CLIMATE-MEDIATED WILDFIRE DISTURBANCE TO A MAMMAL COMMUNITY

WITHIN PROTECTED TEMPERATE CONIFEROUS FORESTS

by

Patrick Burke

B.A., College of William and Mary, 2004

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE AND POSTDOCTORAL STUDIES

(Zoology)

THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

May 2019

The following individuals certify that they have read, and recommend to the Faculty of Graduate and Postdoctoral Studies for acceptance, a thesis/dissertation entitled:

Climate-mediated wildfire disturbance to a mammal community within protected temperate coniferous forests

submitted by   Patrick Burke   in partial fulfillment of the requirements for

the degree of   Master of Science

in   Zoology

Examining Committee:

Dr. Dolph Schluter
Co-supervisor

Dr. Cole Burton
Supervisory Committee Member

Dr. Judy Myers
Additional Examiner

Additional Supervisory Committee Members:

Dr. Karen Hodges
Supervisory Committee Member

Dr. Jedediah Brodie
Supervisory Committee Member

Abstract

Climate disruption is anticipated to impact global biodiversity in the twenty-first century, in part by altering the frequency and intensity of natural disturbances. Wildland fires are climate-mediated disturbances that are increasing in frequency and intensity across western North American coniferous forests due to atmospheric warming and reduced summer precipitation. Coupled climate-fire models predict that climate is driving novel wildfire regimes in this system, but the landscape-level effects of increasing fire size and intensity of burns on wildlife remain unknown. The intermediate disturbance hypothesis suggests that species diversity is maximized when ecological disturbance regimes are moderate through a trade-off between colonization and competitive exclusion. If this hypothesis describes diversity-disturbance relationships in the North Cascades mountains of Canada and the United States, I expected that areas subject to fires of larger extent and greater severity than the historical norm will have reduced species diversity. To test this prediction at the landscape scale, I sampled mammal activity using passive camera traps deployed under a probabilistic sampling design, stratified across land cover type and fire history. I used these data to assess the impact of fire severity, time since fire, and fire extent on mammal species richness. I found that high mammal community diversity can persist following burns of high severity. I also found that the relationship between mammal diversity and wildfire disturbance deviates from the expected unimodal peaked pattern predicted by the intermediate disturbance hypothesis.

Lay Summary

Wildfires occur naturally in forests and grasslands around the world. As the climate warms, new patterns of fire are anticipated in many environments. Dry forests are susceptible to larger and more severe fires. These fires have unknown consequences for animals living in these forests, including forests within national parks and preserves designed to protect animals and their habitat. My research addresses how wildfire changes the number of animal species in the forest by comparing the number of species in burned versus non-burned areas. Additionally, my research explores the specific environmental conditions that might cause such changes in the animal community. Unexpectedly, I found that dry forests of the North Cascades with the highest wildfire severity had greater species diversity than sites with either low disturbance or sites with no disturbance. These results suggest that mammal communities may be resilient to new patterns of wildfire associated with climate change.

Preface

This thesis represents the primary research of Patrick Burke in fulfilling his degree as a Master of Science student at the University of British Columbia. The design of the research program was completed by Patrick Burke and Dr. Jedediah Brodie. Data were collected by Patrick Burke and Nick Hindley. Patrick Burke performed all statistical analyses and wrote the manuscript. No ethics approvals were required for this research.

Table of Contents

List of Tables

List of Figures

List of Abbreviations

ClimateWNA	Climate Western North America software
DEM	Digital Elevation Model
g	gram
GECSC	Geosciences and Environmental Change Science Center
GeoMAC	Geospatial Multi-Agency Coordination Group
GRTS	Generalized random-tessellation stratified survey design
IDH	Intermediate disturbance hypothesis
kg	kilogram
km²	square kilometers
m	meter
MTBS	Monitoring Trends in Burn Severity
PRISM	Parameter Elevation Regression on Independent Slopes Model
STRM	Shuttle Radar Topography Mission
TIB	Theory of Island Biogeography
USGS	United States Geological Survey

Acknowledgements

I acknowledge the support and guidance of the Faculty of the Biodiversity Research Centre at UBC who enriched my understanding of ecological science, supported my thesis research, and broadened my worldview. I specifically thank Dr. Jedediah Brodie for his contributions to the development of my research question, logistical support in the field, and recommendations for analyzing data. Additionally, I sincerely thank Dr. Dolph Schluter for his patience explaining linear regression and for fulfilling a vacancy as co-supervisor on my committee. I thank Dr. Karen Hodges and Dr. Cole Burton for thoughtful recommendations which improved my thesis. I thank Dr. Diane Srivastava for guidance on my manuscript and assistance with community diversity metrics. I thank Dr. Jason Ransom for support organizing field logistics and managing equipment. I thank undergraduates Nick Hindley and Taylor Justason for contributions of invaluable field and lab time, as well as my assistants Alex and Aida Burke who provided comic relief and shared campfire stories. I thank the administrative staff at US National Park Service, BC Parks, and the US Forest Service for helping secure research permits. My research was financially supported by the Skagit Environmental Endowment Commission and the University of British Columbia Botany Department.

Finally, I extend my sincere gratitude to the original inhabitants and stewards of the lands where my study took place, namely the Stó:lō Nation, Nlaka'pamux Nation, Nooksack Nation, Methow Tribe, Chelan Tribe, Entiat Tribe, and the Confederated Tribes and Bands of the Yakama Nation, whose ancestral traditional territories extend across regions of my study area. I also acknowledge the foresight of mid-century citizen activists and land managers in the United States and Canada for enacting legal protections to facilitate the preservation of biodiversity and provision of future ecosystem services on these lands.

Chapter 1. Introduction

Chapter 1 introduces the theory behind the empirical work in Chapter 2, which is my thesis research. Here, I outline the research theme, review the literature, and introduce my research questions in Section 1.2.

1.1   Background and rationale

Fundamental to ecology is understanding the spatial distribution of biodiversity and the mechanisms responsible for observed patterns at multiple scales. Ecology is often defined as the study of the distribution and abundance of organisms (Andrewartha & Birch 1954). One important mechanism driving diversity patterns is disturbance. A succinct and precise definition for ecological disturbance is challenging because many types of disturbances exist and disturbances are relative to a reference condition that must be defined (Rykiel 1985). For my purposes, disturbance refers to a measurable condition that changes the structure and spatial arrangement of habitat in an ecosystem at local, regional, or landscape scales. Disturbances can be biotic or abiotic, brief or extended, frequent or infrequent. Connell (1978) provided examples of disturbance such as forest windfall, landslides, insect plagues, floods, and storms. Shea et al. (2004) succinctly define disturbance as an event that alters niche opportunities available to species in a system. Disturbances can be quantified by frequency, size, intensity, and severity (Turner et al. 1998). The term perturbation is not synonymous with disturbance, but rather describes the effects of disturbances (Rykiel 1985). A disturbance regime refers to the spatial and temporal dynamics of recurring disturbances over time (Turner 2010).

Disturbance affects species by changing the quality and structure of available habitat. Habitat fragmentation describes the landscape-scale process of reconfiguring contiguous natural habitats into patches surrounded by disturbed or converted lands, known as the landscape matrix

(Fahrig 2003). Habitat loss and fragmentation are key topics of ecological research, constituting

as much as 20% of the academic literature between 1994 and 2016 (Fardila et al. 2017).

Generally, habitat loss is a stronger driver of adverse effects to biodiversity than habitat

fragmentation (Fahrig 2003). Disturbance can affect biodiversity through extinction (Barnosky et

al. 2011), alteration of trophic organization (Post 2002), or changes to spatial use of the

landscape (Turner et al. 1997). Disturbance also creates new niches for colonial species and edge

specialists (Hobbs & Huenneke 1992). But what rules or theory dictate the role of disturbance in

shaping community diversity?

The conceptual approach for understanding the ecological processes associated with

disturbance begins with the equilibrium theory of island biogeography (TIB; MacArthur &

Wilson 1967). The TIB predicts that species richness on islands surrounded by areas of non-

habitat is driven by two primary processes: colonization and local extinction. Areas with higher

species richness are characterized by larger land masses (with greater niche diversity) and shorter

inter-patch distances. Although originally conceptualized for oceanic islands, the mechanisms of

island biogeography seem to operate in terrestrial ecosystems at regional spatial scales and short

temporal scales. Empirical tests have validated the theory through experimental reductions of

local species richness and measuring colonization rates following disturbance (Simberloff &

Wilson 1969). In the past five decades, the TIB has been widely used as a conceptual tool to

interpret ecological effects of fragmentation, inform design of protected areas, and drive

ecological research programs (Diamond 1975; Newmark 1987, 1995; Belote et al. 2016; Fardila

et al. 2017).

An important extension to the TIB is the recognition of the value of intermediary

"matrix" habitat in continuous landscapes (Franklin & Lindenmayer 2009). Building from a

meta-analysis by Prugh et al. (2008), which shows that patch size and inter-patch distance are poor predictors of patch occupancy for many species, Franklin & Lindemayer (2009) suggest the processes that structure ecological communities in island systems are weakened by intermediate habitats located between primary habitat patches. These "matrix" habitats provide marginal resources for species dispersal and persistence away from preferred habitats. The recognition of the value of matrix habitats improves the TIB by recognizing that some ecosystems exhibit a gradient of habitat suitability.

The TIB describes patterns of community diversity as a dynamic equilibrium between colonization and extinction. These processes drive landscape-scale patterns of richness but also operate at the patch level (Simberloff & Wilson 1969). Therefore, local extinction from habitat patches and re-colonization can be important at local scales. But how do these processes interact in dynamic systems under active disturbance regimes? What rules govern the structuring of ecological communities in disturbed landscapes? One long-standing approach to answering that question is the intermediate disturbance hypothesis.

1.1.1 Intermediate disturbance hypothesis

Originally described by theoretical ecologists in the 1970's, the intermediate disturbance hypothesis (IDH) asserts that community richness in sessile organisms at local scales is maximized when disturbances are moderate in frequency and intensity (Horn et al. 1975; Connell 1978). Connell's paper explored six hypotheses to explain how local diversity is created and maintained. These six hypotheses are organized in two classes: (1) the equilibrium model, where high-diversity ecological communities exist in a state of balance and return to that state following disturbance and (2) the nonequilibrium model, where high-diversity communities result from perturbations that shuffle resources to provide continually changing ecological

3

niches. The IDH is based on observations of diversity within tropical forests and coral reefs and represents the latter, nonequilibrium, perspective. Connell (1978) noted that in communities where disturbances were rare, competitively dominant species exclude other species from the community. On the other hand, in communities with frequent disturbance, diversity is low because only the most competitive species are able to persist and colonize. The IDH postulates that intermediate disturbance increases diversity through a balance between colonization of disturbed habitats by new species and competitive exclusion by a few dominant species in undisturbed habitats. This hypothesis describes a mechanism that governs biodiversity patterns at local and regional scales.

A competing hypothesis explaining the mechanism behind patterns of richness is the niche partitioning hypothesis (Schoener 1974). The idea suggests that species specialization drives diversity patterns to an equilibrium in which all available niches are filled. Empirical work on niche partitioning shows that similar species differentiate resource use between selected prey items, across time of day and seasons, and within different habitats (MacArthur 1958; Ikeda et al. 2016). Importantly, multiple mechanisms may be working synergistically to drive community diversity (Chesson 2000). Or, mechanisms may be different across taxa or functional group. Niche partitioning describes relationships between coexisting species that utilize different resources to minimize competition. Alternatively, the IDH describes coexistence relationships where one species outcompetes a similar species occupying the same ecological niche, which draws from the competitive exclusion principle (Hardin 1960).

In the decades following the 1970s, the IDH was tested empirically. By 2001, enough primary research had been completed to publish a meta-analysis of disturbance-diversity studies (Mackey & Currie 2001). Surprisingly, Mackey and Currie (2001) found that diversity-

disturbance relationships are not often strong and are not consistently peaked, but rather show a variety of shapes, including monotonic or inverse-peaked. The authors caution that many diversity-disturbance relationships in the literature may reflect sampling design and sample size more than actual ecological relationships. They also question whether the IDH is primarily a patch or regional scale phenomenon. A second review focusing only on experimental studies found a similar result and suggested that feedback patterns between diversity and disturbance may be driving patterns in some systems (Hughes et al. 2007).

While the theory was being tested empirically, theoretical improvements to the IDH were being made. In 2004, researchers identified the need to identify the mechanisms that produce diversity in disturbed systems rather than only describe the observed patterns of diversity (Roxburgh et al. 2004; Shea et al. 2004). Because diversity requires high species coexistence, a more rigorous understanding of coexistence mechanisms in species rich systems is needed. Shea et al. (2004) point out that in most circumstances, the IDH is a simple representation of the sum of many different co-occurring coexistence mechanisms. One such mechanism is niche partitioning, as discussed above. Another mechanism is the storage effect, or the ability of one species to tolerate strong competition by delaying growth until conditions become more favorable. Examples include demographic buffering in population growth (McDonald et al. 2016) or maintenance of seed banks (Castillo & Stevenson 2010). A third coexistence mechanism is relative nonlinearity, which describes a condition where species responses to changes in resource availability follow different trajectories (Chesson 2000; Shea et al. 2004). Careful identification of species coexistence mechanisms improves diversity-disturbance research by describing the processes that drive patterns of species diversity.

Improvements to understanding processes driving diversity patterns is further extended by a 2011 study that identifies the importance of explicitly defining disturbance conditions (Miller et al. 2011). The authors use a simple two-species model to show that multiple diversity-disturbance relationships can be generated by changing the aspect of disturbance used to plot the relationship, namely intensity, timing, duration, and extent of disturbance. As an example, a community may have a peaked diversity-intensity relationship, a linear diversity-extent relationship, and no relationship between diversity and timing or duration of disturbance. The aspects of disturbance measured may independently affect species diversity in a community. In summary, the IDH describes patterns of diversity that are governed by processes of species coexistence and specific aspects of disturbance measured.

Although the IDH is widely known, not all ecologists agree on its validity as a guiding principle in the maintenance of species richness in biological systems. Fox (2013) refutes the theoretical underpinnings of the IDH, arguing that the model is logically flawed. He makes three criticisms of Connell's assumptions about how competitive exclusion shapes diversity-disturbance curves: 1) intermediate disturbance affects species coexistence through changes to strength of competition, not merely due to changes in species densities; 2) differential mortality rates and average growth rates drive competitive exclusion, not linear successional processes; and 3) environmental fluctuations alone are not sufficient to drive long-term competitive outcomes. Fox acknowledges that the competition—colonization interpretation of the IDH is theoretically sound, but interprets the key points of Connell's original formulation, above, as grounds for abandoning the IDH altogether. He also notes that empirical evidence for the IDH is mixed (Mackey & Currie 2001; Hughes et al. 2007). Others defended the hypothesis as a valuable explanation for a few mechanisms that drive diversity-disturbance patterns, while

acknowledging the flaws in Fox's critique (Sheil & Burslem 2013). In summary, the IDH is a simple idea with complex mechanisms that make interpretation across disturbances and ecosystems difficult. Precise, quantitative, general laws in community ecology are rare (Simberloff 2004), but ecologists generally agree that the basic concept underpinning the IDH is sound: that a trade-off between colonization and competitive exclusion in ecological communities can support species coexistence and higher diversity when disturbance is moderate than when disturbance is either too high or too low.

1.1.2 Disturbance in coniferous forests of the North Cascades

Wildland fire, or wildfire, is an ecological process that disturbs large spatial areas of coniferous forests in the North Cascade mountains in western North America. Wildfire is a historically common disturbance in these forests, but catastrophic fires are increasing following decades of fire suppression (Agee & Skinner 2005; Marlon et al. 2012) and climate warming (Dennison et al. 2014; Sheehan et al. 2015). In the North Cascades, the proportion of forests highly suitable for large wildfires is predicted to increase from 2% to approximately 30% in the next century (Davis et al. 2017). Further, the mean fire return interval is estimated to decrease in the next century from 81 years to between 47 and 37 years depending on the climate model selected (Sheehan et al. 2015).

Globally, much of the literature on community response to wildfire addresses succession in plant communities (Eales et al. 2018). Comparatively less is known about the response of vertebrates to wildfire. Wildfire disturbance has most often been assessed at the species-level using radio telemetry (Cunningham et al. 2003; Biggs et al. 2010; Vanbianchi et al. 2017; Brown et al. 2018; Delheimer et al. 2018), pellet counts (Klinger et al. 1989; Biggs et al. 2010; Cheng et al. 2015), and camera traps (Borchert 2012). These studies generally describe spatial and

temporal habitat use following fire disturbances. Many studies in North America occur in shrubland systems (Borchert 2012; van Mantgem et al. 2015; Holbrook et al. 2016) and boreal forests (Schwartz & Franzmann 1989; Nelson et al. 2008; Brown et al. 2018), but a number of studies are relevant to the sub-boreal montane coniferous forests in the North Cascades (Blanchard & Knight 1990; Ripple & Beschta 2012; Cheng et al. 2015; Vanbianchi et al. 2017, 2018). Therefore, I use what is currently known about species responses to wildfire to predict how the mammal community may respond in the North Cascades.

1.2   Hypotheses and predictions

Using the IDH as a framework, I asked whether wildfire disturbance generated a peaked unimodal mammal diversity-disturbance pattern in dry coniferous forests of the North Cascades, and what mechanisms contribute to the observed pattern in this system. Specifically, my research questions were:

1. How do wildfire disturbances change mammal community richness? Does community richness peak at intermediate levels of disturbance, as predicted by ecological theory?

2. Which wildfire disturbance variables and environmental conditions have the strongest relationship to observed species richness across a gradient of disturbance?

I predicted that mammal community richness in temperate coniferous forests affected by wildfires would follow the peaked diversity-disturbance relationship characteristic of the IDH. I expected, but did not test, that two key processes were driving this relationship in the system. First, I expected that competitive exclusion would suppress diversity in undisturbed forests, constraining mammal community richness. Because landscapes dominated by stand replacing

8

fires are nonequilibrium systems (Turner & Romme 1994), habitat heterogeneity increases available habitat niches, reducing competitive exclusion, and supporting species coexistence and community diversity through wildfire disturbance. Second, I predicted the mammal community richness would be reduced by wildfires of high severity, intensity, and frequency that deviate from the historical norm (Figure 1-1). These predictions follow expectations of the IDH and are based on observed species response to wildfire in the literature (Table 1.1).

The regional species pool of terrestrial forest mammals present in montane habitats of the North Cascades is 29 species. The species pool includes terrestrial mammals with average adult body mass greater than 150 g potentially detected at camera traps in the study area. Aquatic mammals, flying mammals, and most small mammals with ranges in the study area are excluded from the species pool due to near-zero detectability by camera traps. I conducted an inexhaustive review of mammal-wildfire literature from studies in sub-boreal montane coniferous forests and similar fire-prone systems. Empirical studies provided information on mammal presence, occupancy, and abundance in forests subject to wildfire using radio telemetry (Cunningham et al. 2003; Biggs et al. 2010; Bunkley et al. 2015), direct counts (Klinger et al. 1989), pellet counts (Cheng et al. 2015), and camera traps (Borchert 2012). Reviews provided additional natural history information and wildfire response (Bull et al. 2001; Nelson et al. 2008; van Mantgem et al. 2015). For each species, I synthesized the available information into predicted density-disturbance relationships. As a brief example, *Martes americana* (American marten) and other members of the Mustelidae use old forests with tree-cavities for resting and reproduction (Delheimer et al. 2018). Non-breeding juvenile marten were found in higher abundance in recently burned boreal forests, possibly due to increased prey abundance (Nelson et al. 2008) or competitive exclusion by breeding adults in higher quality habitat. Given preference of breeding

9

adults for mature forest, I predict densities are highest where disturbance is lowest for this species. This qualitative approach was used for all species within the regional species pool. Where literature was unavailable or not found for a species, I used known habitat preference, reproductive capacity, and other species traits to make density-disturbance predictions. Eighteen species in the pool (62.1%) are predicted to have highest densities at moderate levels of wildfire disturbance based on available literature and expert opinion (Table 1.1). I used the cumulative estimated species density-disturbance curves to predict what the community response would be across a similar gradient of disturbance. This approach makes an assumption that cumulative species densities are correlated with community richness.

Burn severity is important for post-fire vegetation succession in coniferous forests of western North America (Johnstone et al. 2011; Brown et al. 2018). Burn severity has also been shown to induce a measurable response (both positive and negative) on bird and small mammal community diversity (Fontaine & Kennedy 2012). Time since disturbance and spatial extent disturbed are also important factors (Turner et al. 1998). Because disturbance affects seral stage, an important predictor of habitat use for many North Cascades herbivores and their predators (Table 1.1), I predict that burn severity, time since fire, and fire extent are important measures of disturbance driving patterns of richness in the system.
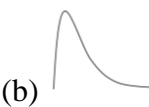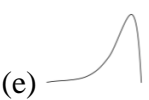
Predicted disturbance response	DD Shape	Species	No. Sp.
Decreasing density with increasing wildfire disturbance	(a)	American marten (Nelson et al. 2008; Delheimer et al. 2018) [red squirrel, Douglas squirrel]	1 [2]
Highest density at low to medium wildfire disturbance	(b)	wolverine (Bull et al. 2001), bobcat (Borchert 2012) [ermine, long-tailed weasel, bushy-tailed woodrat, raccoon, spotted skunk, striped skunk, porcupine]	2 [7]
Highest density at low and high wildfire disturbance	(c)	cougar (Borchert 2012; Jennings et al. 2016)	1
Highest density at medium wildfire disturbance	(d)	American badger (Holbrook et al. 2016), Canada lynx (Koehler & Brittell 1990; Bull et al. 2001; Nelson et al. 2008; Vanbianchi et al. 2017), snowshoe hare (Bull et al. 2001; Cheng et al. 2015), American mink (Malison & Baxter 2010), coyote (Borchert 2012) [golden-mantled ground squirrel, Cascade red fox]	5 [2]
Highest density at medium to high wildfire disturbance	(e)	mule/black-tailed deer (Klinger et al. 1989; Horncastle et al. 2013), grizzly bear (Zager & Habeck 1983; Blanchard & Knight 1990; Nelson et al. 2008)	2
Increasing density with increasing wildfire disturbance	(f)	moose (Schwartz & Franzmann 1989; Nelson et al. 2008; Brown et al. 2018), elk (Biggs et al. 2010; Wan et al. 2014)	2
Equal density across disturbance gradient	(g)	American black bear (Schwartz & Franzmann 1989; Cunningham et al. 2003), wolf (Schwartz & Franzmann 1989; Ballard et al. 2000; Nelson et al. 2008), [hoary marmot, bighorn sheep, mountain goat]	2 [3]

Table 1.1 Summary of predictions for mammal species density across a gradient of wildfire disturbance based on published literature and expert opinion. Twenty-nine mammal species currently or historically present in the North Cascades ecosystem are grouped by predicted response to wildfire disturbance. Predicted response to disturbance is visualized by six density-disturbance relationships (*DD shape*) showing density of animals on the y-axis and wildfire disturbance on the x-axis. Species are categorized within one of seven predicted *DD shape* groups: (a) monotonic decreasing density with increasing disturbance, (b) unimodal, skewed toward low disturbance; (c) unimodal, inverted; (d) unimodal, with density maximum at intermediate disturbance; (e) unimodal, skewed toward high disturbance; (f) monotonic increasing density with increasing disturbance; (g) no relationship between density and disturbance. Only monotonic and unimodal responses are predicted. The total number of species are shown for each group (*No. Sp.*). Species in brackets are species within the species pool that were grouped by the author based on habitat preference and traits.
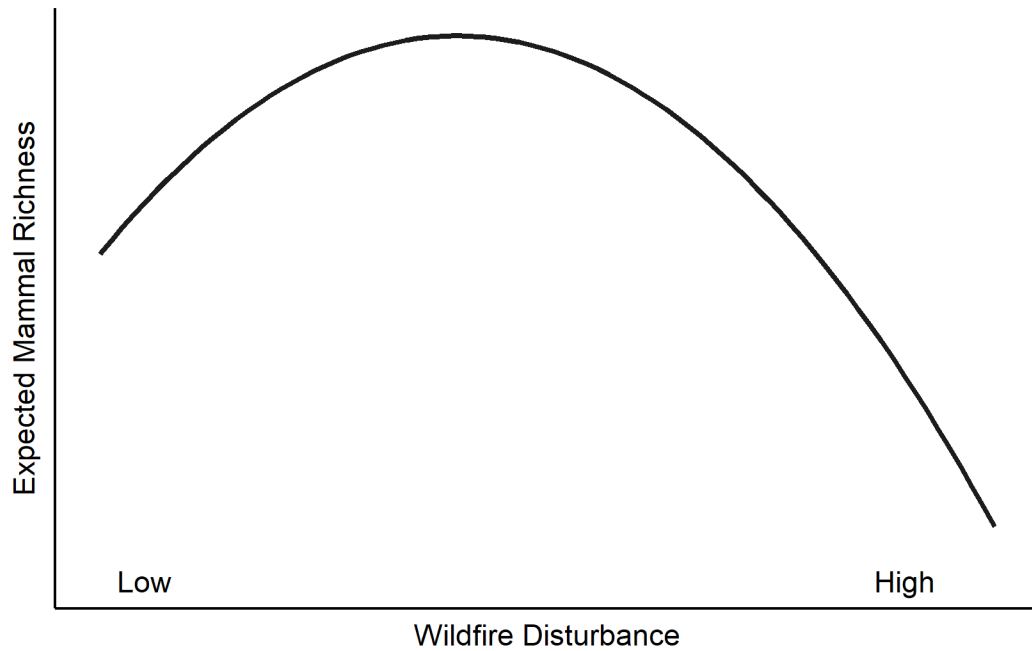
Figure 1-1. Predicted response of mammal community to wildfire disturbance. As disturbance increases in the system, mammal species richness increases to a peak, then decreases. As disturbance approaches extreme or maximum levels, richness is expected to fall below levels at undisturbed patches and/or patches with low severity burns. This same pattern is expected with measuring disturbance severity, frequency, and extent.

Chapter 2. Research Chapter

Chapter 2 addresses the methods, results, and implications of the primary research I conducted for this thesis.

2.1   Introduction

Changing climatic conditions are anticipated to affect global biodiversity in the twenty-first century through a variety of processes, including increasing rates of habitat loss and fragmentation through altered natural disturbance cycles (Thomas et al. 2004; Pereira et al. 2010; Urban 2015). Habitat loss alone is considered the most significant individual global threat to biodiversity (Pimm & Raven 2000; Hanski 2011), but climate change could exacerbate this threat by increasing natural disturbances such as wildfire. Changing climatic conditions increase adverse effects of habitat loss on biodiversity (Mantyka-Pringle et al. 2012) and influence rates of forest recovery after disturbance (Anderson-Teixeira et al. 2013).

Wildfire is a major driver of landscape change in forested ecosystems of western North America (Davis et al. 2017; Littell et al. 2018). Fire affects forests by rearranging the structure and distribution of vegetation (Stevens-Rumann et al. 2018), altering abiotic processes (Santi et al. 2013), and changing habitat availability for numerous species (Driscoll et al. 2010; Fontaine & Kennedy 2012; Lindenmayer et al. 2016). Post-fire vegetation succession is an important driver of habitat quality for mammals (Fisher & Wilkinson 2005), particularly herbivores (Brown et al. 2018). Important factors influencing post-fire succession include the severity, duration, extent, and interval of disturbance (Turner et al. 1998; Stevens-Rumann & Morgan 2016). Recent evidence shows that climate may also influence succession if environmental conditions become unsuitable for stand regeneration (Hansen et al. 2018). Biodiversity is impacted by wildfire through local extirpations of species, changes to habitat structure, altered

species interactions, and indirect effects of abiotic changes. Though species responses to wildfire have been studied in some systems, we still lack a general understanding of community-level responses to wildfire and to altered wildfire regimes (Thom & Seidl 2016). Wildfire regime refers to the process of disturbance and recovery within a system at the landscape level, in particular the ordinary spatial and temporal dynamics in recent history. The processes of disturbance and recovery are closely associated with climatic conditions.

Wildfire regimes have been substantially altered in northwestern North America in the last three decades due to increased fuel availability following years of wildfire suppression in combination with a warming climate and increasing frequency of summer drought (Dennison et al. 2014). In Cascade coniferous forests, large, high severity wildfires are closely linked to climate warming (Cansler & Mckenzie 2014). Historical wildfire regimes in the North Cascades generated patchy habitat mosaics with a diversity of successional states through lower-severity burns (Agee 1993). Modern high severity burns increase post-fire recovery time due to changes in soil biochemistry (Certini 2005), forest regeneration (Hansen et al. 2018), and reduced densities of surviving organisms for recolonization (Turner et al. 1998). The prevalence of large, high-severity wildfires in the North Cascades deviates from the historical norm, possibly indicating a shift into a new ecosystem state (Turner & Romme 1994; Davis et al. 2017). Wildfire regimes in northwestern North America are expected to further intensify over the next half century, with potential for disturbances with no historical analogs in systems such as the western Cascades with high fuel loads but low flammability (Littell et al. 2018).

Recent trends in North Cascades coniferous forests show increases in wildfire duration and size, consistent with trends across the western United States (Dennison et al. 2014). Coupled fire-climate models forecast that wildfire size will increase and wildfire return interval will

15

decrease with warming across the region (Sheehan et al. 2015). Models based on fuels and water availability predict larger areas burned in both the eastern and western Cascades ecosystems (Littell et al. 2018). It is expected that wildfires will continue to burn at rates that exceed historical norms as CO_2 accumulates in the atmosphere, causing increased summer temperatures, decreased summer precipitation, and early spring snow melt. These novel climate regimes may cause regional vegetation shifts where wildfires encroach into forests that historically had low wildfire intensity and where coniferous forests are replaced by mixed conifer-broadleaf forests (Sheehan et al. 2015). Landscape-level effects of wildfire and post-fire recovery may have beneficial or deleterious effects on organisms, depending on life history traits and the extent of disturbance. The characteristics of wildfire disturbance that shape the large forest mammal community in temperate coniferous forests with active wildfire regimes is poorly known.

The intermediate disturbance hypothesis suggests that species diversity in a system is greatest at intermediate levels of environmental disturbance (Connell 1978). Such diversity-disturbance relationships are characterized by a unimodal peaked response across the gradient of disturbance. A meta-analysis of empirically measured diversity-disturbance relationships shows that multiple patterns are observed in nature, including flat, increasing, decreasing, and double-peaked relationships (Mackey & Currie 2001). The shape of these relationships can be explained in part by the aspect of disturbance that is measured (Miller et al. 2011). For wildfire disturbances, the following aspects can be measured: intensity (thermal energy of the fire), severity (heat effect on vegetation and soil), timing (date of fire), duration (length of the fire), extent (area burned), and interval (time since the previous burn).

In this observational study, I assess the effect of wildfire disturbance factors on large forest mammals in the North Cascades by comparing diversity of mammals at sites with varying

wildfire disturbance histories. I use empirical data to test the relationship between species richness and disturbance factors associated with wildfire. I predicted that mammal community richness in the North Cascades has a traditional peaked disturbance-diversity relationship with burn severity and wildfire interval. If this is true, species richness metrics should decline at the highest levels of wildfire disturbance.

2.2   Methods

2.2.1   Study System and Species

I selected dry forests of the North Cascades mountains in Canada and the United States in western North America as a study system given the active wildfire regime and large protected forests. The study area is a 13,000 km^2 region within the North Cascades Level III Ecoregion (Omernik & Griffith 2014), and within the North Cascades, Okanagan, and East Cascades – Modoc Plateau Terrestrial Ecoregions of the World (Olson & Dinerstein 2002). Mean monthly temperatures average 3.7 to 14.0°C and annual summer precipitation averages 140.0 mm, which is 7.6% of total annual precipitation (Sheehan et al. 2015). Forests in the coastal regions west of the study area are notable for large accumulations of forest biomass and high carbon sequestration (Mitchell et al. 2009). Forests east of the Cascade Divide contain xerophytic vegetation and are subject to more frequent wildfires (Agee 1993). The precipitation gradient in the region is pronounced due to a rain shadow, with forests rapidly changing from cool and humid to dry and warm. Sampling occurred primarily east of the Continental Divide in dry, wildfire-prone forests.

Numerous protected areas occur within the study area, within different political jurisdictions and with multiple protection categories, as defined by the International Union for Conservation of Nature (IUCN; Dudley 2008). IUCN Category Ia protected areas include Skagit

River Forest Ecological Reserve, Ross Lake Ecological Reserve, Whipsaw Creek Ecological Reserve, Skagit River Cottonwoods Ecological Reserve, Chilliwack River Ecological Reserve, and Skagit River Rhododendrons Ecological Reserve. Category Ib protected areas include Mount Baker Wilderness, Pasayten Wilderness, Noisy-Diobsud Wilderness, Glacier Peak Wilderness, Lake Chelan-Sawtooth Wilderness, and the Stephen Mather Wilderness. Category II protected areas include North Cascades National Park, Chilliwack Lake Provincial Park, E.C. Manning Provincial Park, and Skagit Valley Provincial Park. Category VI protected areas include Ross Lake and Lake Chelan National Recreation Areas, and Cascade Recreation Area. Together, protected areas cover 10,152 km^2 within my study area.

These protected areas represent native habitat for terrestrial forest mammals with minimal anthropogenic influences, including hunting and habitat conversion. One study found that global species richness is 10.6% higher within protected areas compared to nearby multiple use areas (Contu et al. 2016). Another study found that Category II protected areas effectively prevent extirpations of mammals in western Canada across historical timeframes, but not in smaller, more insular protected areas in eastern Canada (Glenn & Nudds 1989). However, the global network of protected areas is inadequate to protect portions of ranges of all species globally, especially in the tropics (Rodrigues et al. 2004). In order to isolate to effects of wildfire on mammal richness, I selected to sample only within protected areas to reduce confounding variables that may influence species richness. Activities such as hunting, timber extraction, and motorized recreation may directly or indirectly impact mammal community richness. Although these activities were not completely restricted within all types of protected areas in the study area, the extent of direct anthropocentric impacts was significantly reduced.

The mammal community in the study area includes 70 known species in 6 Orders and 20

Families (U.S. National Park Service 2019), including the recently reintroduced *Pekania*

pennanti (fisher). Excluding small rodents, insectivores, aquatic mammals, extirpated species,

Species	Family	ABM (kg)	HR (km^2)	PD (#/km^2)	Trophic Level
Moose, *Alces alces*	*Cervidae*	481.0	64.2	0.40	herbivore
Elk, *Cervus elaphus*	*Cervidae*	240.0	50.5	2.9	herbivore
Grizzly bear, *Ursus arctos*	*Ursidae*	196.0	282.0	0.02	omnivore
American black bear, *Ursus americanus*	*Ursidae*	111.0	27.9	0.73	herbivore
Mule deer, *Odocoileus hemionus*	*Cervidae*	83.8	2.0	16.0	herbivore
Bighorn sheep, *Ovis canadensis*	*Bovidae*	74.6	16.2	1.5	herbivore
Mountain goat, *Oreamnos americanus*	*Bovidae*	71.3	15.7	NA	herbivore
Cougar, *Puma concolor*	*Felidae*	53.9	118.0	0.02	carnivore
Grey wolf, *Canis lupus*	*Canidae*	35.0	21.8	0.01	carnivore
Wolverine, *Gulo*	*Mustelidae*	12.8	306.0	0.01	carnivore
Coyote, *Canis latrans*	*Canidae*	12.0	16.8	0.25	carnivore
Canada lynx, *Lynx canadensis*	*Felidae*	9.8	27.8	0.05	carnivore
American badger, *Taxidea taxus*	*Mustelidae*	7.8	3.1	1.9	carnivore
Porcupine, *Erethizon dorsatum*	*Erethizontidae*	7.4	0.10	3.5	herbivore
Bobcat, *Lynx rufus*	*Felidae*	6.4	28.4	0.10	carnivore
Raccoon, *Procyon lotor*	*Procyonidae*	6.4	4.1	3.3	omnivore
Red fox, *Vulpes vulpes*	*Canidae*	4.8	3.1	1.1	carnivore
Striped skunk, *Mephitis mephitis*	*Mustelidae*	2.4	2.0	8.2	omnivore
Hoary marmot, *Marmota caligata*	*Sciuridae*	2.3	NA	NA	herbivore
Snowshoe hare, *Lepus americanus*	*Leporidae*	1.6	0.03	100.0	herbivore
American mink, *Mustela vison*	*Mustelidae*	0.9	1.9	2.5	carnivore
American marten, *Martes americana*	*Mustelidae*	0.9	3.3	0.67	carnivore

Species	Family	ABM (kg)	HR (km^2)	PD (#/km^2)	Trophic Level
Western spotted skunk, *Spilogale gracilis*	*Mustelidae*	0.6*	0.26*	4.7*	omnivore
Bushy-tailed woodrat, *Neotoma cinerea*	*Muridae*	0.3	0.03	NA	herbivore
Ermine, *Mustela erminea*	*Mustelidae*	0.3	0.10	6.3	carnivore
Red squirrel, *Tamiasciurus hudsonicus*	*Sciuridae*	0.2	0.01	172.0	omnivore
Douglas squirrel, *Tamiasciurus douglasii*	*Sciuridae*	0.2	0.00	44.9	omnivore
Long-tailed weasel, *Mustela frenata*	*Mustelidae*	0.2	0.19	0.76	carnivore
Golden-mantled ground squirrel, *Callospermophilus sp.*	*Sciuridae*	0.2**	NA	NA	omnivore

Table 2.1 Twenty-nine terrestrial mammal species detectable by passive infrared camera traps in the North Cascades. *ABM* **is the average adult body mass (kg).** *HR* **is the average home range size (km^2) for an individual.** *PD* **is the average population density (individuals/ km^2) for the species. Data derived from PanTHERIA mammal database (Jones et al. 2009). *Because** *S. gracilis* **is absent in the database, measurements from a phylogenetically similar species are reported here (***S. putorius***). **ABM for** *C. lateralis* **reported here.**

and species with highly specific habitat requirements, 29 species of mammals were potentially detectable by camera traps in the region during 2016 (Table 2.1). Species excluded were: *Ochotona princeps* (American pika), *Aplodontia rufa* (mountain beaver), *Castor canadensis* (North American beaver), *Lontra canadensis* (North American river otter), *P. pennanti*, 10 species of bat, and 26 species of rodents and insectivores. Singleton et al. (2002) identified important core habitat areas and corridors for four rare carnivore species in the North Cascades: *Lynx canadensis* (Canada lynx), *Gulo gulo* (wolverine), *Canis lupus* (wolf), and *Ursus arctos* (grizzly bear). The study found that the region is an ecologically important landscape of contiguous transboundary habitat for large, wide-ranging mammals. Of 29 terrestrial mammal

species detectable by camera traps in montane habitats of the North Cascades, 19 (65.5%) have highest densities at moderate levels of wildfire disturbance based on available literature (Table 1.1).

2.2.2   Data

Data used in this study include mammal occurrence data from passive camera trap sampling, local site conditions collected at sampling stations, wildfire perimeters, burn severity, a digital elevation model (DEM), and climatic data.

2.2.2.1   Sampling data and site conditions

Sample sites were points with a single camera trap deployed with a minimum linear distance of 1,000 m to adjacent camera. I identified potential sample sites using a generalized random-tessellation stratified (GRTS) survey design using the Spatial Survey Design and Analysis "spsurvey" statistical package (Kincaid & Olsen 2016) in R (R Development Core Team 2016). This survey design provided a spatially stratified sample across variables of interest that maintained stratification when sample locations were dropped due to access limitations. I selected the GRTS design to accommodate sampling in remote terrain within many administrative jurisdictions and access constraints. Stratification was based on bioclimatic land units, the presence of past wildfire, and the time since the last wildfire. GIS shapefiles of wildfire perimeters were collected from the US Geological Survey Geosciences and Environmental Change Science Center (GECSC) Outgoing Datasets of historical wildfires. Sample stations were selected to represent major land cover classes within the study region, wildfire area characteristics (size and age), a latitudinal gradient in precipitation across the Cascade Divide, and an elevational gradient with an upper bound at average maximum wildfire elevation.

Field sampling was conducted in 2016 at 39 sample sites within and adjacent to protected areas in the study region across a variety of habitat types and wildfire histories. Three sites (483-SIRI, 9 trap nights; 570-BORI, 6 trap nights; and 1602-HEOC, 7 trap nights) were excluded from the analysis due to premature equipment failure. The remaining 36 sites had 19 or greater trap nights (Figure 2-1). Five sites (14%) were repeated from previous camera trap surveys (Christophersen 2006) and thirty-one (86%) were identified from the spatially-balanced design. Sampling was conducted between May and October of one year during the period of probable wildfire disturbance. A 3- to 6-month sampling duration is recommended for species richness studies, as a balance between suitable survey effort and minimizing immigration or emigration from the study area (Wearn & Glover-Kapfer 2017).

Mammal detections at each site were recorded with a single Reconyx Hyperfire HC500 passive infrared camera trap at each sample location. Cameras were positioned within 500 m of the pre-determined GRTS locations to maximize detections by orienting the camera detection zone at movement corridors. Cameras were generally not placed on human roads or trails and no baits or attractants were used. Cameras were deployed for up to 6 months and were active 24 hours per day, providing continuous records of animal occurrence at each station. Camera deployments were standardized to minimize detection bias: trigger sensitivity was set to high, delay interval was set to 1 s, and camera height was approximately 30 - 40 cm above ground, adjusting for slope (Rovero et al. 2013). Cameras were oriented northward to maximize lighting of target organisms and minimize false triggers from the sun.

The following habitat features were recorded during deployment for an area 30 m in radius from the camera station: topographic position, percent canopy cover, average stem size, average spacing of tree stems, wildfire fuel load, standing dead timber, and horizontal detection
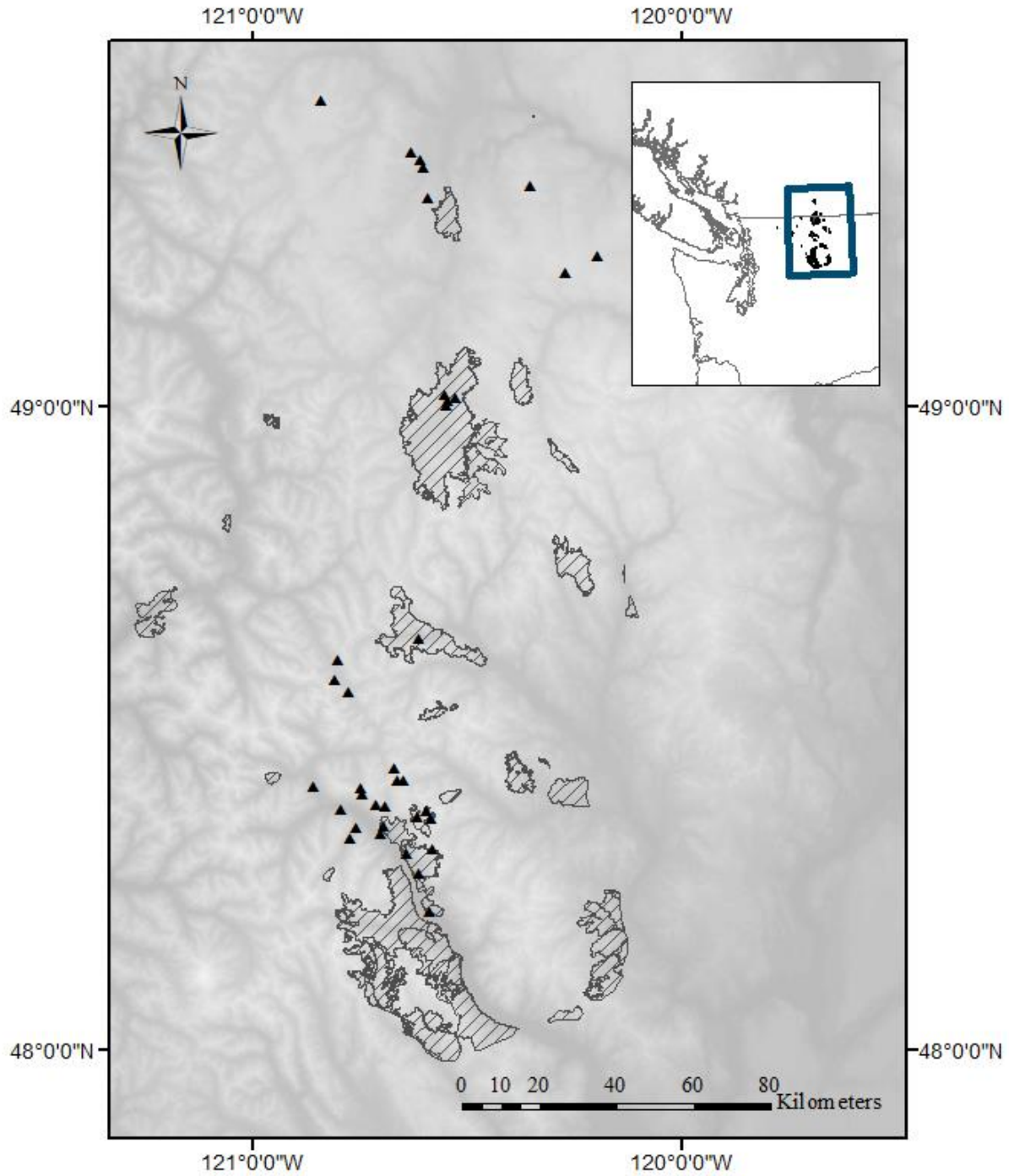
Figure 2-1. Passive infrared camera trap sampling locations (solid triangles) with >19 trap nights in montane coniferous forests along the Cascade Divide in Washington state and British Columbia (n = 36). Hatched regions represent burned areas for large wildfires > 400 ha between 2000 and 2015.

distance. Topographic position was qualitatively assessed as a category: ridge, upper slope, mid-slope, lower slope, and valley. Percent canopy cover was estimated visually from one location.

Average spacing of tree stems was estimated visually from one location, based on the distance between stems of canopy trees. Average stem size was estimated as diameter at breast height by measuring 2 - 5 representative stems of canopy trees. Wildfire fuel load was qualitatively assessed as low, medium, or high based on the quantity of dead forest biomass. Standing dead timber was estimated visually and recorded as a binary variable greater than or less than 10% of total standing trees. Horizontal detection distance was measured using the "Walk test" feature on the camera trap. The maximum distance from the camera that targets could be detected was measured by test-triggering the camera at different distances during deployment. Camera trap detection zones are variable across sites due to differences in slope, vegetation, temperature gradients, and camera deployment orientation (Newey et al. 2015; Welbourne et al. 2016).

Image metadata, including species identifications, were managed using the package "camtrapR" in R (Niedballa et al. 2016). Images were viewed in digiKam (Caulier et al. 2016), an open source digital photo management software, and tagged with custom metadata information. For each image with mammal detections, the species was identified and the number of individuals was recorded. Where possible, sex and age class were determined visually by a single observer (P. Burke). An independent detection was defined as one image or a series of images of an animal separated by 60 or more minutes of time without a record of the same species. Image metadata containing this information was extracted from each image file using ExifTool (Harvey 2016), an open source software for image metadata management.

2.2.2.2 Wildfire data

Fifty-six wildfires occurred in the study area between 2001 and 2015, including 36 large wildfires greater than 4 km² (400 ha) in size. Total area burned by large wildfires was 3517.3 km², or 31.7% of the study area. Wildfires less than 4 km² excluded. Average size of large wildfires was 231.3 ± 163.5 km². Median size of large wildfires was 37.6 km². The largest wildfire, the Farewell fire (Fawn Peak Complex), was 584.0 km² and occurred in 2003. Most large wildfires occurred in drier habitats in the rain shadow east of the Cascade Divide. Only 3% of area burned by large wildfires occurred west of the Cascade Divide. Years with greatest area burned occur in 2003, 2006, and 2015 (Figure 2-2).

Wildfire perimeters were acquired from publicly available databases. Canadian historical wildfire perimeters are available under an Open Government License of British Columbia from the BC Data Catalogue and published by the Ministry of Forests, Lands, Natural Resource Operations and Rural Development and BC Wildfire Service. Historical perimeters within the United States are available from USGS Geosciences and Environmental Change Science Center (GECSC) Outgoing Datasets of historical wildfires. These vector shapefiles are available without access or use constraints from the Geospatial Multi-Agency Coordination Group (GeoMAC).

Wildfire burn severity data were acquired from the Monitoring Trends in Burn Severity (MTBS) database (Eidenshink et al. 2007). Burn severity is defined by Eidenshink et al. (2007) as the "degree to which a site has been altered or disrupted by fire; loosely, a product of fire intensity and residence time." The authors add that burn severity relates principally to visible changes within one growing season as a mosaic within burn area perimeters. This database includes burn severity for large wildfires greater than 404 ha that have occurred since 1984. Severity is classified at 30m resolution by comparing Normalized Burn Ratio values from pre-

and post-fire Landsat bands 4 (near infrared) and 7 (shortwave infrared). The difference in Normalized Burn Ratios (dNBR) is the difference in pre-fire NBR and post-fire NBR. Given local variability in calculated dNBR values, burn severity was averaged across the sample location and eight nearest neighbors, representing a 0.014 km^2 (1.44 ha) region surrounding each sampling location. This area represents the local average burn severity at the sample location.
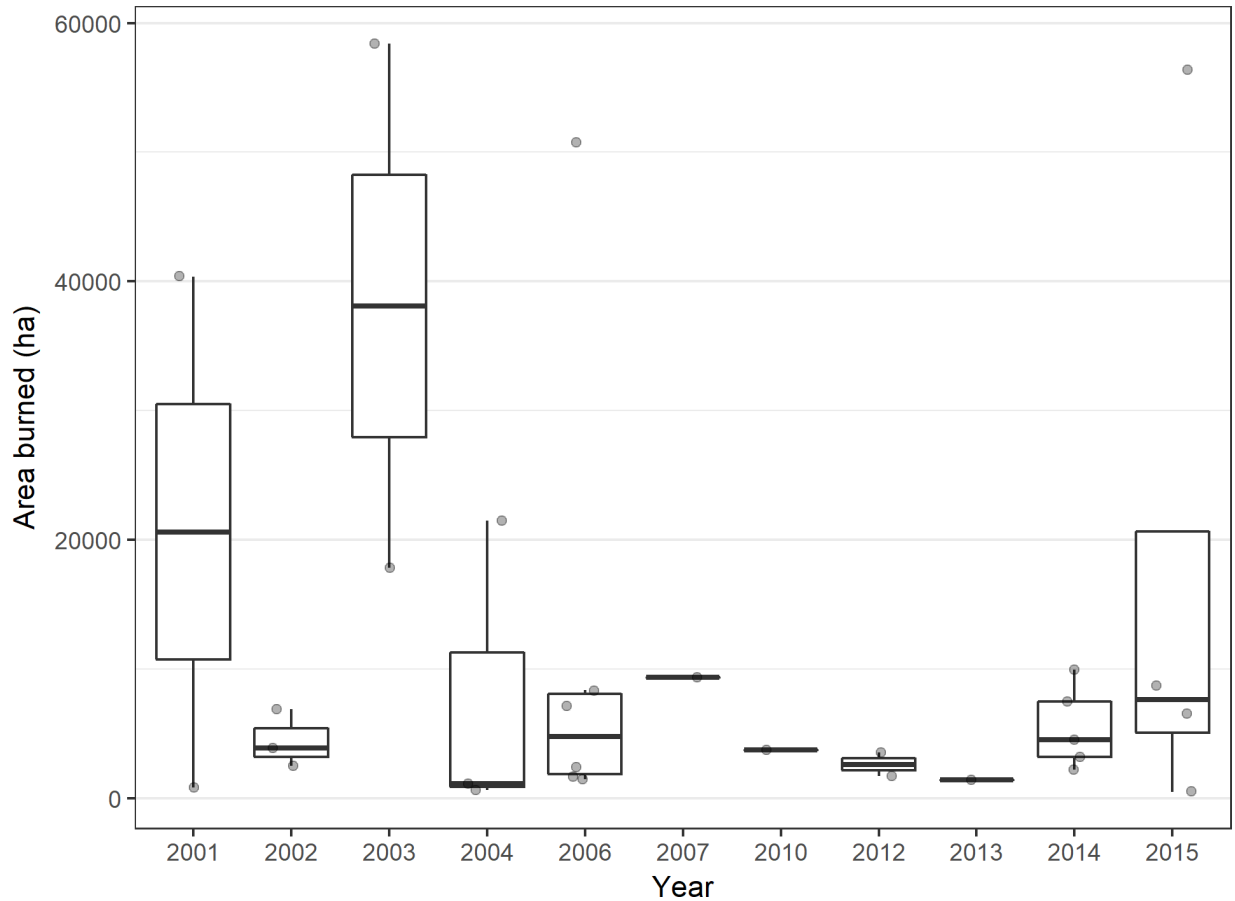
Figure 2-2. Total area burned annually by large wildfires (greater than 4 km², between 2001 and 2015 in the study area. Data points are jittered to show spread.

2.2.2.3   Climate and geographic data

Locally downscaled climate variables were accessed for each sample location using the software package ClimateWNA (version 5.50; Wang et al. 2017). The software calculates

biologically-relevant and scale-free climate variables for locations in western North America (Wang et al. 2016) using high resolution spatial climate data available from the PRISM (Parameter elevation Regression on Independent Slopes Model) statistical mapping system (Daly et al. 2002) at 800 x 800 m resolution. I selected climate normal data averaged annually from 2001 to 2015 to represent average conditions during the period of wildfire history sampled in this study.

A high-resolution DEM for the study region was compiled using Shuttle Radar Topography Mission (SRTM) global 1 arc-second digital elevation data downloaded from the United States Geological Survey (USGS) EarthExplorer. These data were collected from imaging radars orbiting the Earth sampling surface topography at 1 arc-second, or approximately 30 m resolution. A measure of terrain variability, known as the terrain ruggedness index (TRI), was calculated from the DEM. TRI is calculated by mathematically comparing elevation at a point with elevations at eight nearest neighbors (Wilson et al. 2007). TRI therefore represents the elevational variation within a 0.014 km2 (1.44 ha) region, measuring 90 m square around each sampling location.

2.2.3   Quantitative analyses

All quantitative analyses were completed in R (R Development Core Team 2016) using RStudio Version 1.1.442.

2.2.3.1   Observed species richness

Species richness (S) is a count of species within a unit area. For this study, S represents the number of observed mammal species detected by each camera trap, not accounting for detectability. I assessed the relationship between species richness at locations across a continuum of wildfire disturbance metrics. To account for differences in sample effort, I calculated a

sample-based rarefaction curve of time-series species detections for each sampling location using the following expression from Chiarucci et al. (2008):

$$\bar{S}_i = S_n - \binom{n}{i}^{-1} \sum_{k \in G} \binom{n - n_k}{i}, i = 1, \dots, n \tag{2.1}$$

Applied to my data, this model provides an estimate of species richness across trap nights independent of the ordering of species detections. Here, species richness is modeled for i simple random samples without replacement from the total number of trap nights at each camera trap (n). Therefore, S_n describes the total observed number of species at the end of sampling at one camera site. If G represents the set of species observed in n nights, n_k is the number of nights containing at least one individual of species $k \in$ G. I calculated S_i for each of 35 camera stations that had greater than 0 species present. One site was excluded from calculations as no species were detected during sampling. Rarefaction curves were calculated using the "exact" method in the "vegan" package (Oksanen et al. 2018).

The minimum sampling effort across all sites was 19 trap nights. To minimize bias introduced by uneven sample effort without extrapolating from the rarefaction curves, observed species richness at day 19 was adjusted for each site using the formula $S_{adj} = |S_{19}|$. No adjustments were made to species richness to account for differences in detectability between species.

2.2.3.2   Hypothesis model

To test the relationship between wildfire disturbance and species richness of forest mammals using the sampling location as the independent replicate, I used a statistical framework suitable for non-normally distributed data. I used multiple regression and analysis of variance to explore the individual effects of wildfire variables on species richness. I first selected a

generalized linear model using a log link function and Poisson distribution to account for species richness as the response variable, considering that richness is a positive integer representing independent values at each sampling location (i.e. discrete counts). Species richness at each sample location was calculated by summing the presence of unique species detected by a single passive camera trap. This metric, local-scale species richness, is equivalent to α diversity, or the local diversity within a homogenous habitat sampled by the camera equipment (Whittaker 1972; Brown et al. 2016). However, differences in sampling effort among camera trap stations introduce bias into richness calculations. To account for this bias, species richness was estimated for each sample location using rarefaction curves (Section 2.2.3.1). Correlation among covariates was assessed using Spearman rank correlation coefficients (ρ) to account for monotonic relationships in the non-normal data. All covariates had correlation coefficients < 0.4. Spatial autocorrelation was also assessed among the points sampled using two tests: Moran's I and Geary's C (Moran 1950; Geary 1954).

I first used generalized linear regression to test the prediction that wildfire disturbance in protected areas of the North Cascades follows a unimodal response with greatest mammal species richness occurring at intermediate levels of disturbance. The hypothesis model included three factors influencing succession and associated post-fire ecological effects: 1) a measure of burn severity, 2) a measure of time since disturbance, and 3) a measure of disturbance extent (Turner et al. 1998; Stevens-Rumann & Morgan 2016). In this model, burn severity is measured by dNBR. Disturbance timing was measured as the number of growing seasons since the wildfire, and all sites had the same disturbance interval because no sites were repeatedly burned during the study interval. Disturbance extent was quantified by canopy closure, a point estimate of forest canopy coverage at the sampling location. The data did not show evidence of

overdispersion, but were slightly underdispersed when tested with the R package 'AER' (Kleiber & Zeileis 2017; *alpha* = -0.61), so quasi-likelihood estimation was not needed. Goodness-of-fit (pseudo-R^2, or *pR²*) was estimated by calculating the difference between the residual and null deviance, divided by the null deviance (Hagle & Mitchell 1992). This *hypothesis model* represents a test of the prediction that species richness is maximized by intermediate levels of disturbance in protected coniferous montane forests of the North Cascades. This Poisson regression with log-link can be described mathematically as:

$$S_{adj} = e^{\beta + \beta_1 x_1^2 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_4} \tag{2.2}$$

Here, adjusted species richness for each camera trap station (S_{adj}) is dependent on a quadratic term for *average dNBR* (x_1^2), *years since wildfire*, a measure of disturbance frequency (x_2), *canopy closure*, a measure of disturbance extent at the patch level (x_3), and horizontal *detection distance* (x_4). A moderate correlation was found between model terms *year since wildfire* and *canopy closure* ($\rho = 0.56$, $p = 0.0004$), suggesting a moderate positive relationship between these variables associated with increasing vegetation cover during post-fire forest succession. The covariate for horizontal detection distance was included to account for differences in the camera detection zone between sites.

2.2.3.3   Stepwise model

Disturbance may be measured across a variety of ecological conditions, including spatial, temporal, site level, or landscape level characteristics, among many others. My hypothesis model focused on three measures: disturbance severity, disturbance extent, and time since disturbance. I used stepwise regression to assess an additional suite of variables potentially affecting community richness in burned habitats. The purpose of this modeling exercise was to identify

other variables that may influence species richness in the system. For these models, the response variable is observed species richness at each site, the hypothesis model covariates were retained, with an independent variable added for survey effort, and three additional environmental variables. Bayesian Information Criterion (BIC) was used to select the most parsimonious model at each step by selecting the model with lowest BIC score. The global *stepwise model* used Poisson regression with log-link can be described as:

$$S_{adj} = e^{\beta + \beta_1 x_1^2 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_4 + \beta_5 x_5 + \beta_6 x_6 + \beta_7 x_7} \tag{2.3}$$

Here, the total observed number of species at the end of sampling at one camera site (S_{adj}) is dependent on a quadratic term for *average dNBR* (x_1^2), a term for *sample effort* (x_2), *average spacing* of tree stems (x_3), *canopy closure* (x_4), horizontal *detection distance* (x_5), *mean annual precipitation* (x_6), and *topographic ruggedness* (x_7). I used backward- and forward-selection stepwise regression to identify one final model. The covariate for horizontal detection distance was included to account for differences in the camera detection zone between sites.

2.2.3.4   Hierarchical model

In both previous models, species detectability is assumed to be equal for all 29 species in Table 2.1 after 19 trap nights. However, species in the North Cascades likely have differing camera trap detectability given differences in body size, population density, and behavior. To address this limitation, I used a model that explicitly accounts for imperfect detection by estimating species accumulation from multispecies state models of occurrence and detection (Dorazio et al. 2006a). Models of species occurrence and detection were fit using R and WinBUGS (Lunn et al. 2000) according to Dorazio et al. (2006). The model specifies a Gibbs sampler which computed 55,000 random draws for each of 4 different Markov chains (Dorazio et al. 2006b).

2.3 Results

Eighteen species of mammals were recorded during 2,551 trap nights in 2016 (Table 2.2). The most frequently detected species was *Odocoileus hemionus* (mule deer), present at 86% of sites. The subspecies *O. h. columbianus* (black-tailed deer) was identified visually in camera images, but was not differentiated for species richness calculations because it is a subspecies. Mammal species richness varied between 0 and 7 species across sample locations ($\bar{x}$ = 2.7 SE = 1.5). Most mammals in the study region were infrequently detected by camera traps. Total detections of mammal species varied from 488 detection-events for *O. hemionus* to 1 detection each for three species: *Erethizon dorsatum*, *Oreamnos americanus*, and *Lynx canadensis*. Nine species were detected three or fewer times, representing 2.6% of all detections in the study. Twelve species were detected at three or fewer sites, representing 66.7% of all species detected in the study. Of 36 sample locations, 6 sites (16.7%) had low severity, 6 sites (16.7%), had high severity and 24 sites (66.7%) had no wildfire disturbance since 2001. Total animal detections varied by camera, with an average of 0.29 ± 0.23 species detections per 10 survey nights (minimum: 0.00; maximum: 1.01).

Species	Det.	Sites	PD
Mule deer, *Odocoileus hemionus*	488	31	16.00
American black bear, *Ursus americanus*	48	19	0.73
Coyote, *Canis latrans*	39	11	0.25
Snowshoe hare, *Lepus americanus*	29	4	100.00
Elk, *Cervus canadensis*	20	3	2.90
American badger, *Taxidea taxus*	16	2	1.98
Moose, *Alces alces*	12	6	0.40
Bushy-tailed woodrat, *Neotoma cinerea*	8	2	NA
Bobcat, *Lynx rufus*	7	5	0.10
Cougar, *Puma concolor*	3	2	0.02
Hoary marmot, *Marmota caligata*	3	1	NA
Golden mantled ground squirrel, *Callospermophilus lateralis*	3	2	NA
Striped skunk, *Mephitis mephitis*	2	1	8.21
Douglas' squirrel, *Tamiasciurus douglasii*	2	2	44.90
American marten, *Martes americana*	2	2	0.67
Porcupine, *Erethizon dorsatum*	1	1	3.50
Mountain goat, *Oreamnos americanus*	1	1	NA
Canada lynx, *Lynx canadensis*	1	1	0.05

Table 2.2 Species detected by passive infrared camera traps at 36 sampling locations during 2,551 trap nights. *Det.* is the number of detection-events for each species across all sampling locations. *Sites* is the number of unique sites where each species was detected. *PD* is the average population density (individuals/ km^2) from PanTHERIA mammal database (Jones et al. 2009).

Cameras were operational during the wildfire season, from late May through November. Average sample time at camera stations was 70.86 ± 24.56 trap nights, with a minimum of 19 nights and a maximum of 143 nights out of 2,551 trap nights across all stations in 2016. Survey effort was determined by battery life and the frequency of camera triggers, which varied greatly

across sites. Species rarefaction curves for most sites did not fully saturate during the sample period, suggesting incomplete sampling at these sites (Figure 2-3). Therefore, species richness was estimated at day 19 for all sampling stations, reducing the effective sample effort for the survey to 684 trap-nights.
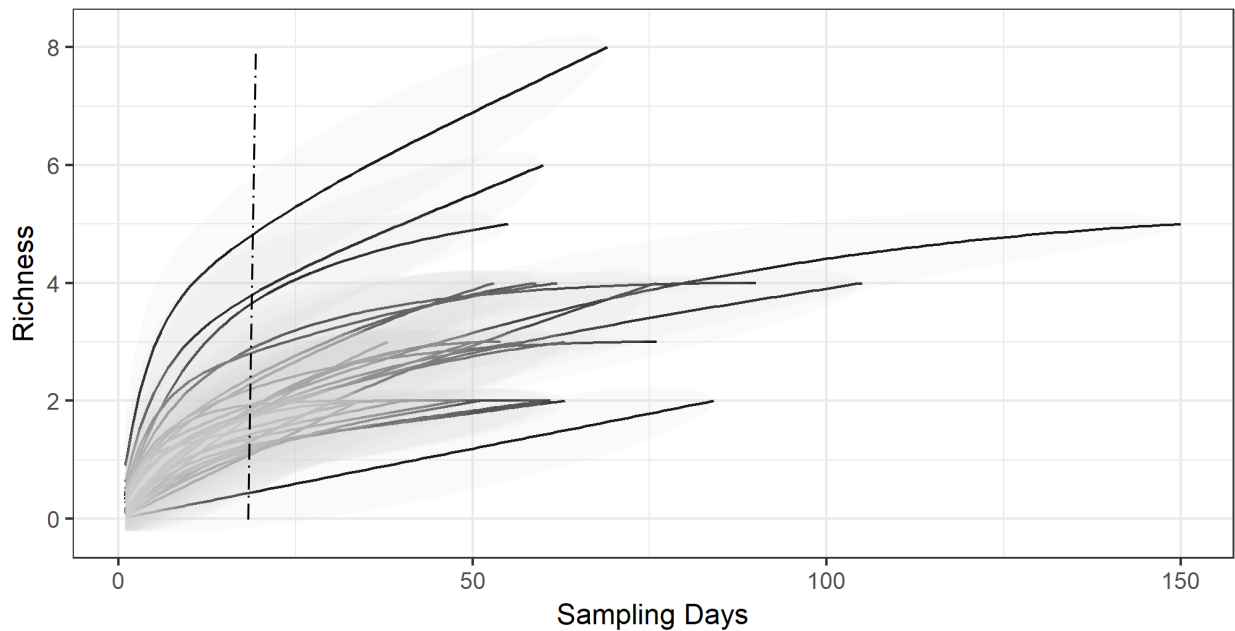
Figure 2-3. Solid lines represent sample-based rarefaction curves with 95% standard error of time-series detections at each of 36 sampling locations (Chiarucci et al. 2008). Species richness at day 19 was estimated by calculating the intersection between the dashed line and each curve.

2.3.1   Hypothesis model results

Species richness was correlated with $dNBR^2$ ($p < 0.01$, F value = 11.8) and canopy closure ($p < 0.01$, F value = 10.1), but not years since wildfire ($p = 0.40$, F value = 0.7) or detection distance ($p = 0.23$, F value = 1.5). The model had a *pseudo-R²* = 0.38 with 30 degrees of freedom. A unimodal response was found, but the relationship was inverse to the pattern predicted by the IDH when measuring dNBR as a disturbance variable (Figure 2-4). Richness was lowest, rather than highest, at intermediate levels of disturbance. Sites with the highest

dNBR had greater observed species richness than sites with either low disturbance or sites with no disturbance in the prior 15 years.
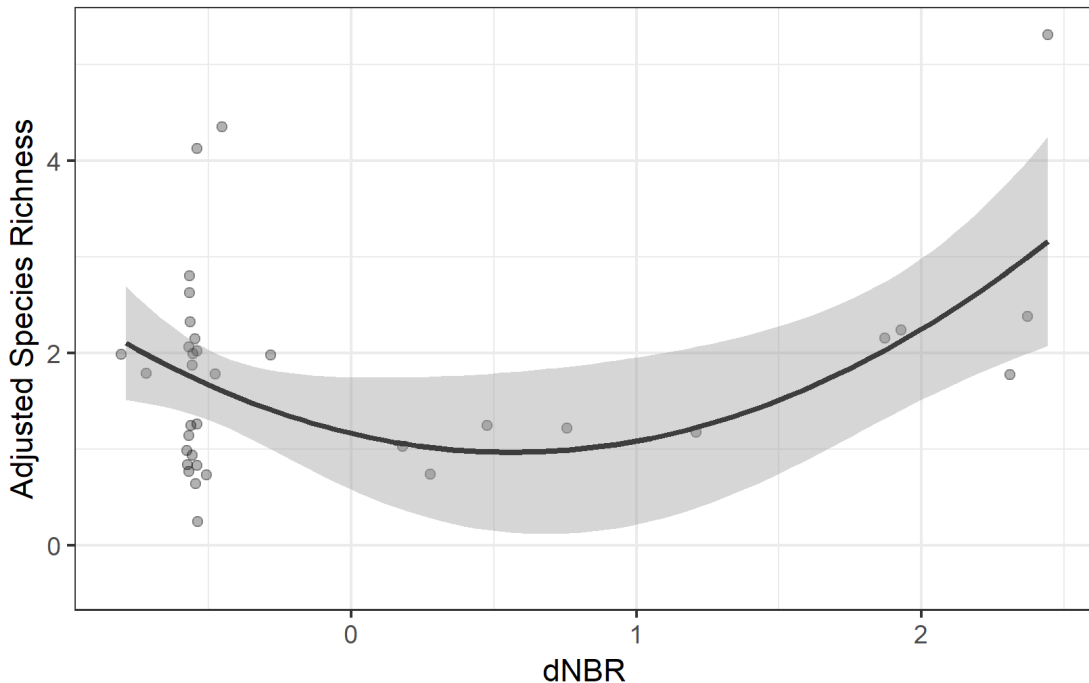
Figure 2-4. Adjusted species richness at 36 sampling sites across a range of dNBR, a measure of burn severity. Richness was estimated by rarefaction at day 19 of sampling for all sites. High dNBR reflects greater change between pre-fire and post-fire conditions, indicating a more severe wildfire. Data points are jittered to show spread.

No strong spatial correlation was found among sites sampled in this study. Based on Moran's I analysis, I found no autocorrelation between species richness and proximity to nearby sites (z-score = 0.12; p = 0.03). Geary's C found a positive and very slight autocorrelation among nearby sites (z-score = 0.78; p = 0.03). Therefore, a model without incorporating spatial weights was deemed suitable for the study, as sites appear independent.

2.3.2 Stepwise model results

Stepwise regression was used to fit the most parsimonious model from a global model by removing non-significant variables in order of lowest BIC. Seven hypotheses were tested during this exercise. The final model included a quadratic term for *average dNBR* ($\beta_1 = 0.21$, 95% CI = 0.12, 0.30) and *canopy closure* ($\beta_2 = 0.32$, 95% CI = 0.15, 0.49) as important variables (Table 2.3). In this model, all terms were significant in that the 95% confidence intervals did not include zero. Observed species richness was quadratically related to *dNBR*. Two variables influencing detectability of mammals at camera traps, total trap nights and horizontal detection distance, made no significant contribution to the model. Additional independent variables average spacing of tree stems, topographic ruggedness, and mean annual precipitation also made no significant contribution. The final model selected by stepwise regression is consistent with the findings in the hypothesis model, suggesting that burn severity and canopy closure may be important variables associated with mammal richness in the system.

Model	r.df.	BIC	ΔBIC	*pR²*
$\log(S) = dNBR^2 + CC$	32	122.99	0.00	0.32
$\log(S) = dNBR^2 + AS + CC$	31	125.17	2.11	0.34
$\log(S) = dNBR^2 + TN + AS + CC$	30	128.61	5.62	0.38

Table 2.3 Three top-ranking generalized linear mixed models with Poisson link used to estimate species richness response to wildfire. *r.df.* = the number of residual degrees of freedom, *BIC* = Bayesian Information Criteria, *ΔBIC* = difference in BIC from top-raking model, and *pR²* = pseudo-*R²* calculated by dividing null deviance by the difference between null deviance and residual deviance. Regression coefficients include dNBR², canopy cover (CC), average spacing of tree stems (AS), and site trap nights (TN).

2.3.3 Hierarchical model results

Estimated species richness is maximized at unburned sites and high severity burns when accounting for imperfect detection using a hierarchal multispecies occupancy framework to predict species accumulation (Figure 2-5). The median and mean estimated number of species present at the 24 unburned sites is 37.0 and 38.4 respectively across all model results. At high severity sites, the estimates are 31.0 and 34.3 respectively. And at low severity sites, the estimates are 23.0 and 27.3 respectively. These estimates are higher than the regional species pool, which suggests heterogeneity within species occurrence at sampling stations as well as within species detectability in the community. Prediction intervals on the estimates are wide due to uncertainty in both the observation parameters and the population parameters.
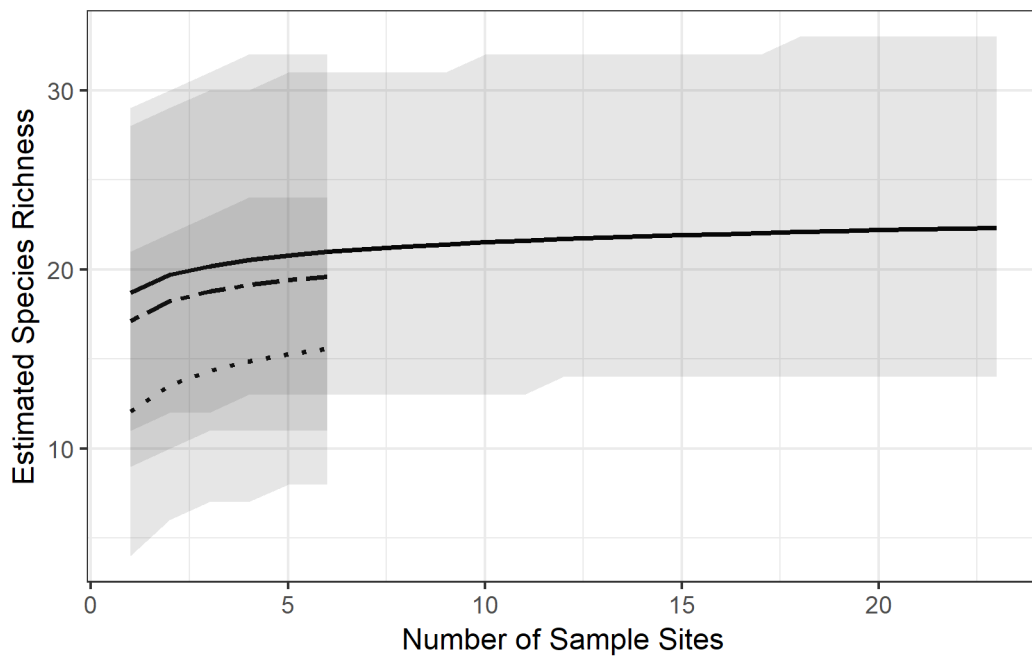

Figure 2-5. Species accumulation curves accounting for imperfect detection in not-recently-burned (solid), high dNBR (dashed), and low dNBR (dotted) sites. Species richness was estimated using a multispecies occupancy modeling framework and error bars show 90% prediction interval.

2.4   Discussion

Results of this study suggest with empirical data that habitat patches disturbed by high severity wildfire in dry coniferous forests of the eastern North Cascades may support higher species richness than patches with low levels of disturbance. Observed species richness was found to be lowest at intermediate levels of disturbance when measuring burn severity (Figure 2-4). This result was supported when estimating species richness with a hierarchical model that accounts for species detectability (Figure 2-5). Although species detectability is variable within the community, sites with low dNBR have lower estimated richness when controlled for survey effort and imperfect detection. Therefore, my research hypothesis that mammal richness is maximized at intermediate levels of burn severity in North Cascade forests is rejected. For these data, the unimodal peaked IDH pattern was not found. These results suggest that forest mammal communities may be resilient to climate-mediated wildfires predicted to increase in size, severity, and extent in this region. However, caution is advised when interpreting these findings for three reasons: (1) the sample size for burned sites was low, (2) the entire gradient of wildfire disturbance was not sampled, and (3) imperfect detection of species may confound observed community richness.

Low sample size at burned sites in this study may have multiple effects on the results of my statistical analyses. Power to detect a medium effect size (ES = 0.7) at the standard significance level ($\alpha = 0.05$) given my sample size of burned sites (N = 13) is very low when calculated with the 'pwr' package (Ekstrom et al. 2018): 32%. Thus, the likelihood of a committing a Type II error—failure to reject a false null hypothesis—is about one out of three for my data (Cohen 1992). In order to achieve 80% power, my sample would need to increase by 33 sites which would have been possible with one additional season of field sampling. Although

I found significant results in my hypothesis model, the low power of my study reflects low precision in these results.

My research hypothesis model tested the effect of three important wildfire disturbance variables on mammal species richness: burn severity, years since wildfire, and canopy cover. I found a significant relationship between richness and burn severity as well as richness and canopy cover. However, I did not find a significant relationship between species richness and years since wildfire ($p = 0.2938$, $F_2 = 1.14$). As discussed, disturbance is a multivariate phenomenon. My study design stratified sample sites across land classification and history of wildfire, but could not include all disturbance variables as strata. As a result, my sample population had an uneven distribution of sites with burn severity and time since the last burn. For sites burn severity history, 3 (23.1%) occurred in the lower half of the range of values. Further, the time since the last burn was sampled unevenly. Wildfires burned in my study system in every year between 2001 and 2015 and the largest wildfires, measured in total burned area, occurred in 2001, 2003, and 2015. I had one sample site (7.6%) from a 2001 burn and one (7.6%) from a 2003 burn, but no sampling occurred in 2015 burned areas. A disproportionately high amount of sampling (53.8%) occurred in 2006 burns. An increased sampling effort would have evened out the distribution of sampling along these disturbance gradients.

The small sample size in the data also imposed a limitation in the statistical framework used in this study. I was unable to test model accuracy of the model selected by stepwise regression because not enough data was available to create a training data set. As a result, the validity of the selection of variables deemed important by this method is questionable. Additional data on mammal richness in my study system are available through collaborators in the Wildlife Camera Network Northwest (Section 3.1.2), although these data are not suitable for

training data because they do not occur in burned habitats. Data from future sampling in burned

regions would be required for this purpose. Further, the likelihood of a false negative finding, or

Type I error, is very high for stepwise regression with small sample size (Forstmeier et al. 2017).

A general rule of thumb based on data simulations (Forstmeier & Schielzeth 2011) is that

Bonferroni corrections may be used reliably to prevent over-fit when there are three or more data

points per model predictor. My stepwise regression used 13 data points for 7 predictors.

Low sample size at burned sites in my study was due to access limitation, remoteness of

sampling locations, equipment limitations, and financial resources. Thirteen sites with burn

history were sampled across 864 nights during a single year, which represents 28.7% of total trap

nights and 36.1% of total sampling sites. Access prohibitions prevented data collection in 2017 at

the most recent and severe wildfire in my study area, the Wolverine fire of 2015 (214.4 km²).

The next most recent burned areas sampled were sites in the Lone Mountain 1 fire of 2014 (9.9

km²). Most sampling locations occurred in remote locations requiring overnight hikes to access.

Sampling time at each site was dependent on battery life, which averaged 70.8 ± 24.6 nights.

Three sites were dropped due to less than 19 trap nights due to premature power failure.

Importantly, four of the seven high severity sites were located in a single wildfire complex that

burned 10 years prior to sampling—the Tatoosh Complex fires of 2006 (164.6 km² in

Washington and British Columbia). Nine total species were detected at these sites. Species

richness averaged 4.5 ± 1.5 at these four sampling sites. The site with the highest diversity of all

sites sampled for this study also occurred at one of these sites (1168-PARI3). A rare species, *T.*

taxus, was detected only here and one nearby site. The camera at this site was placed along an

old road, which may have increased observed diversity due to ease of travel. Sites with low

severity had average species richness of 1.5 ± 1.2. These sites all had mule deer present, but little

else. One site had bobcat and one site had American black bear. Rare species were not detected at low severity sites.

In addition to low sample size in burned sites, the sample effort at most sites was incomplete, as demonstrated by few species rarefaction curves approaching an asymptote (Figure 2-3). Of the 29 species of mammals potentially detectable by camera traps in the region (Table 2.1), eight of these species were not detected by camera traps (27.5%): wolverine, gray wolf, bighorn sheep, western spotted skunk, ermine, long-tailed weasel, American mink, raccoon. Two of these species, gray wolf and wolverine, are wide ranging species with low abundance (each with a population density of 0.01 animals per kilometer; Table 2.1). More extensive spatial and temporal sampling would increase the probability of detecting these rare species. The smaller Mustelidae species, long-tailed weasel (0.2 kg), ermine (0.3 kg), spotted skunk (0.6 kg), and American mink (0.9 kg), may have gone undetected due to their small size. For species with small size or large home ranges, the probability of imperfect detection is probably equal for all sites. However, if a species with low detectability has a preference for one habitat type across a range of habitats sampled, this association may be lost due to low sample effort. My study collected data across 2,551 trap nights in 2016, which is reported in Table 2.2. My study estimated species richness at 36 sites after 19 days of sampling, which is a total sampling effort of 689 trap nights, which is the total effort for all estimated species richness modeling. The recommended camera trap survey effort for diversity studies is 1,000 trap nights (Wearn & Glover-Kapfer 2017).

Generally, species richness was low across sample sites. Therefore, small changes in the number of species detected at sample sites may have disproportionate changes to the modeled ecological relationships (Kéry 2011). Mammal detectability at camera traps can be influenced by

41

temperature (Welbourne et al. 2016), orientation of the camera trap (Rowcliffe et al. 2011), placement along trails (Kolowski & Forrester 2017), camera type (Rovero & Marshall 2009; Newey et al. 2015), local species abundance (Kéry 2011), and size of the detection zone (Burton et al. 2015). Where possible, I controlled for these factors during sampling by using a single model of camera trap, measuring the detection zone, and deploying cameras using the same methodology across sites. However, the body size and home range of animals in the community could not be controlled. Mammal species detectable by camera traps in the North Cascades range in size, life history traits, and average home range (Table 2.1), but species-specific detectability for this community in this region is not available in the literature. Some species were likely missed at unburned sites due to size and camera orientation: Douglas squirrel, bushy-tailed woodrat, and snowshoe hare. Other species in the community are rare, occurring at low density is large home ranges or in patches: wolverine, Canada lynx, and wolf. These species likely have low detectability in this system. Very few species were observed in low severity burn sites, which may be due to habitat selection or species detectability. If species with low detectability prefer specific successional stages, the absence of these species at camera traps may influence patterns of observed species richness. However, I show that patterns of estimated richness accounting for imperfect detection match patterns of observed richness, suggesting detectability is not confounding comparisons of richness across habitats.

In Table 1.1, I made predictions about the relationship between animal density and disturbance to inform a hypothesis for this study. These predictions were made on the assumption that average species densities across a gradient of disturbance would correlate to observed species richness at the site level. Using observed relative abundance from camera traps detections, I estimated a curve for each species of relative abundance adjusted for survey effort

across a range of burn severity values (Table 2.4). The observed relative abundance matched predictions for 3 out of 18 species detected. The shape of most density-burn severity species curves was monotonic decreasing (Table 2.4(a)), suggesting that species abundances for most montane forest mammals in the North Cascades are higher in undisturbed sites. Five species had highest observed abundances at high severity burn sites: American badger, Canada lynx, coyote, moose, and mule deer. For the ungulates, this observation may be due to better foraging opportunities in stands regenerating form high severity burns. For American badger, solar exposure and habitat quality at open sites with previous high severity crown fires increases habitat suitability. Most species were predicted to have greatest densities at intermediate levels of disturbance in Table 1.2, but zero species were observed with this expected peaked curve (Table 2.4(d)). Because species density-disturbance predictions only matched observed abundance-disturbance patterns for 3 species, it is not unexpected that the predicted humped IDH pattern was not observed.

My results suggest that many forest mammals respond positively to burn severity a population level but also at a community level. However, the mechanisms that drive mammal habitat selection in high burn severity patches remains unknown. With more data, other improvements could be made to this study. It has been shown that the shape of diversity-disturbance relationship depends on the disturbance variables being measured (Miller et al. 2011). Additional disturbance variables could be tested with more sampling locations to understand the most important disturbance mechanisms driving community assembly. More data would provide the opportunity to explore the relationship between species evenness (e.g. Pielou's J) and measures of combined species richness-evenness (e.g. Shannon-Wiener's H′) on
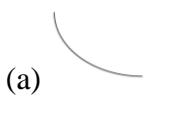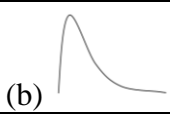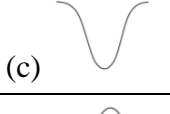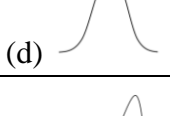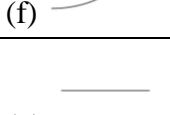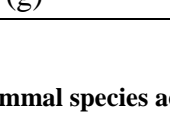
Observed disturbance response	DD Shape	Species	Obs. Sp.
Decreasing density with increasing wildfire disturbance	(a)	American marten*, bushy-tailed woodrat, Douglas squirrel*, elk, golden-mantled ground squirrel, hoary marmot, mountain goat, porcupine, and striped skunk	9 *(3)*
Highest density at low to medium wildfire disturbance	(b)	Not calculated	NA *(9)*
Highest density at low and high wildfire disturbance	(c)	American black bear, cougar*, coyote, moose, mule deer, snowshoe hare	7 *(1)*
Highest density at medium wildfire disturbance	(d)	None	0 *(7)*
Highest density at medium to high wildfire disturbance	(e)	Not calculated	NA *(2)*
Increasing density with increasing wildfire disturbance	(f)	badger, Canada lynx	*2* *(2)*
Equal density across disturbance gradient	(g)	bobcat	1 *(5)*

Table 2.4 Relative abundance of mammal species across wildfire burn severity. Eighteen mammal species were observed during the study. Observed response to disturbance is visualized by seven density-disturbance relationships (*DD shape*) showing relative abundance adjusted by survey effort on the y-axis and burn severity on the x-axis. Species are categorized within one of five of the seven predicted *DD shape* groups, as described in Table 1.1. Not enough observational data were collected to assess the skew of distributions for category (b) or (e) because abundance is available for only three

categories: no disturbance, low, and high levels of disturbance. The asterisk (*) denotes a species with an observed DD shape that matches the predicted shape. The number of observed species (*Obs. Sp.*) is given for each *DD shape*, as well as the number of predicted species for each group (italicized in parentheses).

wildfire disturbance. Similarly, an extension to assess phylogenetic or functional diversity may elucidate other mechanisms underlying the diversity-disturbance relationship in this system.

My study used mammal presence data only from protected areas, which limits inference to multiple-use lands around protected areas. The shape of diversity-disturbance curves outside of protected areas may change with increased hunting pressure, greater habitat modification, or intensified fire management activities. Further, abundances of species within and outside protected areas most likely differ, affecting detectability. The apparent resilience of mammals to burn severity within protected areas in my study cannot be extrapolated to unprotected areas where additional disturbances contribute to mammal community assembly.

2.4.1   Data Accessibility

The data used in this study may provide a benchmark of mammal occurrence during the early decades of a changing wildfire regime in Cascade coniferous forests. Raw data in tabular format – analyzed in digiKam and processed through camtrapR – were archived with the Environmental Data Initiative (EDI), a secure environmental data repository and member node for DataONE. Data are available for use with attribution under a Creative Commons Attribution-NonCommercial 4.0 International Public License. Data are archived as Package ID: d46d8ece-36d0-11e9-b191-91314e814857. Image metadata are archived in Ecological Metadata Language according to the Camera Trap Metadata Standard (Forrester et al. 2016).

Chapter 3. Conclusions

Chapter 3 places my thesis research in the context of the broader discipline, explores limitations of the research, identifies opportunities for future research direction, and assesses the management implications of my research findings.

3.1   Research conclusions

Climate-mediated wildfire has potential long-term implications for forest resilience (Whitlock et al. 2003; Stevens-Rumann et al. 2018), human health (Liu et al. 2015; Cascio 2018), and persistence of wildlife (Driscoll et al. 2010; McKenzie et al. 2011). My research provides early empirical evidence that species diversity in burned forests of the Cascade mountains can persist after high severity wildfires. Although my data lacks strong statistical power, the data will be available to land managers and researchers for future applied and academic ecological research.

3.1.1   Limitations

My project involved collection of valuable primary ecological data on mammals in a rugged transboundary ecosystem spanning multiple management jurisdictions. Logistical constraints and access restrictions limited the volume of data that I was able to collect in one field season. Ultimately, my statistical modeling was based on a small sample size of 13 sites burned by wildfire. My data were not statistically spatially autocorrelated and I used a randomized, spatially-stratified design to select sampling sites. However, constraints for the project resulted in a sample that may or may not be representative of the full distribution of diversity-disturbance phenomena in the system for three reasons: 1) a complete gradient of disturbance was not sampled when burn severity and time since disturbance was considered, 2)

small sample size of burned sites, and 3) imperfect detection of species. These limitations were discussed in detail in Section 2.4 above.

3.1.2 Future directions

My research is part of a collaborative network of ecologists using camera traps in the North Cascades on a wide variety of research initiatives. The Wildlife Camera Network Northwest (WCN-NW) is an association of scientists and conservationists using remote camera technology to assess the status of wildlife in the urban-wildland interface, quantify the density and distribution of species of conservation concern, monitor mitigation projects such as wildlife crossing structures, and involve the public in citizen scientist research programs. The WCN-NW facilitates data sharing, supports the development of standardized camera methodology, and encourages communication among researchers. A parallel initiative is also developing between academic, government, and non-profit researchers in British Columbia.

I believe these types of research networks will be important for future ecological studies. A key component of these networks is public data accessibility. Quality camera trap data can be expensive and timely to collect, and combined data sets may provide new scientific insights. Best practices for data sharing ecological data focus on ensuring datasets are complete, interpretable, and accessible (Whitlock 2011; White et al. 2013; Michener 2015). However, a recent meta-analysis found that high rates of incomplete data and unusable ecological data are available in publicly accessible repositories (Roche et al. 2015). Research networks may serve social functions to which encourage researchers to see beyond individual research interests to support benefits in the larger scientific community. Additionally, these networks support the development and use of metadata standards (Forrester et al. 2016) and best practices for data management (Scotson et al. 2017). An important future direction for these organizations is

developing survey design recommendations that facilitate multiple analytical frameworks in data analysis workflows.

My research explored the influence of a few disturbance variables on a small component of the ecological community in my study system. We know that the aspect of disturbance measured influences the shape of the diversity-disturbance curve observed (Miller et al. 2011). I expect that increasing the scope of the research to include more vertebrates would further influence the shape of the diversity-disturbance relationship. The presence of small mammals, herpetofauna, and fish could be detected at camera sites using environmental DNA (eDNA; Rees et al. 2014; Thomsen & Willerslev 2015). The presence of vocal birds, bats, and mammals could be detected using passive bioacoustic monitoring (Pijanowski et al. 2011; Gibb et al. 2018). These techniques would increase the species pool in the study by over 800% and capture most of the vertebrate biodiversity in the system. We could further extend efforts to measure the diversity of woody and herbaceous plants at each sampling location. These techniques would allow us to examine the effects of disturbance variables on a more comprehensive representation of biodiversity in the system.

Much of the ecological literature on the IDH includes observational and experimental tests of disturbance on single, well-defined communities (Shea et al. 2004). Stream invertebrates, alpine plants, intertidal marine organisms, and bacterium are common communities for research. Connell's original hypothesis was framed on tropical forest and coral systems. These communities are easily observable, accessible, and generally stationary. These systems provide opportunity to control for confounding variables such as herbivory, invasive species, or trophic cascades. For observational studies at larger scales with mobile organisms, these factors are not easily controlled and researchers must use knowledge about their study system to justify

assumptions about such variables. However, as methodologies to collect and process large volumes of passive ecological data become more accessible, researchers will be able to make direct measurements of these variables to incorporate into models built from empirical data.

In Chapter 1, I introduced the idea of interspecies competition as a key mechanism of the IDH. In the context of the IDH, competition is generally thought of as niche competition over limited resources. Communities are generally studied as functional groups within a trophic system, such as corals (ecosystem architects) or plants (producers). In large systems, particularly in studies where the community of interest includes species of high trophic levels, the processes of predation, herbivory, and trophic cascades should be taken into account. One way to begin to do this is formally describe and measure the community-disturbance relationships for multiple trophic levels across multiple gradients of disturbance (e.g., Figure 3-1).
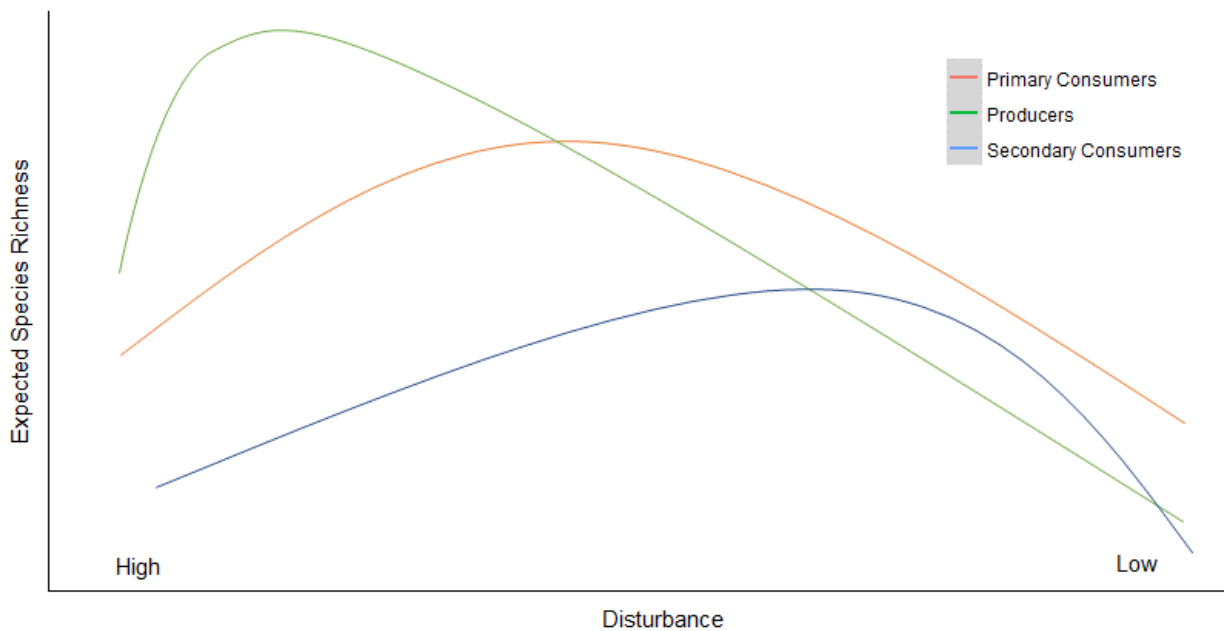

Figure 3-1. Theoretical model of diversity-disturbance curves for multiple trophic levels within an ecological community.

Finally, the data available from my study is starting point for understanding wildfire disturbance on mammals in North American protected areas, but it does not meaningfully test the IDH in a robust way. Because experiments to test the relationship between wildfire and species richness are impractical and unethical, future research must make use of natural experiments and well-designed observational studies. One approach to this endeavor would be longitudinal studies of changes to the mammal community in the half-century following a burn. Logistical and analytical methods used in this study could be used at long-term monitoring sites set up before the first winter following a summer wildfire. These data would track community richness changes over time following disturbance. Data collected for my thesis and other data available from regional collaboration networks could provide pre-disturbance reference data.

3.1.3 Management implications

Findings from this study should be interpreted with caution, given the problems associated with small sample size and differences in species detectability. The management implications of my research are that more long-term monitoring data are needed to understand the effects of climate change on wildlife in protected areas. The need for long-term monitoring data is widely acknowledged to understand temporal turnover and the mechanisms driving community changes (Magurran et al. 2010; Lindenmayer et al. 2016; Proença et al. 2017; Haase et al. 2018). In systems with small incremental changes over time, such as under climate change, ecological effects can go unnoticed until tipping points and regime shifts are reached. In systems with alternative stable states (Beisner et al. 2003), such as fire-mediated forest/savannah systems, the timing of management action can be critical to maintenance of desired ecosystem states.

3.2 Concluding Remarks

I believe the field of ecology is poised to grow rapidly in the next century considering the growth in processing power of advanced computers, rapid development of novel ecological sensors, and availability of open source modeling and analysis software. I also believe an even greater opportunity exists in the democratization of scientific institutions, as universities, publishers, and funding organizations increasingly commit to principles of transparency, accountability, and accessibility in science. A thoughtful approach to incorporating these principles will contribute to increased rigor of published ecological research. Ultimately, increased rigor will support improved ecological theory and applied ecological research. But without improved scientific rigor, methodological advances and exponential computing gains will do little to improve the field.

Some researchers have identified a "crisis of confidence" associated with low reproducibility in science (Baker 2016; Forstmeier et al. 2017). In the field of ecology, one study shows that very little variance is explained by studies published in the ecological literature (Møller & Jennions 2002). One important finding from Baker's surveys of 1,500 participants was that selective reporting of data is a widespread problem, potentially exacerbated cultural values around academic publication. Policy reforms to improve use of statistical methods by editorial boards of ecological journals lags behind other fields (Fidler et al. 2004). Although the field of ecology has matured over the past century, significant cultural precedential values are inhibiting some growth in the discipline. I believe that transparency and accessibility of all steps in the research process is fundamental to address these problems present in the ecological sciences.

To that end, I believe the strongest contribution of this graduate research to the field of ecology is the publicly available primary data I collected in 2016. The data and metadata are robust and follow accepted current best practices and have been archived for public use in a high-quality, stable data archive. I believe the findings from my research, although statistically significant, do not have strong relevance to applied ecology (e.g. species or ecosystem management) or to theoretical ecology (e.g. interpretations of the IDH). However, the exercise of analyzing, reinterpreting, and reanalyzing my data post hoc in a new theoretical context developed new analytical and conceptual skills that will be valuable for my future scientific endeavors.

References

Agee JK. 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington DC, United States.

Agee JK, Skinner CN. 2005. Basic principles of forest fuel reduction treatments. Forest Ecology and Management **211**:83–96.

Anderson-Teixeira KJ, Miller AD, Mohan JE, Hudiburg TW, Duval BD, DeLucia EH. 2013. Altered dynamics of forest recovery under a changing climate. Global Change Biology **19**:2001–2021.

Andrewartha HG, Birch LC. 1954. The Distribution and Abundance of Animals. University of Chicago Press, Chicago, United States.

Baker M. 2016. Is there a reproducibility crisis? Nature News **533**:452–454.

Ballard WB, Krausman PR, Boe S, Cunningham S, Whitlaw HA. 2000. Short-term response of gray wolves (*Canis lupus*) to wildfire in Northwestern Alaska. The Canadian Field-Naturalist **114**:241–247.

Barnosky AD, Matzke N, Tomiya S, Wogan GUO, Swartz B, Quental TB, Marshall C, Mcguire JL, Lindsey EL, Maguire KC, Mersey B, Ferrer EA. 2011. Has the Earth's sixth mass extinction already arrived? Nature **471**:51–57.

Beisner BE, Haydon DT, Cuddington K. 2003. Stable states in ecology. Frontiers in Ecology and the Environment **1**:376–382.

Belote TR, Dietz MS, McRae BH, Theobald DM, McClure ML, Hugh IG, McKinley PS, Gage JA, Aplet GH. 2016. Identifying corridors among large protected areas in the United States. PLoS ONE **11**:1–16.

Biggs JR, VanLeeuwen DM, Holechek JL, Valdez R. 2010. Multi-scale analyses of habitat use by elk following wildfire. Northwest Science **84**:20–32.

Blanchard BW, Knight RiR. 1990. Reactions of grizzly bears, *Ursos arctos horribilis*, to wildfire in Yellowstone National Park, Wyoming. The Canadian Field-Naturalist **104**:592–594.

Borchert MI. 2012. Mammalian carnivore use of a high-severity burn in conifer forests in the San Bernardino Mountains of southern California, USA. Hystrix **23**:50–56.

Brown CL, Kielland K, Euskirchen ES, Brinkman TJ, Ruess RW, Kellie KA. 2018. Fire-mediated patterns of habitat use by male moose (*Alces alces*) in Alaska. Canadian Journal of Zoology **96**:183–192.

Brown RL, Jacobs LA, Peet RK. 2016. Species Richness: Small Scale. Encyclopedia of Life Sciences. John Wiley & Sons, Ltd., Chichester, United Kingdom.

Bull EL, Aubry KB, Wales BC. 2001. Effects of disturbance on forest carnivores in eastern Oregon and Washington. Northwest Science **75**:180–184.

Bunkley JP, Mcclure CJW, Kleist NJ, Francis CD, Barber JR. 2015. Anthropogenic noise alters bat activity levels and echolocation calls. Global Ecology and Conservation **3**:62–71.

Burton AC, Neilson E, Moreira D, Ladle A, Steenweg R, Fisher JT, Bayne E, Boutin S. 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. Journal of Applied Ecology **52**:675–685.

Cansler CA, Mckenzie D. 2014. Climate, fire size, and biophysical setting control fire severity and spatial pattern in the northern Cascade Range, USA. Ecological Applications **24**:1037–1056.

Cascio WE. 2018. Wildland fire smoke and human health. Science of the Total Environment **624**:586–595.

Castillo LS, Stevenson PR. 2010. Relative importance of seed-bank and post-disturbance seed
dispersal on early gap regeneration in a Colombian amazon forest. Biotropica **42**:488–492.

Certini G. 2005. Effects of fire on properties of forest soils: a review. Oecologia **143**:1–10.

Cheng E, Hodges KH, Mills LS. 2015. Impacts of fire on snowshoe hares in Glacier National
Park, Montana, USA. Fire Ecology **11**:119–136.

Chesson P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology
and Systematics **31**:343–66.

Chiarucci A, Bacaro G, Rocchini D, Fattorini L. 2008. Discovering and rediscovering the
sample-based rarefaction formula in the ecological literature. Community Ecology **9**:121–
123.

Christophersen RG. 2006. Supplemental forest carnivore surveys in North Cascades National
Park Service Complex, Washington. USDI National Park Service. Sedro Woolley, WA.
NPS/PWR-NCCN/INV-2006/01. NPS D280.

Cohen J. 1992. A power primer. Quantitative Methods in Psychology **112**:155–159.

Connell JH. 1978. Diversity in tropical rain forests and coral reefs. Science **199**:1302–1310.

Contu S et al. 2016. Local biodiversity is higher inside than outside terrestrial protected areas
worldwide. Nature Communications **7**:1–7.

Cunningham SC, Ballard WB, Monroe LM, Rabe MJ, Bristow KD. 2003. Black bear habitat use
in burned and unburned areas, central Arizona. Wildlife Society Bulletin **31**:786–792.

Daly C, Gibson WP, Taylor GH, Johnson GL, Pasteris P. 2002. A knowledge-based approach to
the statistical mapping of climate. Climate Research 22:99–113.

Davis R, Yang Z, Yost A, Belongie C, Cohen W. 2017. The normal fire environment—modeling environmental suitability for large forest wildfires using past, present, and future climate normals. Forest Ecology and Management **390**:173–186.

Delheimer MS, Slauson KM, Szykman Gunther M, Zielinski WJ. 2018. Use of artificial cavities by Humboldt marten. Wildlife Society Bulletin **42**:510–517.

Dennison PE, Brewer SC, Arnold JD, Moritz MA. 2014. Large wildfire trends in the western United States, 1984–2011. Geophysical Prospecting **41**:2928–2933.

Diamond JM. 1975. The island dilemma: lessons of modern geographical studies for the design of nature preserves. Biological Conservation **7**:129–146.

Dorazio RM, Royle JA, Söderström B, Glimskär A. 2006a. Estimating species richness and accumulation by modeling species occurrence and detectability. Ecology **87**:842–854.

Dorazio RM, Royle JA, Söderström B, Glimskär A. 2006b. Supplement: R and WinBUGS code for fitting the model of species occurrence and detection and example data sets.

Driscoll DA et al. 2010. Fire management for biodiversity conservation: Key research questions and our capacity to answer them. Biological Conservation **143**:1928–1939.

Dudley N. 2008. Guidelines for applying protected area management categories. Pages 1–23 in S. Stolton, P. Shadie, and N. Dudley, editors. IUCN WCPA Best Practice Guidance on Recognizing Protected Areas and Assigning Management Categories and Governance Types, Best Practice Protected Area Guidelines Series No. 21. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.

Eales J, Haddaway NR, Bernes C, Cooke SJ, Jonsson BG, Kouki J, Petrokofsky G, Taylor JJ. 2018. What is the effect of prescribed burning in temperate and boreal forest on

biodiversity, beyond tree regeneration, pyrophilous and saproxylic species? A systematic review. Environmental Evidence **7**:1–33.

Eidenshink J, Schwind B, Brewer K, Zhu Z-L, Quayle B, Howard S. 2007. A project for monitoring trends in burn severity. Fire Ecology Special Issue **3**:3–21.

Ekstrom C, Dalgaard P, Gill J, Weibelzahl S, Ford C, Volcic R. 2018. Package 'pwr': basic functions for power analysis. Version 1.2-2.

Fahrig L. 2003. Effects of Habitat Fragmentation on Biodiversity. Annual Review of Ecology, Evolution, and Systematics **34**:487–515.

Fardila D, Kelly LT, Moore JL, Mccarthy MA. 2017. A systematic review reveals changes in where and how we have studied habitat loss and fragmentation over 20 years. Biological Conservation **212**:130–138.

Fidler F, Geoff C, Mark B, Neil T. 2004. Statistical reform in medicine, psychology, and ecology. Journal of Socio-Economics **33**:615–630.

Fisher JT, Wilkinson L. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. Mammal Review **35**:51–81.

Fontaine JB, Kennedy PL. 2012. Meta-analysis of avian and small-mammal response to fire severity and fire surrogate treatments in U.S. fire-prone forests. Ecological Applications **22**:1547–1561.

Forrester T, O'Brien T, Fegraus E, Jansen P, Palmer J, Kays R, Ahumada J, Stern B, McShea W. 2016. An open standard for camera trap data. Biodiversity Data Journal **4**:e10197.

Forstmeier W, Schielzeth H. 2011. Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. Behavioral Ecology and Sociobiology **65**:47–55.

Forstmeier W, Wagenmakers EJ, Parker TH. 2017. Detecting and avoiding likely false-positive findings – a practical guide. Biological Reviews **92**:1941–1968.

Franklin JF, Lindenmayer DB. 2009. Importance of matrix habitats in maintaining biological diversity. Proceedings of the National Academy of Sciences of the United States of America **106**:349–350.

Geary RC. 1954. The Contiguity Ratio and Statistical Mapping. The Incorporated Statistician **5**:115–127.

Gibb R, Browning E, Glover-Kapfer P, Jones KE. 2018. Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring. Methods in Ecology and Evolution DOI: 10.1111/2041–210X.13101: 1–17.

Glenn SM, Nudds TD. 1989. Insular biogeography of mammals in Canadian parks. Journal of Biogeography **16**:261–268.

Haase P, Tonkin JD, Stoll S, Burkhard B, Frenzel M, Geijzendorffer IR, Häuser C, Klotz S, Kühn I, McDowell WH, Mirtl M, Müller F, Musche M, Penner J, Zacharias S, Schmeller DS. 2018. The next generation of site-based long-term ecological monitoring: linking essential biodiversity variables and ecosystem integrity. Science of the Total Environment **613–614**:1376–1384.

Hagle TM, Mitchell GE. 1992. Goodness-of-fit measures for probit and logit. American Journal of Political Science **36**:762–784.

Hansen WD, Braziunas KH, Rammer W, Seidl R, Turner MG. 2018. It takes a few to tango: changing climate and fire regimes can cause regeneration failure of two subalpine conifers. Ecology **99**:966–977.

Hanski I. 2011. Habitat loss, the dynamics of biodiversity, and a perspective on conservation. Ambio **40**:248–255.

Hardin G. 1960. The competitive exclusion principle. Science **131**:1292–1297.

Harvey P. 2016. ExifTool. Version 11.20. Available from http://owl.phy.queensu.ca/~phil/exiftool/.

Hobbs RJ, Huenneke LF. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology **6**:324–337.

Holbrook JD, Arkle RS, Rachlow JL, Vierling KT, Pilliod DS, Wiest MM. 2016. Occupancy and abundance of predator and prey: implications of the fire-cheatgrass cycle in sagebrush ecosystems. Ecosphere **7**:1–21.

Horn HS, Cody M., Diamond JM. 1975. Markovian properties of forest succession. Pages 196–211 in H. S. Horn, M. L. Cody, and J. M. Diamond, editors. The ecology and evolution of communities. Harvard University Press, Boston, United States.

Horncastle VJ, Yarborough RF, Dickson BG, Rosenstock SS. 2013. Summer habitat use by adult female mule deer in a restoration-treated ponderosa pine forest. Wildlife Society Bulletin **37**:707–713.

Hughes AR, Byrnes JE, Kimbro DL, Stachowicz JJ. 2007. Reciprocal relationships and potential feedbacks between biodiversity and disturbance. Ecology Letters **10**:849–864.

Ikeda T, Uchida K, Matsuura Y, Takahashi H, Yoshida T, Kaji K, Koizumi I. 2016. Seasonal and diel activity patterns of eight sympatric mammals in northern Japan revealed by an intensive camera-trap survey. PLoS ONE **11**:1–17.

Jennings MK, Lewison RL, Vickers TW, Boyce WM. 2016. Puma response to the effects of fire and urbanization. Journal of Wildlife Management **80**:221–234.

Johnstone JF, Rupp TS, Olson M, Verbyla D. 2011. Modeling impacts of fire severity on successional trajectories and future fire behavior in Alaskan boreal forests. Landscape Ecology **26**:487–500.

Jones KE, Bielby J, Cardillo M, Fritz SA, O'Dell J, Orme CDL, Safi K, Sechrest W, Boakes EH, Carbone C, Connolly C, Cutts MJ, Foster JK, Grenyer R, Habib M, Plaster CA, Price SA, Rigby EA, Rist J, Teacher A, Bininda-Emonds ORP, Gittleman JL, Mace GM, Purvis A. 2009. PanTHERIA: A species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecological Archives **E090-184-D**:1-96.

Kéry M. 2011. Species richness and community dynamics: a conceptual framework. Pages 207–231 in A. F. O'Connell, J. D. Nichols, and K. U. Karanth, editors. Camera Traps in Animal Ecology: Methods and Analyses. Springer, Tokyo, Japan.

Kincaid TM, Olsen AR. 2016. Package 'spsurvey': spatial survey design and analysis. Version 3.3.

Kleiber C, Zeileis A. 2017. Package 'AER': applied econometrics with R. Version 1.2-5.

Klinger RC, Kutilek MJ, Shellhammer HS. 1989. Population responses of black-tailed deer to prescribed burning. Journal of Wildlife Management **53**:863–871.

Koehler GM, Brittell JD. 1990. Managing spruce-fir habitat for lynx and snowshoe hare. Journal of Forestry **88**:10–14.

Kolowski JM, Forrester TD. 2017. Camera trap placement and the potential for bias due to trails and other features. PLoS ONE **12**:1–20.

Lindenmayer DB et al. 2016. Temporal trends in mammal responses to fire reveals the complex effects of fire regime attributes. Ecological Applications **26**:557–573.

Littell JS, McKenzie D, Wan HY, Cushman SA. 2018. Climate change and future wildfire in the western United States: an ecological approach to nonstationarity. Earth's Future **6**:1097–1111.

Liu JC, Pereira G, Uhl SA, Bravo MA, Bell ML. 2015. A systematic review of the physical health impacts from non-occupational exposure to wildfire smoke. Environmental Research **136**:120–132.

Lunn DJ, Thomas A, Best N, Spiegelhalter D. 2000. WinBUGS – A Bayesian modelling framework: concepts, structure, and extensibility. Statistics and Computing **10**:325–337.

MacArthur RH. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology **39**:599–619.

MacArthur RH, Wilson EO. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, United States.

Mackey RL, Currie DJ. 2001. The diversity-disturbance relationship: is it generally strong and peaked? Ecology **82**:3479–3492.

Magurran AE, Baillie SR, Buckland ST, Dick JMP, Elston DA, Scott EM, Smith RI, Somerfield PJ, Watt AD. 2010. Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. Trends in Ecology and Evolution **25**:574–582.

Malison RL, Baxter C V. 2010. The fire pulse: wildfire stimulates flux of aquatic prey to terrestrial habitats driving increases in riparian consumers. Canadian Journal of Fisheries and Aquatic Sciences **67**:570–579.

Mantyka-Pringle CS, Martin TG, Rhodes JR. 2012. Interactions between climate and habitat loss

    effects on biodiversity: a systematic review and meta-analysis. Global Change Biology

    18:1239–1252.

Marlon JR, Bartlein PJ, Gavin DG, Long CJ, Anderson RS, Briles CE, Brown KJ, Colombaroli

    D, Hallett DJ, Power MJ, Scharf EA, Walsh MK. 2012. Long-term perspective on wildfires

    in the western USA. Proceedings of the National Academy of Sciences of the United States

    of America **109**:E535–E543.

McDonald JL, Bailey T, Delahay RJ, McDonald RA, Smith GC, Hodgson DJ. 2016.

    Demographic buffering and compensatory recruitment promotes the persistence of disease

    in a wildlife population. Ecology Letters **19**:443–449.

McKenzie D, Gedalof Z, Peterson DL, Mote P. 2011. Climatic change, wildfire, and

    conservation. Conservation Biology **18**:890–902.

Michener WK. 2015. Ecological data sharing. Ecological Informatics **29**:33–44.

Miller AD, Roxburgh SH, Shea K. 2011. How frequency and intensity shape diversity-

    disturbance relationships. Proceedings of the National Academy of Sciences of the United

    States of America **108**:5643–5648.

Mitchell SR, Harmon ME, O'Connell KEB. 2009. Forest fuel reduction alters fire severity and

    long-term carbon storage in three Pacific Northwest ecosystems. Ecological Applications

    19:643–655.

Møller AP, Jennions MD. 2002. How much variance can be explained by ecologists and

    evolutionary biologists? Oecologia **132**:492–500.

Moran PAP. 1950. Notes on Continuous Stochastic Phenomena. Biometrika **37**:17–23.

Nelson JL, Zavaleta ES, Chapin FS. 2008. Boreal fire effects on subsistence resources in Alaska and adjacent Canada. Ecosystems **11**:156–171.

Newey S, Davidson P, Nazir S, Fairhurst G, Verdicchio F, Irvine RJ, van der Wal R. 2015. Limitations of recreational camera traps for wildlife management and conservation research: a practitioner's perspective. Ambio **44**:S624-635.

Newmark WD. 1987. A land-bridge island perspective on mammalian extinctions in western North American parks. Nature **325**:430-431.

Newmark WD. 1995. Extinction of mammal populations in western North American National Parks. Conservation Biology **9**:512–526.

Niedballa J, Sollmann R, Courtiol A, Wilting A. 2016. Package `camtrapR`: an R package for efficient camera trap data management. Methods in Ecology and Evolution **7**:1457–1462.

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, Hara RBO, Simpson GL, Solymos P, Stevens MHH, Wagner H. 2018. Package 'vegan': community ecology package. Version 2.5-3.

Olson DM, Dinerstein E. 2002. The Global 200: Priority Ecoregions for Global Conservation. Annals of the Missouri Botanical Garden **89**:199–224.

Omernik JM, Griffith GE. 2014. Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. Environmental Management **54**:1249–1266.

Pereira HM, Leadley PW, Proenca V, Alkemade R, Scharlemann JPW, Fernandez-Manjarres JF, Araujo MB, Balvanera P, Biggs R, Cheung WWL, Chini L, Cooper HD, Gilman EL, Guenette S, Hurtt GC, Huntington HP, Mace GM, Oberdorff T, Revenga C, Rodrigues P, Scholes RJ, Sumaila UR, Walpole M, Proença V, Alkemade R, Scharlemann JPW, Fernandez-Manjarrés JF, Araújo MB, Balvanera P, Biggs R, Cheung WWWL, Chini L,

Cooper D, Gilman EL, Guénette S, Hurtt GC, Huntington HP, Mace GM, Oberdorff T, Revenga C, Rodrigues P, Scholes RJ, Sumaila UR, Walpole M. 2010. Scenarios for global biodiversity in the 21st century. Science **330**:1496–1501.

Pijanowski BC, Villanueva-Rivera LJ, Dumyahn SL, Farina A, Krause BL, Napoletano BM, Gage SH, Pieretti N. 2011. Soundscape ecology: the science of sound in the landscape. BioScience **61**:203–216.

Pimm SL, Raven P. 2000. Extinction by numbers. Nature **403**:843–845.

Post DM. 2002. The long and short of food-chain length. Trends in Ecology and Evolution **17**:269–277.

Proença V, Proença V, Martin LJ, Pereira HM, Fernandez M, McRae L, Belnap J, Böhm M, Brummitt N, García-Moreno J, Gregory RD, Honrado JP, Jürgens N, Opige M, Schmeller DS, Tiago P, van Swaay CAM. 2017. Global biodiversity monitoring: From data sources to essential biodiversity variables. Biological Conservation **213**:256–263.

Prugh LR, Hodges KE, Sinclair ARE, Brashares JS. 2008. Effect of habitat area and isolation on fragmented animal populations. Proceedings of the National Academy of Sciences of the United States of America **105**:20770–20775.

R Development Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.r-project.org/.

Rees HC, Maddison BC, Middleditch DJ, Patmore JRM, Gough KC. 2014. The detection of aquatic animal species using environmental DNA - a review of eDNA as a survey tool in ecology. Journal of Applied Ecology **51**:1450–1459.

Ripple WJ, Beschta RL. 2012. Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. Biological Conservation **145**:205–213.

Roche DG, Kruuk LEB, Lanfear R, Binning SA. 2015. Public data archiving in ecology and evolution: how well are we doing? PLoS Biology **13**:1–12.

Rodrigues ASL, Andelman SJ, Bakarr MI, Boitani L, Brooks TM, Cowling RM, Fishpool LDC, da Fonseca GAB, Gaston KJ, Hoffmann M, Long JS, Marquet PA, Pilgrim JD, Pressey RL, Schipper J, Sechrest W, Stuart SN, Underhill LG, Waller RW, Watts MEJ, Yan X. 2004. Effectiveness of the global protected area network in representing species diversity. Nature **428**: 640–643.

Rovero F, Marshall AR. 2009. Camera trapping photographic rate as an index of density in forest ungulates. Journal of Applied Ecology **46**:1011–1017.

Rovero F, Zimmermann F, Berzi D, Meek P. 2013. Which camera trap type and how many do I need? A review of camera features and study designs for a range of wildlife research applications. Hystrix **24**:148–156.

Rowcliffe JM, Carbone C, Jansen PA, Kays R, Kranstauber B. 2011. Quantifying the sensitivity of camera traps: An adapted distance sampling approach. Methods in Ecology and Evolution **2**:464–476.

Roxburgh SH, Shea K, Wilson JB. 2004. The Intermediate Disturbance Hypothesis: Patch dynamics and mechanisms of species coexistence. Ecology **85**:359–371.

Rykiel EJ. 1985. Towards a definition of ecological disturbance. Australian Journal of Ecology **10**:361–365.

Santi P, Cannon S, DeGraff J. 2013. Wildfire and landscape change. Pages 262–287 in J. Shroder, L. James, C. Harden, and J. Clague, editors. Treatise on Geomorphology:

Geomorphology of Human Disturbances, Climate Change, and Natural Hazards. Academic Press, San Diego, United States.

Schoener TW. 1974. Resource partitioning in ecological communities. Science **185**:27–39.

Schwartz CC, Franzmann AW. 1989. Bears, wolves, moose, and forest succession, some management considerations on the Kenai Peninsula, Alaska. Alces **25**:1–10.

Scotson L, Johnston LR, Iannarilli F, Wearn OR, Mohd-Azlan J, Wong WM, Gray TNE, Dinata Y, Suzuki A, Willard CE, Frechette J, Loken B, Steinmetz R, Moßbrucker AM, Clements GR, Fieberg J. 2017. Best practices and software for the management and sharing of camera trap data for small and large scales studies. Remote Sensing in Ecology and Conservation **3**:158–172.

Shea K, Roxburgh SH, Rauschert ESJ. 2004. Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. Ecology Letters **7**:491–508.

Sheehan T, Bachelet D, Ferschweiler K. 2015. Projected major fire and vegetation changes in the Pacific Northwest of the conterminous United States under selected CMIP5 climate futures. Ecological Modelling **317**:16–29.

Sheil D, Burslem DFRP. 2013. Defining and defending Connell's intermediate disturbance hypothesis: A response to Fox. Trends in Ecology and Evolution **28**:571–572.

Simberloff D. 2004. Community ecology: is it time to move on? The American Naturalist **163**:787–799.

Simberloff DS, Wilson EO. 1969. Experimental zoogeography of islands: the colonization of empty islands. Ecology **50**:278–296.

Singleton PH, Gaines WL, Lehmkuhl JF. 2002. Landscape permeability for large carnivores in Washington: a geographic information system weighted-distance and least-cost corridor

assessment. Res. Pap. PNW-RP-549. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, United States. 89p.

Stevens-Rumann C, Morgan P. 2016. Repeated wildfires alter forest recovery of mixed-conifer ecosystems. Ecological Applications **26**:1842–1853.

Stevens-Rumann CS, Kemp KB, Higuera PE, Harvey BJ, Rother MT, Donato DC, Morgan P, Veblen TT. 2018. Evidence for declining forest resilience to wildfires under climate change. Ecology Letters **21**:243–252.

Thom D, Seidl R. 2016. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. Biological Reviews **91**:760–781.

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, de Siqueira MF, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL, Williams SE. 2004. Extinction risk from climate change. Nature **427**:145–148.

Thomsen PF, Willerslev E. 2015. Environmental DNA - An emerging tool in conservation for monitoring past and present biodiversity. Biological Conservation **183**:4–18.

Turner MG. 2010. Disturbance and landscape dynamics in a changing world. Ecology 91:2833–2849.

Turner MG, Baker WL, Peterson CJ, Peet RK. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. Ecosystems **1**:511–523.

Turner MG, Romme WH. 1994. Landscape dynamics in crown fires ecosystems. Landscape Ecology **9**:59–77.

Turner MG, Romme WH, Gardner RH, William W, Turner MG, Romme WH, Gardner RH, Hargrove WW. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs **67**:411–433.

U.S. National Park Service. 2019. Species checklist for North Cascades National Park. Available from https://irma.nps.gov/npspecies/search/specieslist/noca (accessed July 1, 2019).

Urban MC. 2015. Accelerating extinction risk from climate change. Science **348**:570–573.

van Mantgem EF, Keeley JE, Witter M. 2015. Faunal responses to fire in chaparral and sage scrub in California, USA. Fire Ecology **11**:128–148.

Vanbianchi C, Gaines WL, Murphy MA, Hodges KE. 2018. Navigating fragmented landscapes: Canada lynx brave poor quality habitats while traveling. Ecology and Evolution **8**:11293–11308.

Vanbianchi CM, Murphy MA, Hodges KE. 2017. Canada lynx use of burned areas: conservation implications of changing fire regimes. Ecology and Evolution **7**:2382–2394.

Wan HY, Olson AC, Muncey KD, St. Clair SB. 2014. Legacy effects of fire size and severity on forest regeneration, recruitment, and wildlife activity in aspen forests. Forest Ecology and Management **329**:59–68.

Wang T, Hamann A, Spittlehouse D. 2017. ClimateWNA: A program to generate climate normal, annual, seasonal, and monthly data for historical and future periods in western North America. Version 5.50.

Wang T, Hamann A, Spittlehouse D, Carroll C. 2016. Locally downscaled and spatially customizable climate data for historical and future periods for North America. PLoS ONE **11**:1–17.

Wearn OR, Glover-Kapfer P. 2017. Camera-trapping for conservation: a guide to best practices. WWF Conservation Technology Series 1(1). WWF-UK, Woking, United Kingdom.

Welbourne DJ, Claridge AW, Paull DJ, Lambert A. 2016. How do passive infrared triggered camera traps operate and why does it matter? Breaking down common misconceptions. Remote Sensing in Ecology and Conservation **2**:77–83.

White EP, Baldridge E, Brym ZT, Locey KJ, McGlinn DJ, Supp SR. 2013. Nine simple ways to make it easier to (re)use your data. Ideas in Ecology and Evolution **6**:1–10.

Whitlock C, Shafer SL, Marlon J. 2003. The role of climate and vegetation change in shaping past and future fire regimes in the northwestern US and the implications for ecosystem management. Forest Ecology and Management **178**:5–21.

Whitlock MC. 2011. Data archiving in ecology and evolution: best practices. Trends in Ecology and Evolution **26**:61–65.

Whittaker RJ. 1972. Evolution and measurement of species diversity. Taxon **32**:213–251.

Wilson MFJ, O'Connell B, Brown C, Guinan JC, Grehan AJ. 2007. Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. Marine Geodesy **30**:3–35.

Zager P, Habeck J. 1983. Logging and wildfire influence on grizzly bear habitat in northwestern Montana. Pages 124–132 Bears: Their Biology and Management, Vol. 5. A Selection of Papers from the Fifth International Conference on Bear Research and Management, Madison, Wisconsin, USA, February 1980. International Association for Bear Research and Management, Missoula.