–601.

Ignace, M. 2014. "SSN Cultural Heritage Study – Final Report."

Ignace, M. B., and R. E. Ignace. 2017. *Secwépemc People, Land and Laws*. Montreal: McGill-Queen's University Press.

Invasive Species Council of BC. 2021. "Field Guide to Noxious Weeds and Other Selected Invasive Plants of British Columbia." https://bcinvasives.ca/wp-content/uploads/2021/02/Field_guide_to_Noxious_Weeds_11th_2021.pdf.

Keeley, J. E. 2009. "Fire Intensity, Fire Severity and Burn Severity: A Brief Review and Suggested Usage." *International Journal of Wildland Fire* 2009(18): 116–126.

Kerns, B. K., W. G. Thies, and C. G. Niwa. 2006. "Season and Severity of Prescribed Burn in Ponderosa Pine Forests: Implications for Understory Native and Exotic Plants."

Ecoscience 13(1): 44–55. https://doi.org/10.2980/1195-6860(2006)13[44:SASOPB]2.0.CO;2.

Key, C. H., and N. C. Benson. 2006. "FIREMON – Landscape Assessment." In *FIREMON: Fire Effects Monitoring and Inventory System. General Technical Report RMRS-GTR-164-CD*, edited by D. C. Lutes, R. E. Keane, J. F. Caratti, C. H. Key, N. C. Benson, S. Sutherland, and L. J. Gangi, 1–55. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station.

Knight, C. A., L. Anderson, M. J. Bunting, M. Champagne, R. M. Clayburn, J. N. Crawford, A. Klimaszewski-Patterson, et al. 2022. "Land Management Explains Major Trends in Forest Structure and Composition over the Last Millennium in California's Klamath Mountains." *Proceedings of the National Academy of Sciences of the United States of America* 119(12): 1–11. https://doi.org/10.1073/pnas.2116264119.

Kuhnlein, H., and N. J. Turner. 1991. *Traditional Plant Foods of Canadian Indigenous Peoples: Nutrition, Botany and Use*. Amsterdam: Gordon and Breach Publishers.

Lenth, R. V., B. Bolker, P. Buerkner, I. Giné-Vazquez, M. Herve, M. Jung, J. Love, F. Miguez, H. Riebl, and H. Singmann. 2023. "Estimated Marginal Means, aka Least-Squares Means." Version 1.8.5. https://cran.r-project.org/web/packages/emmeans/index.html.

Lepofsky, D., D. Hallett, K. Washbrook, A. McHalsie, and K. Lertzman. 2005. "Documenting Precontact Plant Management on the Northwest Coast: An Example of Prescribed Burning in the Central and Upper Fraser Valley, British Columbia." In *Keeping It Living: Traditions of Plant Use and Cultivation on the Northwest Coast*, edited by D. E. Deur and N. J. Turner. Seattle, WA: University of Washington Press.

Levine, J. I., B. M. Collins, Z. L. Steel, P. de Valpine, and S. L. Stephens. 2022. "Higher Incidence of High-Severity Fire In and Near Industrially Managed Forests." *Frontiers in Ecology and the Environment* 1–8: 397–404. https://doi.org/10.1002/fee.2499.

Linley, G. D., C. J. Jolly, T. S. Doherty, W. L. Geary, D. Armenteras, C. M. Belcher, R. Bliege Bird, et al. 2022. "What Do You Mean, 'Megafire'?" *Global Ecology and Biogeography* 31: 1–17. https://doi.org/10.1111/geb.13499.

Lozon, J. D., and H. J. MacIsaac. 1997. "Biological Invasions: Are They Dependent on disturbance?" *Environmental Reviews* 5(2): 131–144. https://doi.org/10.1139/a97-007.

Marcoux, H. M., L. D. Daniels, S. E. Gergel, E. Da Silva, Z. Gedalof, and P. F. Hessburg. 2015. "Differentiating Mixed- and High-Severity Fire Regimes in Mixed-Conifer Forests of the Canadian Cordillera." *Forest Ecology and Management* 341: 45–58. https://doi.org/10.1016/j.foreco.2014.12.027.

Marcoux, H. M., S. E. Gergel, and L. D. Daniels. 2013. "Mixed-Severity Fire Regimes: How Well Are They Represented by Existing Fire-Regime Classification Systems?" *Canadian Journal of Forest Research* 43(7): 658–668. https://doi.org/10.1139/cjfr-2012-0449.

Mariani, M., S. E. Connor, M. Theuerkauf, A. Herbert, P. Kuneš, D. Bowman, M.-S. Fletcher, et al. 2022. "Disruption of Cultural Burning Promotes Shrub Encroachment and Unprecedented Wildfires." *Frontiers in Ecology and the Environment* 20: 292–300. https://doi.org/10.1002/fee.2395.

Marks-Block, T., F. K. Lake, and L. M. Curran. 2019. "Effects of Understory Fire Management Treatments on California

Hazelnut, an Ecocultural Resource of the Karuk and Yurok Indians in the Pacific Northwest." *Forest Ecology and Management* 450: 117517. https://doi.org/10.1016/j.foreco.2019.117517.

McCune, B., J. B. Grace, and D. L. Urban. 2002. *Analysis of Ecological Communities*, Vol. 28. Gleneden Beach, OR: MjM Software Design.

McLauchlan, K. K., P. E. Higuera, J. Miesel, B. M. Rogers, J. Schweitzer, J. K. Shuman, A. J. Tepley, et al. 2020. "Fire as a Fundamental Ecological Process: Research Advances and Frontiers." *Journal of Ecology* 108(5): 2047–69. https://doi.org/10.1111/1365-2745.13403.

Meunier, G., and C. Lavoie. 2012. "Roads as Corridors for Invasive Plant Species: New Evidence from Smooth Bedstraw (*Galium mollugo*)." *Invasive Plant Science and Management* 5(1): 92–100. https://doi.org/10.1614/ipsm-d-11-00049.1.

Midgley, J. J., L. M. Kruger, and R. Skelton. 2011. "How Do Fires Kill Plants? The Hydraulic Death Hypothesis and Cape Proteaceae "Fire-Resisters"." *South African Journal of Botany* 77: 381–86. https://doi.org/10.1016/j.sajb.2010.10.001.

Miller, J. E. D., and H. D. Safford. 2020. "Are Plant Community Responses to Wildfire Contingent upon Historical Disturbance Regimes?" *Global Ecology and Biogeography* 29(10): 1621–33. https://doi.org/10.1111/geb.13115.

Morgan, P., M. Moy, C. A. Droske, S. A. Lewis, L. B. Lentile, P. R. Robichaud, A. T. Hudak, and C. J. Williams. 2015. "Vegetation Response to Burn Severity, Native Grass Seeding, and Salvage Logging." *Fire Ecology* 11(2): 31–58. https://doi.org/10.4996/fireecology.1102031.

Nimmo, D. G., A. N. Andersen, S. Archibald, M. M. Boer, L. Brotons, C. L. Parr, and M. W. Tingley. 2022. "Fire Ecology for the 21st Century: Conserving Biodiversity in the Age of Megafire." *Diversity and Distributions* 28(3): 350–56. https://doi.org/10.1111/ddi.13482.

Nolan, R. H., L. Collins, A. Leigh, M. K. J. Ooi, T. J. Curran, T. A. Fairman, V. Resco de Dios, and R. Bradstock. 2021. "Limits to Post-Fire Vegetation Recovery under Climate Change." *Plant Cell and Environment* 44(11): 3471–89. https://doi.org/10.1111/pce.14176.

Oksanen, J., G. L. Simpson, F. G. Blanchet, R. Kindt, P. Legendre, R. B. O'Hara, P. Solymos, et al. 2022. "Vegan: Community Ecology Package." CRAN.

Parisien, M. A., Q. E. Barber, K. G. Hirsch, C. A. Stockdale, S. Erni, X. Wang, D. Arsenault, and S. A. Parks. 2020. "Fire Deficit Increases Wildfire Risk for Many Communities in the Canadian Boreal Forest." *Nature Communications* 11(1): 1–9. https://doi.org/10.1038/s41467-020-15961-y.

Peacock, S. L., M. B. Ignace, and N. Turner. 2016. "Re Secwépemc re syecwmenúl'ecwems: Secwepemc Stewardship of Land and Resources." In *Secwepemc People and Plants: Research Papers in Shuswap Ethnobotany*, edited by M. B. Ignace, N. J. Turner, and S. L. Peacock, 177–217. Tacoma: Society of Ethnobiology.

Peeler, J. L., and E. A. H. Smithwick. 2018. "Exploring Invasibility with Species Distribution Modeling: How Does Fire Promote Cheatgrass (*Bromus tectorum*) Invasion within Lower Montane Forests?" *Diversity and Distributions* 24(9): 1308–20. https://doi.org/10.1111/ddi.12765.

Peppin, D., P. Z. Fulé, C. H. Sieg, J. L. Beyers, and M. E. Hunter. 2010. "Post-Wildfire Seeding in Forests of the Western United States: An Evidence-Based Review." *Forest Ecology and Management* 260(5): 573–586. https://doi.org/10.1016/j.foreco.2010.06.004.

Pogue, A. M. 2017. *Humans, Climate and an Ignitions-Limited Fire Regime at Vaseux Lake*. Vancouver: University of British Columbia.

Poos, M. S., and D. A. Jackson. 2012. "Addressing the Removal of Rare Species in Multivariate Bioassessments: The Impact of Methodological Choices." *Ecological Indicators* 18: 82–90. https://doi.org/10.1016/j.ecolind.2011.10.008.

Pyke, D. A., T. A. Wirth, and J. L. Beyers. 2013. "Does Seeding after Wildfires in Rangelands Reduce Erosion or Invasive Species?" *Restoration Ecology* 21(4): 415–421. https://doi.org/10.1111/rec.12021.

R Core Team. 2022. *R: A Language and Environment for Statistical Computing (4.1.2)*. Vienna: R Foundation for Statistical Computing.

Reimer, R. 2000. *Extreme Archaeology: The Results of Investigations at High-Elevation Regions in the Northwest*. Burnaby: Simon Fraser University.

Richter, C., M. Rejmanek, J. E. D. Miller, K. R. Welch, J. Weeks, and H. Safford. 2019. "The Species Diversity × Fire Severity Relationship Is Hump-Shaped in Semiarid Yellow Pine and Mixed Conifer Forests." *Ecosphere* 10(10): e02882. https://doi.org/10.1002/ecs2.2882.

Roberts, M. 2004. "Response of the Herbaceous Layer to Natural Disturbance in North American forests." *Canadian Journal of Botany* 82(9): 1273–83.

Ryan, K. C. 1982. "Techniques for Assessing Fire Damage to Trees." In *Proceedings of Joint Fire Council Meeting. Fire - its Field Effects*, edited by J. E. Lotan, 1–11. The Intermountain Fire Council and The Rocky Mountain Fire Council: Jackson, WY.

Seidl, R., and M. G. Turner. 2022. "Post-Disturbance Reorganization of Forest Ecosystems in a Changing World." *Proceedings of the National Academy of Sciences of the United States of America* 119(28): 1–10.

Stark, K., A. Arsenault, and G. Bradfield. 2006. "Soil Seed Banks and Plant Community Assembly Following Disturbance by Fire and Logging in Interior Douglas-Fir Forests of South-Central British Columbia." *Canadian Journal of Botany* 84(10): 1548–60.

Stephan, K., M. Miller, and M. B. Dickinson. 2010. "First-Order Fire Effects on Herbs and Shrubs: Present Knowledge and Process Modeling Needs." *Fire Ecology* 6(1): 95–114. https://doi.org/10.4996/fireecology.0601095.

Stephens, S. L., N. Burrows, A. Buyantuyev, R. W. Gray, R. E. Keane, R. Kubian, S. Liu, et al. 2014. "Temperate and Boreal Forest Mega-Fires: Characteristics and Challenges." *Frontiers in Ecology and the Environment* 12(2): 115–122. https://doi.org/10.1890/120332.

Stewart, O. C. 2009. In *Forgotten Fires: Native Americans and the Transient Wilderness*, edited by H. T. Lewis and M. K. Anderson. Norman: University of Oklahoma Press.

Strand, E. K., K. L. Satterberg, A. T. Hudak, J. Byrne, A. H. Khalyani, and A. M. S. Smith. 2019. "Does Burn Severity Affect Plant Community Diversity and Composition in Mixed Conifer Forests of the United States Intermountain West One Decade Post Fire?" *Fire Ecology* 15: 25.

Thomas, J. W. 1979. "Wildlife Habitats in Managed Forests in the Blue Mountains of Oregon and Washington." In *Agriculture*, edited by J. L. Parker, R. A. Mowrey, G. M. Hansen, and B. J. Bell. Washington, DC: U.S. Department of Agriculture – Forest Service.

Tortorelli, C., J. Kim, N. M. Vaillant, K. Riley, A. Dye, K. C. Vogler, R. Lemons, M. Day, M. A. Krawchuk, and B. K. Kerns. 2023. "Feeding the Fire: Annual Grass Invasion Facilitates Modeled Fire Spread across Inland Northwest Forest-Mosaic Landscapes." *Ecosphere* 14: 1–19. https://doi.org/10.1002/ecs2.4413.

Turner, M. G. 2010. "Disturbance and Landscape Dynamics in a Changing World." *Ecology* 91(10): 2833–49. https://doi.org/10.1358/dot.2011.47.2.1576694.

Turner, N. 1999. ""Time to Burn": Traditional Use of Fire to Enhance Resource Production by Aboriginal Peoples in British Columbia." In *Indians, Fire and the Land*, edited by R. Boyd, 185–219. Corvallis, OR: Oregon State University Press.

Turner, N. J., D. Deur, and C. R. Mellott. 2011. ""Up on the Mountain": Ethnobotanical Importance of Montane Sites in Pacific Coastal North America." *Journal of Ethnobiology* 31(1): 4–43. https://doi.org/10.2993/0278-0771-31.1.4.

Turner, N. J., M. B. Ignace, and S. L. Peacock. 2016. "Introduction to the Volume." In *Secwepemc People and Plants: Research Papers in Shuswap Ethnobotany*, edited by M. B. Ignace, N. J. Turner, and S. L. Peacock, 1–26. Tacoma, WA: Society of Ethnobiology.

Turner, N. J., D. Lepofsky, and D. Deur. 2013. "Plant Management Systems of British Columbia's First Peoples." *BC Studies: The British Columbian Quarterly* 179: 107–133. http://ojs.library.ubc.ca.ezproxy.library.uvic.ca/index.php/bcstudies/article/view/184112/184174.

Tyhurst, R. 1992. "Traditional and Contemporary Land and Resource Use by Ts'kw'aylaxw and Xaxli'p Bands." In *A Complex Culture of the British Columbia Plateau*, edited by B. Hayden, 355–404. Vancouver: UBC Press.

United Nations Environment Programme (UNEP). 2022. *Spreading Like Wildfire: The Rising Threat of Extraordinary Wildfires*. Nairobi: A UNEP Rapid Response Assessment. https://doi.org/10.1038/news000413-8.

US Forest Service. 2022. "Fire Effects Information System." https://www.feis-crs.org/feis/.

US Geological Survey. 2018. "Landsat Collection 2 – Landsat 8 Operational Land Imager." https://www.usgs.gov/landsat-missions/landsat-collection-2.

Wang, G. G., and K. J. Kemball. 2005. "Effects of Fire Severity on Early Development of Understory Vegetation." *Canadian Journal of Forest Research* 35(2): 254–262.

Weeks, J., J. E. D. Miller, and H. D. Safford. 2023. "High-Severity Fire Drives Persistent Floristic Homogenization in Human-Altered Forests." *Ecosphere* 14(2): 1–13. https://doi.org/10.1002/ecs2.4409.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.