SHOULD I STAY OR SHOULD I GO? ASSESSING RANGE STASIS VERSUS RANGE SHIFTS OF PLANTS IN THE NORTH CASCADES

by

Rachel Wilson

B.Sc., Queen's University, 2014

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE AND POSTDOCTORAL STUDIES

(Botany)

THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

January 2017

Abstract

Under the pressure of anthropogenic climate change, species that are negatively impacted must rapidly respond or risk extirpation. The most immediate option for many species will be to track changing distributions of suitable habitat. Comparisons of contemporary data to historical baseline data indicate that climate change has already altered ranges and abundances of numerous species. Though general patterns are slowly emerging, there is still considerable variation in responses among species. Further, a number of species do not appear to be undergoing any change in their distributions or abundances, despite possible fitness costs of stasis. Given this variation, mechanisms underlying whether species shift or do not shift must be elucidated to allow for the creation of a predictive framework that can be extended to other systems. One way to achieve this end is to associate species functional traits with their magnitude of response. To detect elevational range shifts and changes in abundance of plant species, I and a team of surveyors resurveyed historical vegetation plots in North Cascades National Park. Since the original 1983 survey, the area has warmed by approximately 0.8 ° C. I then tested whether variation in range shifts among species could be associated with functional traits. Overall, most species exhibited range stasis. Of the species that initially appeared to exhibit a range shift, more than half were eliminated after accounting for fires and differences in survey effort between years. Species tended to decrease in abundance within their range, though this trend was often not significant. Predictions from trait models were inconsistent, depending on the modeling framework, the metric used for range shifts, and the inclusion of an outlying species. Range stasis was likely driven by dispersal limitation, but may have also resulted from acclimation, slow demographic processes, microclimate buffering of atmospheric temperatures by landscape features, or some combination of these and other factors. The variation in the degree of range shifts could not be explained satisfactorily by functional traits, casting doubt on their use in a general framework to predict future responses.

Preface

This thesis contains the original, unpublished work of the author, Rachel Wilson. The research program was designed by Dr. Amy Angert and Rachel Wilson. Field surveys were directed by Dr. Amy Angert, Dr. Christopher Kopp and Rachel Wilson with the assistance of Miquel Anglès-Marín, Jennifer Chen, Erin Fitz, Gabrielle Hindley, Peter Lambert, Laura Super, Erin Warkman, Derek Wiens, and Jecoliah Williams. Historical data were obtained with permission from Jim Agee.

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Acknowledgements

Heartfelt thanks to Dr. Amy Angert for her tireless support, invaluable expertise, and good humour in advising me through the ups and downs of a Master's degree. Thanks to Dr. Chris Kopp for advice, organizational skills in the field, and cooking a mean Dutch oven chicken. This work could not have been completed without the aid of an army of dedicated and talented field assistants: Miquel Anglès-Marín, Jennifer Chen, Erin Fitz, Gabrielle Hindley, Peter Lambert, Catriona Leven, Laura Super, Erin Warkman, Derek Wiens, and Jecoliah Williams. Many thanks to committee members Dr. Chris Harley and Dr. Greg Henry for their expert guidance and prompt responses to my frantic, statistics-related emails. Thanks to lab members past and present, official and honorary, for indispensable insight, advice, and commiseration: Matthew Bayly, Megan Bontrager, Barb Gass, Dr. Rachel Germain, Dr. Anna Hargreaves, Evan Hersch, Qin Li, Dr. Chris Muir, and Cora Skaien. Thanks also to Dr. Mary O'Connor for commentary on this thesis. I am grateful to Dr. Janneke Hille-Ris Lambers for support and guidance, and to her lab for helping me get acquainted with Pacific Northwest flora. I am also grateful to staff in the North Cascades National Park Service Complex for logistical assistance, accommodations, and access to their geodatabase of historical fires. Thanks to Dr. Jim Agee for undertaking the original survey work, without which this research would not have been possible, and for answering questions such as, "what are non-dimensional plots?" I am forever grateful for the support of my parents, Jack and Lauren, as well as my sister, Hannah, for their unflagging encouragement and ability to ask probing questions about the status of my degree. Thanks to my boyfriend, Alex, for supporting me through many adrenaline-fueled tirades about the fickle nature of R. And finally, thanks to countless individuals who supported me both socially and academically – you know who you are.

This research was generously funded by the National Sciences and Engineering Research Council of Canada, a Cordula and Gunter Paetzold UBC-Affiliated Fellowship, and a Mazamas Research Grant. This thesis has been supported by the TRY initiative on plant traits (http://www.try-db.org). The TRY initiative and database is hosted, developed and maintained by J. Kattge and G. Bönisch (Max Planck Institute for Biogeochemistry, Jena, Germany). TRY is currently supported by DIVERSITAS/Future Earth and the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig.

I dedicate this thesis to every pet in my life, past and present: cats Jasper (R.I.P.), Cleo (R.I.P.), Molly (R.I.P.), Jesse, and Nala; fish Mars (R.I.P.), Zephyr (R.I.P.), Blue Moon (R.I.P.), Noodle (R.I.P.), Spike, and Spock; and several nameless plants (mostly, R.I.P.).

Chapter 1: Introduction

Understanding and predicting biological responses to anthropogenic climate change is a pressing goal in ecology. At the current rate of climate change, as many as one in six species globally are likely to face extinction (Urban 2015), and a number of species extinctions have already been directly or indirectly attributed to climate change (Pounds et al. 2006, Sinervo et al. 2010, Cahill et al. 2012, Gynther et al. 2016). Under this urgent threat, species negatively impacted by climate change must be able to rapidly respond in order to persist on the landscape (Jump and Penuelas 2005). Viable responses include swiftly adapting or acclimatizing to novel climate. Species may also respond by dispersing from newly unsuitable habitat into unchanged or newly suitable habitat, possibly leading to range expansions or contractions (i.e., shifts) on a larger scale. For ranges determined primarily by climate, tracking of suitable habitat should be largely limited by dispersal ability of the species, but if ranges are also determined by biotic factors, unanticipated patterns of shifts may arise. Regardless, given that the rapid pace of climate change may negate the ability of all but the most short-lived or plastic species to adapt or acclimatize, the immediately viable option for many species will be to track suitable habitat by shifting their range. Preliminary but widespread change in the ranges and abundances of species have already been documented, with measurable consequences for community structure and functioning (Walther et al. 2002, Parmesan 2006, Damschen et al. 2010, Elmendorf et al. 2012b). However, there appears to be considerable heterogeneity in responses among species and systems, and much of this variation is unexplained (Angert et al. 2011). As climate change continues to progress, attempting to manage biological responses requires rigorous projections

for the likely direction and magnitude of these responses among species and, more generally, among functional groups.

A common method for predicting how distributions will respond to climate change is to model a species probability of occurrence on the landscape given some combination of climatic variables, and then to model predicted distributions based on likely alterations of those variables under climate change scenarios (Iverson and Prasad 2001, Elith and Leathwick 2009). The ability of these distribution models to accurately predict species future distributions has been questioned (Pearson and Dawson 2003), prompting tests of existing models (Araújo et al. 2005, Pearman et al. 2008) and the development of more realistic models (Boulangeat et al. 2012). However, many models attempting to forecast distributions still ignore important factors such as overlap between a shifting species and novel competitors (Alexander et al. 2015), the role of pollen dispersal in facilitating adaptation and slowing range expansion (Aguilee et al. 2016), and habitat modification (Archaux 2004). These factors and others may give rise to lagged responses or counterintuitive patterns of movement such as downslope elevational range shifts (Lenoir et al. 2010). Another approach has been to experimentally warm communities in the field and measure responses (Walker et al. 2006, Elmendorf et al. 2012a). The ability of these experiments to predict climate change responses has been variable. Comparisons of warming experiments to long-term observational records suggest that experiments may under-predict phenological advances in response to warming (Wolkovich et al. 2012), but Elmendorf et al. (2015) found that experimental community responses were in good agreement with long-term observations.

Ultimately, the only way to reliably test the validity of predictions is to wait for the species to respond, which is obviously not practical from a conservation standpoint. As such, historical surveys of presence and abundance of species provide an invaluable baseline against which to

measure shifts that have already occurred due to recent climate change (Vellend et al. 2013). Ideally, these recent shifts can be used to predict future responses with the greatest degree of accuracy available to us. There are numerous challenges associated with resurveying historical plots, such as the ability to relocate plots, taxonomic discrepancies, and outdated surveying methods (Vellend et al. 2013). Despite this, a considerable number of resurveys of historical plots have been undertaken. Often, the goal of these surveys is to characterize responses of community composition to climate change or anthropogenic disturbance (for example, Rogers et al. 2009, Keith et al. 2009, Damschen et al. 2010). More rarely, the historical plots covered sufficient latitudinal or elevational breadth for modern surveyors to assess changes in species ranges (for example, Lenoir et al. 2008, Moritz et al. 2008, Tingley et al. 2012, Ash et al. 2016). In general, many surveys report an overall trend of species shifting higher in latitude or elevation, in accordance with the expectation that increasing temperatures will improve suitability at upper range edges and decrease suitability at lower range edges (for example, Beckage et al. 2008, Kelly and Goulden 2008, Lenoir et al. 2008). However, a number of species do not follow these patterns and vary in their magnitude and direction of responses (Angert et al. 2011). Observational and experimental abundance responses to warming have also been shown to vary among functional groups, such that forbs and shrubs tend to respond positively while mosses, ferns and lichens tend to respond negatively (Walker et al. 2006, Elmendorf et al. 2012b). These idiosyncratic responses present a significant challenge to making general predictions of distributional shifts under climate change.

Most surprisingly, many species have shown little to no change in distribution or abundance. These species are rarely the focal point of publications, even if the majority of sampled species appear to show no measurable climate change response (for example, Wolf et al.

2016), so the frequency of this response may be overlooked. However, a number of resurveys have reported no response or a response lagging behind the pace of climate change, particularly among trees (Bertrand et al. 2011, Forero-Medina et al. 2011, Zhu et al. 2011, Devictor et al. 2012, Ash et al. 2016). An absent response (hereafter referred to as stasis) may be driven either by "resistance", referring to internal or external factors that buffer the immediate fitness consequences of climate change, or time lags that create delayed susceptibility to climate change. Resistance may be conferred by the ability of a species to rapidly acclimatize or adapt (Jump and Penuelas 2005), or by having a broad thermal niche, the extremes of which extend beyond current conditions (Sunday et al. 2012). Additionally, buffering of atmospheric warming by geologic features or dense forest may create cooler microhabitats for sheltered species, negating the need for a measurable climate change response (De Frenne et al. 2013, Frey et al. 2016). Stasis driven by time-lagged susceptibility is more concerning from a conservation perspective, as it may arise if slow demography (for example, that of trees) prevents immediate population extinctions at the trailing edge. Slow demography may also delay colonization at the expanding edge, though long-distance dispersal or increasing their reproductive effort may compensate for this. Colonization at the expanding edge may also be delayed if established species are generally able to outcompete newcomers (Bjorkman et al. 2016) or if species are dispersal-limited (Schloss et al. 2012).

Given the variation in responses, a simple, predictive framework is urgently needed so that management decisions can be informed with a high degree of accuracy and a negligible expenditure of resources. One way to achieve this end is to associate species functional traits with known responses (i.e., those measured from a historical baseline), then extrapolate those responses to other species possessing similar traits. Functional traits have been increasingly

employed in attempts to produce general principles and predictions for ecology (Westoby and Wright 2006, McGill et al. 2006), leading to the expansion of data available through online databases (for example, the TRY database; Kattge et al. 2011). Predictions for how traits relate to range shifts may be drawn from invasion biology, as certain traits are likely to influence both invasions and range shifts via their effects on colonization or persistence. For example, species with a high dispersal capacity may be more likely to colonize new habitat, and highly dispersive individuals often characterize populations at the leading edge of invasions (Simmons and Thomas 2004). As such, species with traits enhancing dispersal may be more likely to undergo range shifts. Similarly, propagule pressure, or the number of offspring released into the environment, increases the likelihood of colonization during invasions by increasing the number of dispersal events (Simberloff 2009). Species with high fecundity and frequent reproductive bouts may therefore be better able to shift their range. Ecological generalization is also likely to aid species in range shifts, since generalists may be better able to persist in novel habitat and take advantage of diverse resources.

Despite well-developed predictions for how traits may relate to range shifts (Aubin et al. 2016), support for the ability of traits to predict observed responses to climate change is highly conflicting among and even within studies. Generalizing is further complicated by the fact that studies often use slightly different metrics to quantify range shifts. Early research suggested that individual traits may associate with range shifts in some cases (Perry et al. 2005, Dulvy et al. 2008, Lenoir et al. 2008, Pöyry et al. 2009) but not others (Hill et al. 2002, Moritz et al. 2008, Forero-Medina et al. 2011). For example, a synthesis of four resurvey studies of plants, birds and mammals by Angert et al. (2011) found that a few traits did associate with range shifts for each taxonomic group. However, even multivariate trait models generally had low power to explain

variation among shifts (Angert et al. 2011). A review by Buckley and Kingsolver in 2012 found only ten published records of attempts to relate traits to range shifts, four of which were undertaken by Angert et al. (2011), with poor agreement of trait predictive ability among and within taxonomic groups. More recent studies have often found that one or more traits can associate with range shifts, though some studies do not evaluate the explanatory power of trait models (Betzholtz et al. 2012, Reif and Flousek 2012, Feary et al. 2013, Powney et al. 2014, Sunday et al. 2015, Aguirre-Gutiérrez et al. 2016). Others have found the relationships to be weak (Zhu et al. 2011, Ash et al. 2016) or counter to theoretical expectations (Tingley et al. 2012). Only five studies have used resurvey data across a distributional gradient to relate traits to range shifts for plants, all of which occurred in the Swiss alps, the Eastern U.S., or Britain, and only two of which assessed elevational gradients (Lenoir et al. 2008, Angert et al. 2011, Zhu et al. 2011, Powney et al. 2014, Ash et al. 2016). Given the confusing picture that arises when comparing among and even within study systems and taxonomic groups, much more replication and expansion to other systems is needed, with range shifts quantified using a variety of metrics and numerous traits tested for associations.

In this thesis, I aim to use resurvey data to characterize range and abundance shifts of Pacific Northwest plants in response to recent climate change, then relate functional traits to five different metrics of range shifts. To achieve this, I and a team of surveyors relocated historical vegetation plots in and around the North Cascades (NOCA) National Park Service Complex in Washington, USA (Fig. 1.1). These plots were originally surveyed in 1983 and are ideal for detecting elevational range shifts, as they encompass a wide range of elevations (162 m – 2122 m), show considerable topographic variation, and are supplemented by detailed notes from the original surveyors (Agee and Kertis 1987). Further, the area has experienced approximately a 0.8

° C increase in warming since the original survey (based on unpublished analyses conducted in ClimateWNA; Wang et al. 2012), a temperature change equivalent to descending approximately 125 m in elevation. We resurveyed these plots in a manner parallel to the original survey, then constructed historical and contemporary distributions of the presence of 42 species plus the functional group moss. We also assessed temporal change in species abundances within their ranges. To determine whether functional traits might predict range shifts, I assembled data on dispersal syndrome, growth form, leaf texture, plant height, shade tolerance, specific leaf area, and seed mass from the TRY database (Kattge et al. 2011) and supplemented those data by collecting trait measurements in the field and collating from other sources. I then tested whether magnitude of species shifts associate with their traits. I also evaluated whether associations vary among different range shift metrics in magnitude or direction.

I expect my findings to generally support those of other elevational resurveys, such that species show variation in their magnitude and direction of responses. On average, however, I suspect that (1) most species will tend to shift their range higher in elevation, and (2) shrubby species will tend to increase in cover while ferns and moss will tend to decrease in cover. Considering the variable conclusions from the literature, I tentatively hypothesize that (3) traits will only weakly associate with climate change responses, though traits strongly affecting colonization ability or persistence in novel habitat may show some importance. Colonization ability may be affected by: dispersal syndrome, such that dispersal strategies involving wind (anemochory), animal consumption (endozoochory), or sticking externally to animals (epizoochory) have greater potential for long-distance dispersal than passive dispersal (barochory); seed mass, in which smaller seeds may be more easily carried by dispersal vectors; plant height, such that seeds released from a greater height are more likely to travel farther; and

growth form, where groups with faster generation times may undergo more colonization events. Persistence in novel habitat may be affected by traits known to directly or indirectly associate with ecological generalism or competitive ability, such as: leaf texture, such that species with fine-textured leaves may be more susceptible to herbivory than competitors (Cornelissen et al. 1999); plant height, for example that taller species may outcompete smaller ones for light; shade tolerance, such that intermediately tolerant species may be able to capitalize on a greater variety of niches; specific leaf area, such that photosynthetic rates increase with increasing SLA (Reich et al. 1997); and seed mass, where heavier seeds may reflect improved maternal provisioning and increased likelihood of establishment. Ultimately, my thesis aims to add to the relatively scarce literature relating traits to range shifts and to characterize climate change responses of flora in the Pacific Northwest of North America. These responses and their trait associations could be used to predict future change.

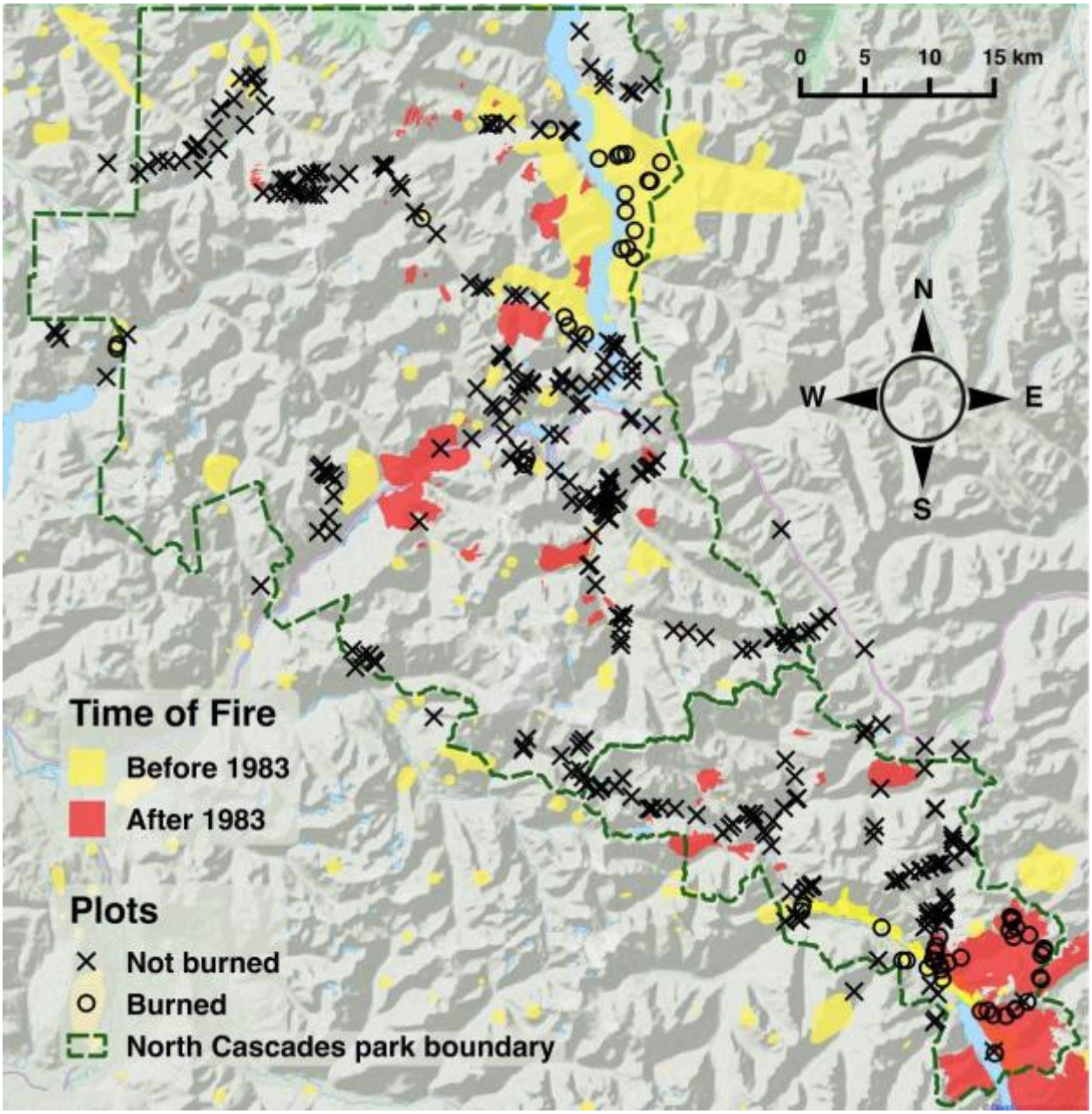

Figure 1. Location of legacy plots in North Cascades National Park (boundary shown in dashed green) in relation to historical fires. Yellow polygons indicate areas that burned prior to 1983 and red polygons indicate areas that burned after 1983. Plots that overlap with historical fires are drawn with O's and plots that were never burned are drawn with X's. Blue polygons represent lakes and rivers. Map created in QGIS version 2.14.3-1 using OpenStreetMap as the topographic base layer.

Chapter 2: Should I stay or should I go? Assessing range stasis versus range shifts of plants in the North Cascades

2.1 Synopsis

In 2014 and 2015, I and a team of surveyors resurveyed historical vegetation plots (established and sampled in 1983) to detect temporal changes in plant elevational ranges and abundances. Plots were surveyed using methods analogous to the original survey to allow for direct comparisons between years (Agee and Kertis 1987). At each plot, presence and percent cover (abundance) were recorded for understory species. Elevations were then associated with plots to create elevational distributions of species presence/absence and abundance.

Change in species elevational distributions were quantified both as "raw" shifts (i.e., absolute change in range edge based on highest- or lowest-elevation presence in each survey year) and "modelled" shifts. Modelled shifts were measured from temporal change in predicted probability of presence based on elevation, elevation^2, survey year, survey year*elevation, survey year*elevation^2, and fires (see below). Top models (ΔAIC < 2) predicting species probability of presence were averaged based on Akaike weight, and species whose model-averaged coefficients included an interaction between survey year and elevation were interpreted as likely to have exhibited a range shift. Shifts in range edges and elevations of peak presence were also calculated for each species based on their AIC-averaged model. I then assessed whether percent cover of species varied between survey years using a similar AIC model selection framework.

Although the region has experienced ~0.8 °C of climate warming since 1983 (climateWNA; Wang et al. 2012), temporal changes may not be entirely attributable to climate change. First, many more species were detected in 2014/2015 surveys than in 1983 surveys, suggesting an overall greater ability of 2014/2015 surveyors to detect presence of species. To account for this difference, 2014/2015 survey data were rarefied and presence analyses were repeated, then compared to results from unrarefied data. Second, numerous plots have historically experienced fires. To account for this, fire history of the plot was included as a covariate in models of species presence and cover. I also assessed whether fire interacted with year to affect probability of presence or percent cover for each species.

I was additionally interested in the ability of species functional traits to associate with magnitude and direction of range shifts. For all my species of interest, I downloaded data on traits (dispersal syndrome, growth form, leaf texture, plant height, shade tolerance, specific leaf area, and seed mass) from the TRY database (Kattge et al. 2011). As a number of traits were not measured for my focal species, I supplemented the TRY data using values from the literature and my own measurements from the field. Traits were then tested for the ability to predict five different range shift metrics in both a univariate and multivariate context.

Across range metrics, most species did not show strong evidence of range shifts, though there was some variation in magnitude and direction of shifts among species. Of the few species that did exhibit shifts, over half were no longer characterized as such after rarefying and accounting for fire. Most species appeared to decrease in cover between survey years, though these models often had low explanatory power. Univariate and multivariate analyses of associations between traits and shifts were inconsistent among range metrics, and removing an outlying species substantially altered any definitive patterns. Ultimately, overwhelming range

stasis and a trend of abundance decreases suggest many species are suffering fitness consequences of climate change within their ranges, but are limited in their ability to disperse to mitigate these consequences. Furthermore, traits cannot reliably explain what little variation was observed.

2.2 Methods

2.2.1 Field resurveys

My colleague, Dr. Christopher Kopp, and I led two survey teams (each including 2-4 assistants) to resurvey 374 legacy vegetation plots in the NOCA (Fig. 1). Originally surveyed in 1983, these plots were ideal for resurvey as they encompassed a wide range of elevations and topographic variation and were supplemented by detailed notes from the original surveyors (Agee and Kertis 1987). Furthermore, the region has experienced an increase of ~0.8°C in mean annual temperatures since the original survey, while mean annual precipitation has not changed (climateWNA; Wang et al. 2012).

We resurveyed 60 plots from mid-July 2014 to August 2014 and resurveyed the remaining plots from June 2015 to September 2015. Plots surveyed each year were chosen to span a range of elevations to ensure that inter-annual variation was not confounded with elevational variation. Sampling methods were designed to be analogous to the 1983 survey (Agee and Kertis 1987; Agee 2014, pers. comm.), with two exceptions. First, the original survey consisted of circular plot ranging in size from 25 – 400 m^2 depending on stand density, while our circular plots were uniformly 500 m^2 in size. However, we recorded trees as occurring either inside or outside of the historical plot radius to allow for direct comparison with historical data. Second, the original survey assessed cover within a 50 m^2 circle (Agee 2014, pers. comm.), whereas we assessed

cover within four 1 m^2 quadrats. These differences were necessary to allow comparison between our resurvey and a parallel resurvey in Mount Rainier National Park.

We relocated historical plots using Universal Transverse Mercator (UTM) data transferred from pencil dots on paper maps by the NOCA National Park Service and site descriptions provided by the original surveyors. In the absence of permanent, on-site markers, some uncertainty in relocating plots remained. However, as I am focusing on elevational distributions of species and not plot-specific comparisons (e.g., richness), this uncertainty is unlikely to affect my results. Furthermore, other resurveys have been shown to be robust to relocation error (Kopecký and Macek 2015).

Once we reached the approximate historical plot area, we established the plot centre haphazardly by throwing a flag and recorded its coordinates using a GPS device (GPSmap76CSx). The 500 m^2 plot was established by using an electronic distance-measuring tool (Sonin 10300) to measure a radius of 12.62 m from the plot centre. We placed flags in each cardinal direction at this distance (Fig. 2). The radius of the historical plot was also marked with flagging tape in each cardinal direction to help distinguish whether trees fell inside or outside the historical plot. Photographs were taken at each outmost flag facing the plot centre to help future researchers relocate our plots. We recorded slope and aspect using an inclinometer and compass. Since some plots were historically subject to logging and forest fires, we noted evidence of natural and anthropogenic disturbance, such as charring or cut trees.

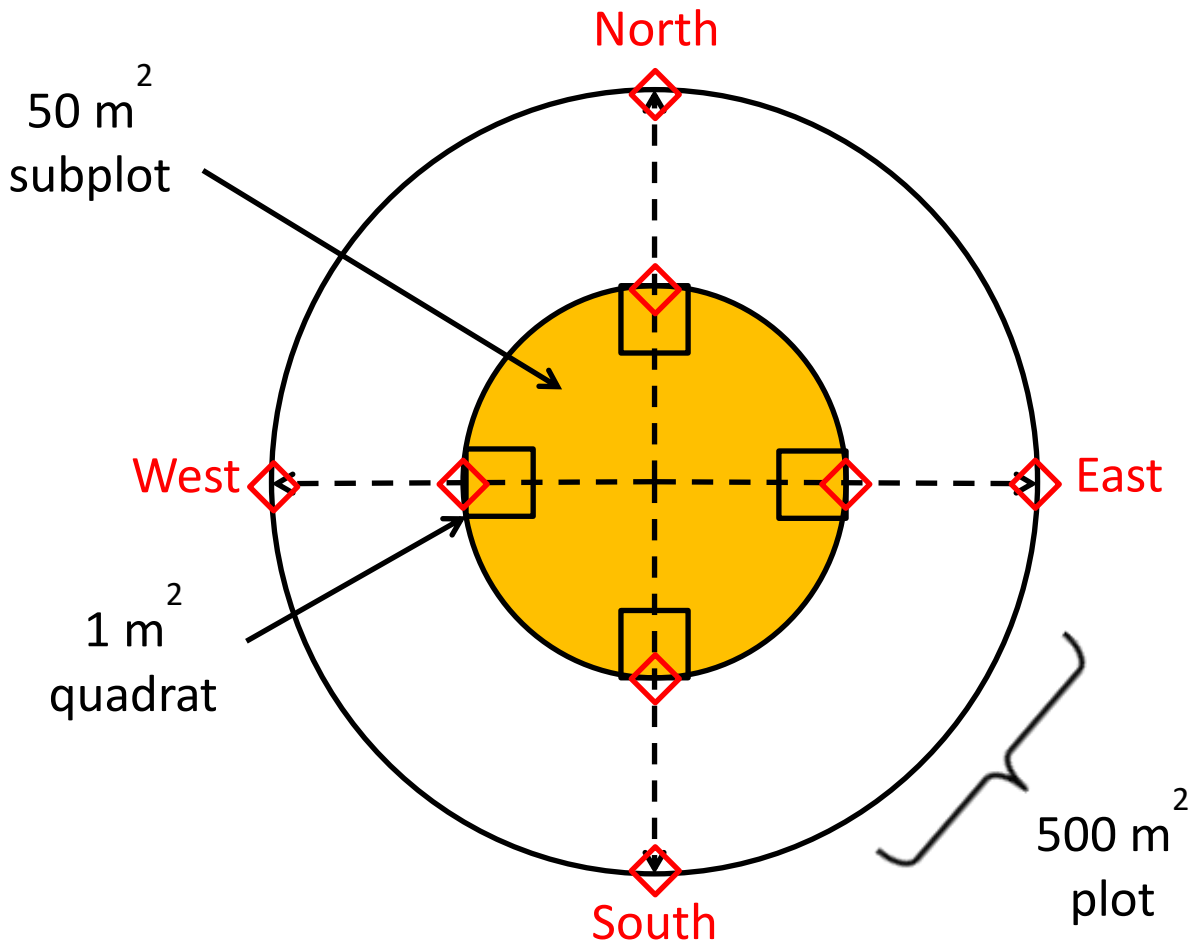

Figure 2. Schematic showing setup of resurvey plots. Flags (red diamonds) were placed in each cardinal direction at distances of 12.62 m and 3.98 m from the plot centre. Trees were surveyed within the 500 m^2 plot (white and yellow circles), understory species were surveyed within the 50 m^2 subplot (yellow circle), and understory species cover and tree seedling tallies were surveyed within the 4 x 1 m^2 quadrats (yellow squares).

After the plot was established, we surveyed understory and tree species. Note that the analysis of tree data was beyond the scope of this thesis, but I describe the sampling procedure here anyway for transparency and completeness. Trees taller than 1.4 m whose centre fell within the 500 m^2 plot area were identified and measured for diameter at breast height (DBH). We additionally recorded whether these trees fell inside or outside the historical plot radius. Next, a

circular subplot of 50 m^2 was established by placing flags at a distance of 3.98 m from the centre in each cardinal direction (Fig. 2). Within this subplot, we recorded the presence of understory vascular plant species and moss (as a functional group, not identified to species). Finally, 1 m^2 quadrats were set up at each of the 4 flags marking the 50 m^2 subplot (Fig. 2). We recorded percent cover of understory species and moss within each of the four quadrats. Since estimations of percent cover can vary among individuals, percent cover was assessed by more than one person for each of the first several quadrats until estimations became consistent among all observers. We also identified and counted tree seedlings within each quadrat, defining seedlings as trees less than 1.4 m tall. From this point forward, I will focus on the understory species data.

2.2.2 Curation and collection of trait data

Traits hypothesized to directly or indirectly affect species elevational shifts (see *Changes in presence*) were downloaded from the TRY database on June 6, 2016 (Kattge et al. 2011). In total, seven traits (dispersal syndrome, growth form, leaf texture, plant height (m), shade tolerance, specific leaf area (SLA; mm^2/mg), and seed mass (mg)) were assessed. A number of species had not been measured for my traits of interest, so I filled gaps wherever possible using published materials. I also incorporated observations, collections and measurements I made during the summers of 2015 and 2016 (details in Appendix A). Traits were condensed to a single value per species. For categorical variables, species were assigned their most commonly reported classification across TRY datasets. For numerical variables, a mean was calculated among all measurements. In cases of species redundancy between my collected data and TRY data, I used my data only. Although this potentially overlooks relevant intraspecific variation, my data were based on samples collected from plants at or near my study sites, and are therefore more likely to

be relevant to my study. Moss was excluded from all trait analyses, as few traits can be confidently assigned to such a general group.

2.2.3 Statistical analyses

All analyses were conducted in R (version 3.3.1). I first adapted the 2014/2015 measurements to be directly comparable with 1983 data (see *Data manipulation*). I accounted for confounding disturbances (see *Controlling for disturbance*). Next, I associated plot locations with elevations, then constructed elevational distributions for species at both timepoints to detect range shifts (see *Changes in presence*). 2014/2015 data were rarefied to account for increased resurvey effort relative to the historical survey (see *Rarefaction*). I also assessed change in species abundance between surveys (see *Changes in cover*). Finally, I associated functional traits with species magnitude of shifts (see *Traits*).

2.2.3.1 Data manipulation

The 1983 survey assessed species cover per plot in six unequally divided classes (0.1-5%, 5-25%, 25-50%, 50-75%, 75-95%, and 95-100%) for one sample area, whereas the 2014/2015 survey assessed cover to the nearest 1% in four quadrats. To standardize the 2014/2015 covers to the 1983 covers, I averaged a given species cover among our four quadrats and then assigned this value to its corresponding 1983 cover class, repeating this process for all species in all plots. If a species was present only in our 50 m^2 subplot but not in the four quadrats, then I included it in analyses of presence/absence but excluded it from cover analyses. Elevations associated with 2014/2015 plot coordinates were obtained from Google Earth (version 7.1.5.1557) and assigned to corresponding 2014/2015 and 1983 plots to create elevational distributions. Finally, a set of focal species were selected from the total set of species. As the goal of this study was, in part, to assess changes in species distributions, I excluded any species with fewer than 10 occurrences in

either survey, resulting in a focal set of 42 species plus moss (Table D1). This safeguarded against the possibility that any changes observed in a species range were due to sampling error alone. Non-native species, putative hybrids, and species that were unable to be classified beyond genus were also excluded.

2.2.3.2 Controlling for disturbance

Because a number of plots were subject to prior disturbances, some of the observed changes between survey years may be successional and unrelated to climate change. For example, two plots were inferred to have a history of clearcutting based on uniform stand age, proximity to logging roads, and observations from the 1983 surveyors. These plots were excluded from the final set of plots for analysis. A more difficult confounding factor was fire, to which numerous plots had historically been subjected. It was important to distinguish between fires occurring before the 1983 survey and after the 1983 survey. For example, old growth forest that experienced a severe fire after the 1983 survey would appear to have progressed "backwards" in successional time upon resurvey, whereas the same forest burned before the 1983 survey would appear to have progressed "forwards". Either may confound estimates of a given species climate change response, depending on whether that species is positively or negatively affected by fire or climate change.

To account for the effect of fires, a geodatabase containing polygons of natural and human-prescribed fires was obtained from the National Park Service and joined to plot coordinates in QGIS (version 2.14.3-1). Plots were categorized as unburned, burned before 1983, and burned after 1983. The year of most recent fire was used for the few plots that burned multiple times. Fire was then included as a covariate in analyses of species presence and cover.

2.2.3.3 Changes in presence

Range shifts are here defined as temporal change in a species probability of presence as a function of elevation. Describing range shifts of species can be challenging, as shifts may be measured as shifts in elevation of the peak probability of occurrence of a given species, or expansion or contraction at a species upper range edge, lower range edge, or both edges. Furthermore, detecting the position of range edges is sensitive to sampling effort and species detectability. To account for this complexity, I quantified range shifts as (1) range edge displacement in metres at upper and/or lower range edges, with range edges defined from a species highest and lowest recorded elevations in each survey period; and (2) in a formal modelling context to detect whether a year*elevation interaction affected probability of presence.

Upper range edge displacement for a given species was measured by subtracting that species highest historical occurrence from its highest contemporary occurrence. For example, a positive value would indicate a shift upwards in the range boundary (i.e., a range expansion at the upper edge). Lower elevational range displacement was calculated in a similar manner, such that a positive difference would indicate a range contraction at the lower edge. These values will be referred to as "raw" shifts from this point onwards.

Range shifts were also more formally quantified using a generalized linear model (glm) with a binomial distribution testing for the effect of elevation, elevation^2, year, fires, year*elevation interaction, and year*elevation^2 interaction on a given species probability of presence. A subset of "top" models (those having Δ Akaike Information Criterion < 2; Burnham and Anderson 2002) were obtained from the full set of possible models. Pseudo-R-squared based on McFadden's log likelihood was calculated for each top model. To obtain model-averaged coefficients, I calculated Akaike weights for each top model, multiplied by each coefficient in

that model, and then summed across models for each coefficient (Burnham and Anderson 2002). Variables not present in models were assigned a value of zero before summing across models to avoid inflating the Akaike weights of rarely-included coefficients. I interpret species whose model-averaged coefficients include a non-zero year*elevation interaction term to be likely to have undergone a range shift, such that their probability of presence as a function of elevation has changed through time.

To shape modelling results into a format more analogous to the raw shifts, I also calculated range edge displacement from my modelled predicted values. In this framework, range edges were considered to be the elevation at which the predicted probability of a species presence dropped below 0.05 in a given model. For each top model, elevations corresponding to predicted upper and lower range edges were calculated for 1983 and 2014/2015, then the difference between years was taken following the raw shift framework above. This yielded upper and lower edge displacement for each top model. If presence did not drop below 0.05 at a given edge, that edge was assigned the elevation of the lowest or highest survey plot. Similarly, if the top model did not include an effect of year, lower and upper edges were assigned the elevation of the lowest and highest survey plot. The elevation at which a given species had the greatest probability of presence was also calculated for each survey year, then the difference was calculated. This yielded peak-presence displacement for each top model. For models not including an effect of year, peak-presence was assumed to be the mean elevation of plots at which the species was present. Finally, these upper and lower range edge displacements and peak-presence displacements were weighted by the associated model's Akaike weight and summed across models. These values will be referred to as "modelled" shifts from this point onwards. Ideally, this approach controls for situations in which one far-outlying occurrence causes the measured

raw shift to be greatly inflated. Furthermore, the correlation between raw and modelled shifts was significant but less than 0.7 (upper: Pearson's $r = 0.56$, $P = 0.0001$; lower: Pearson's $r = 0.34$, $P = 0.03$), indicating that analyzing both raw and modelled shifts is not redundant. To assess magnitude and direction of change overall, among-species means of the raw lower edge displacement, raw upper edge displacement, modelled lower edge displacement, modelled upper edge displacement, and peak-presence displacement were calculated. One-sample t-tests were used to assess whether most species have expanded, contracted, or remained unchanged at either range edge for raw or modelled range metrics. A one-sample t-test was also used to test whether species have shifted in their point of peak presence.

2.2.3.4 Rarefaction

Many more species were detected in the 2014/2015 surveys compared to the 1983 survey (210 species and 356 species, respectively; refer to Results – *Rarefaction*). In particular, small or hard-to-see species tended to be recorded in many more 2014/2015 plots than in the 1983 survey. The enhanced ability of 2014/2015 surveyors to detect species may increase the likelihood of erroneously describing range expansions at either edge, as many species tend to be sparsely distributed at range edges; these edge individuals may have been overlooked in 1983, yet detected in 2014/2015 surveys. To compensate for this problem, I rarefied the 2014/2015 data, recomputed all analyses, and compared results from rarefied to unrarefied datasets.

A subset of species consisting of those common to both surveys were used for rarefaction analysis, excluding non-native species, hybrids, and species not identified beyond the family level. Among these, mean richness per plot was calculated for the 1983 survey and the 2014/2015 survey. Note that here I include individuals classified to the level of genus, whereas I excluded these individuals when compiling the set of focal species. While genus-level

classifications of individuals may mask true species richness per plot only rarely, it is possible that they more frequently underestimate species richness across the scope of each survey. For example, a low-elevation and high-elevation species pair belonging to the same genus will rarely occur in the same plot, but an inability to distinguish between the two will result in only one genus-level record across the full scope of the survey, and will also mask range shifts experienced by either species. For that reason, genus-level IDs were excluded from the focal set of species for analysis, but included when generally estimating species richness in and among plots. The difference in mean richness per plot between surveys was considered to be a proxy for the difference in survey effort, and so was used as the number of species to be randomly removed from each 2014/2015 plot. A species probability of random removal from the plot increased with decreasing percent cover recorded at that plot in 2014/2015, such that rare or otherwise hard-to-see species were more likely to be discarded during rarefaction. Species recorded in the 50 m^2 subplot only were assumed to be rare and so were assigned a proxy cover of 0.1%, though this likely underestimates the abundance of large, patchily distributed species. *Acer circinatum* and *A glabrum* were only measured for DBH in 2014 surveys and so did not have cover values associated with those plots. As a proxy, I calculated the mean cover among plots in 2015 for both *A. circinatum* and *A. glabrum* and assigned those cover values to the 2014 plot occurrences.

To perform the rarefaction, species were randomly removed from each 2014/2015 plot using the "sample" function, incorporating percent cover as a probability weight. For plots containing as many as or fewer than the designated number of species for removal, no species were removed. The new, rarefied 2014/2015 dataset was then joined to the original 1983 dataset and analyzed following the previously-described procedure (see *Changes in presence*),

ultimately producing model-averaged coefficients for each species. The rarefaction and subsequent analysis were repeated 100 times, giving each species 100 sets of model-averaged coefficients. Finally, for each species, the median value and the 5th and 95th percentiles of the set of rarefied coefficients were compared to the original, un-rarefied coefficients.

2.2.3.5 Changes in cover

As cover was recorded in unequally-sized classes, with each class representing a range of possible values (see *Data Manipulation*), I used interval regression (package "survival"; Therneau 2014) to test for an effect of elevation, elevation^2, survey year, fires before and after 1983, year*elevation interaction, and year*elevation^2 interaction on species cover. Interval regression is appropriate when analyzing variables with distinct upper and lower bounds but exact values are unknown.

First, all possible models incorporating elevation, year, fire, and/or a year*elevation interaction were computed. This full set of models was reduced to a subset of top models with ΔAIC < 2. Pseudo-R-squared for each model was calculated from the correlation between each model's predicted cover values and the true cover values. Since true cover values were intervals rather than discrete values, the interval's midpoint was used in the calculation of pseudo-R-squared. Model-averaged coefficients were calculated following the previously described procedure (*Changes in presence*). I interpret species whose model-averaged coefficients included an effect of year or a year*elevation interaction as likely to have responded to climate change. Unlike interpretations of the range shift models, year alone is also considered to be of importance here, as increases or decreases in abundance may occur irrespective of elevation as a result of climate change. Rarefaction was not performed on the cover data, as the 2014/2015 survey bias arguably lies in detectability and not cover assessment. However, this leaves the possibility that

the 2014/2015 survey recorded greater cover of species growing underneath other species, which may inflate 2014/2015 abundance measures.

2.2.3.6 Traits

First, using univariate linear models, I tested for the ability of individual traits to predict range shifts among species. A total of five metrics for range shifts were used: (1) raw lower edge displacement, (2) raw upper edge displacement, (3) modelled lower edge displacement, (4) modelled upper edge displacement, and (5) modelled peak-presence displacement. Each of these five metrics were assessed for a relation with each of the seven previously described traits. A Bonferroni-adjusted significance threshold was used to correct for multiple comparisons (Dunnett 1955).

Next, a multivariate analysis was performed in an AIC model-selection framework to assess which combinations of traits best predict range shifts. Most traits were missing values for a few species, which was problematic as the AIC framework cannot incorporate missing values. After excluding plant height, which contained the most missing values, the total number of species for which all traits were available was 28 (reduced from 42, and moss was not included). Dispersal syndrome was also excluded from multivariate analyses as it was nearly perfectly collinear (aliased) with growth form (for example, all ferns were anemochorous). Generalized variance inflation factors (GVIFs) were calculated to assess for collinearity among the remaining set of predictors (growth form, leaf texture, shade tolerance, seed mass, and SLA) and were concluded to be acceptable (Table D2; package "car"; Fox and Monette 1992, Fox and Weisberg 2011); additionally, correlation among numerical variables was found to be acceptably low (Pearson's $r < 0.7$). AIC corrected for small sample sizes (AICc) was used to rank models. Models were restricted to include no more than three predictor variables (approximately one-

tenth the sample size). Top models (delta AIC < 2) were identified using the "dredge" function and model averages were calculated using the "model.avg" function (package "MuMIn"; Bartoń 2016).

2.3 Results

2.3.1 Changes in presence

Among 42 focal species and moss, mean raw shift at the lower edge was marginally significantly less than zero ($P < 0.1$), although there was considerable variation (mean: -32.4 m ± 38, minimum: -376 m, maximum: 216 m; Fig. 3a). Mean raw shifts at the upper edge did not differ from zero among species, though a few species exhibited a substantial contraction or expansion (mean: 13.0 m ± 59, minimum: -544 m, maximum: 669 m; Fig. 3b).

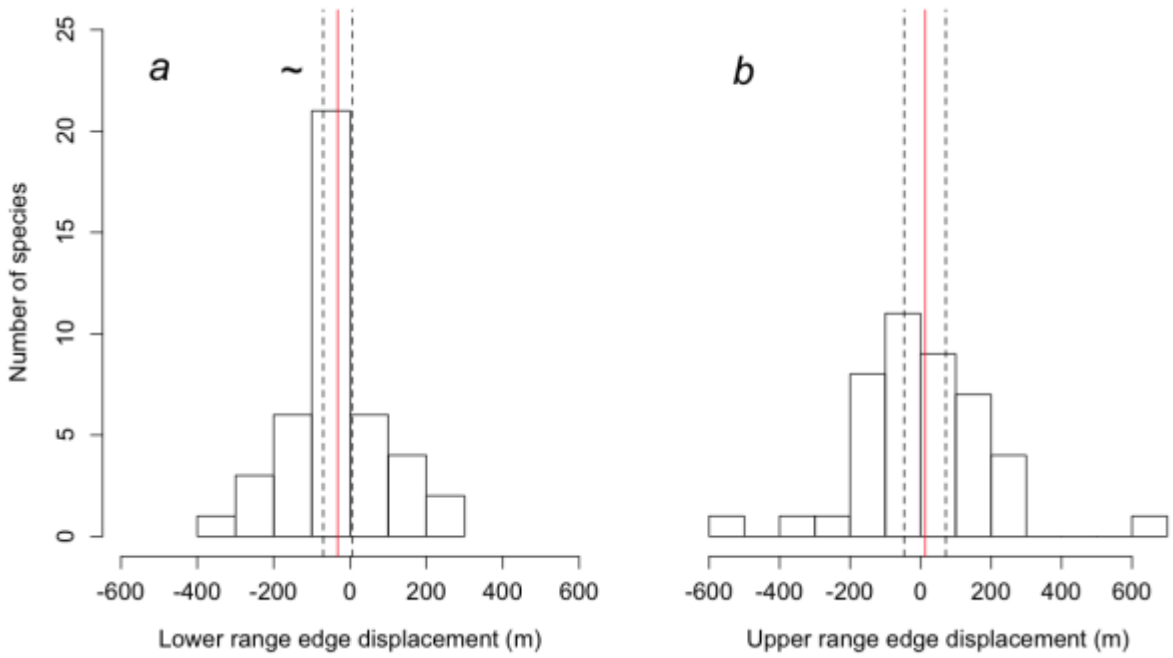

Figure 3. Raw edge displacement among species at the (a) lower and (b) upper range edge. Mean displacement among species is indicated by the red line. Confidence intervals from a one-sample t-test are indicated by the black dashed lines. ~ indicates a marginally significant trend ($P < 0.1$).

Formal modeling revealed similar patterns, with only 15 of 42 species and moss including a year*elevation interaction term in their set of top models (Table 1). Explanatory power of models varied considerably among species (Table D3). Of the species that showed evidence of range shifts (those that included a year*elevation interaction term), direction and magnitude of responses were highly variable (Fig. 4) and only 5 species interaction coefficients were significant predictors of presence in their respective models (Table D3). Furthermore, the range shift observed for *Chamerion angustifolium* was found to be largely attributable to fire (see *Controlling for disturbance* and Appendix B); excluding it from the previous counts results in only 14 total species showing evidence of range shifts, with 4 species including a significant interaction coefficient.

Table 1. Number of species that include each coefficient in their set of model-averaged coefficients predicting presence, separated by direction of effect.

	Intercept	Year	Elevation (m)	Elevation (m^2)	Fires After 1983	Fires Before 1983	Year X Elevation	Year X Elevation^2
+	3	29	36	1	9	17	9	7
–	40	14	7	42	30	22	6	8
Total (43)	43	43	43	43	39	39	15	15

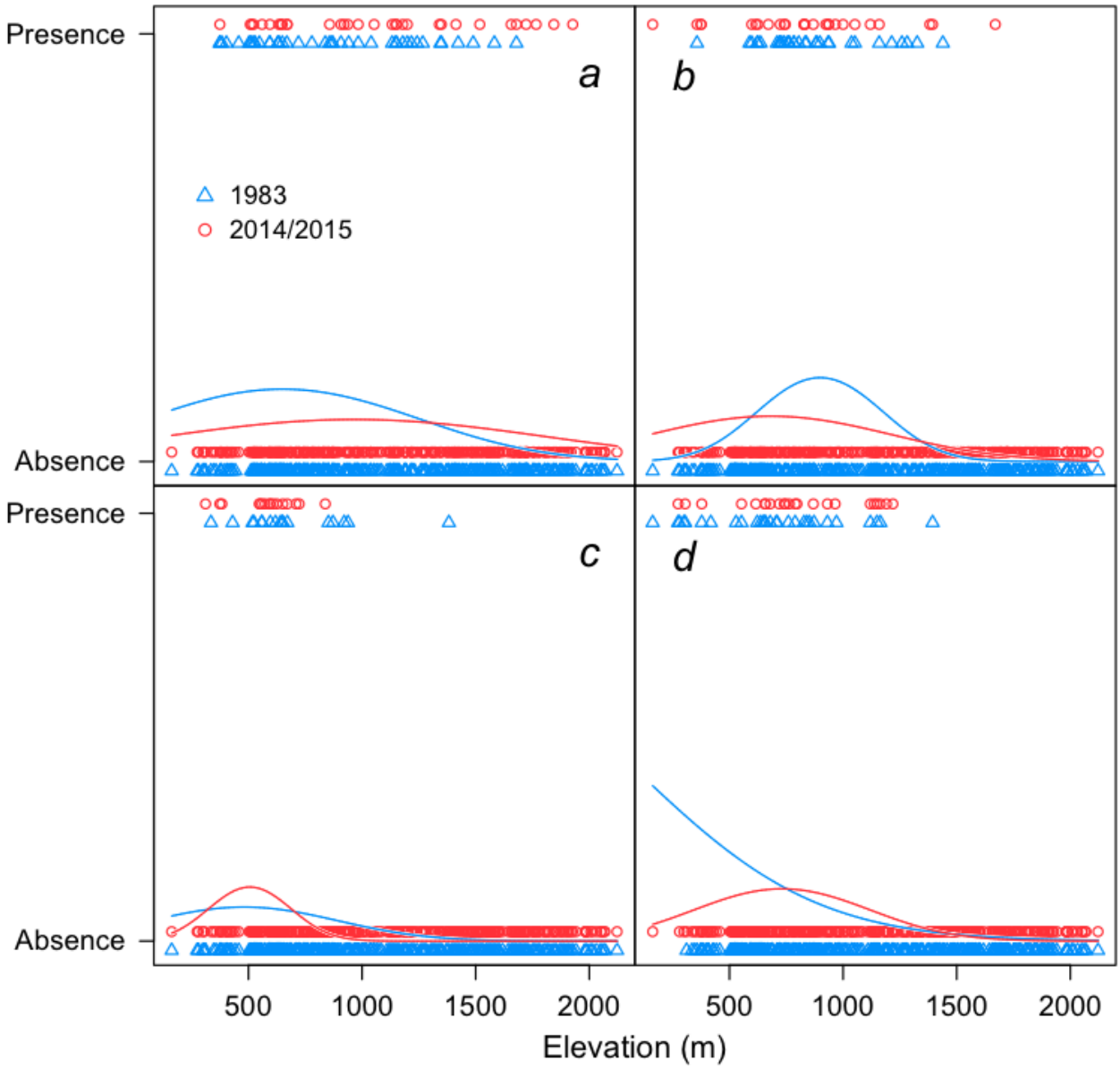

Figure 4. Probability of presence with elevation for (a) *Arctostaphylos uva-ursi*, (b) *Rubus parviflorus*, (c) *Holodiscus discolor*, and (d) *Oplopanax horridus*. All four species include a year*elevation coefficient in their suite of model-averaged coefficients. Points indicate plots at which the species was either present or absent, with the 1983 survey indicated with blue triangles and the 2014/2015 survey indicated with red circles. Points have been displaced for clarity. Lines indicate probability of presence based on top models.

Following patterns similar to those observed for raw shifts, mean modelled shift at the lower edge was significantly ($P < 0.05$) less than zero, again with some variation among species (mean: -47.6 m ± 39, minimum: -504 m, maximum: 229 m; Fig. 5a). Unlike the pattern observed for raw upper edge shifts, however, mean modelled shift at the upper edge was significantly ($P < 0.01$) greater than zero (mean: 77.8 m ± 48, minimum: -220 m, maximum: 696 m; Fig. 5b). Peak-presence shift did not differ significantly from zero (mean: 9.7 m ± 32, minimum: -214 m, maximum: 695 m; Fig. 5c).

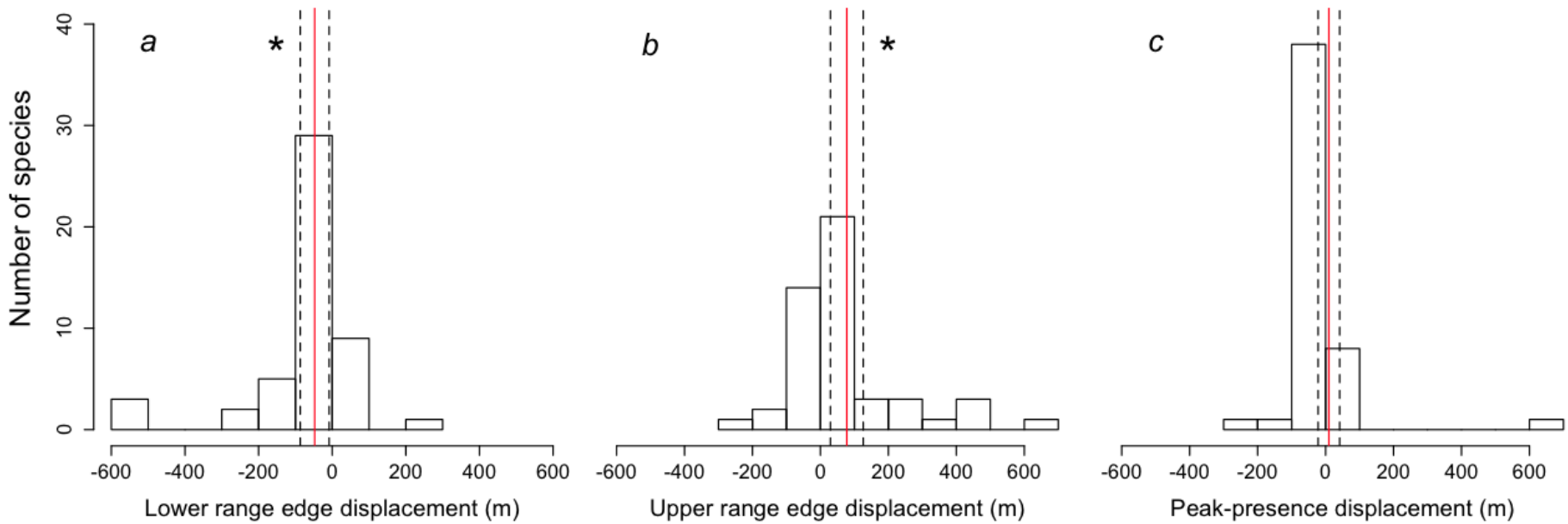

Figure 5. Modelled displacement among species at the (a) lower range edge, (b) upper range edge, and (c) elevation of peak presence. Mean displacement among species is indicated by the red line. Confidence intervals from a one-sample t-test are indicated by the black dashed lines. * indicates a significant trend ($P < 0.05$).

2.3.2 Rarefaction

In 1983, a total of 210 species were recorded with an average of 6.9 species per plot, while in the 2014/2015 surveys, a total of 356 species were recorded with an average of 10.2 species per plot. Only 131 species were recorded in both surveys, of which a mean of 5.7 were recorded per 1983 plot and 7.6 were recorded per 2014/2015 plot. As such, 2 species were removed from each 2014/2015 plot, unless that plot contained 2 or fewer species. After 100 permutations of rarefaction, of the 14 species that originally showed evidence of range shifts, 11 species median rarefied year*elevation coefficients did not significantly differ from their original model-averaged year*elevation coefficients, such that the rarefied coefficient's 5th and 95th percentiles overlapped with the original coefficient (Table D4). Thus, rarefaction did not significantly change the magnitude of range shift we originally observed for most species. However, the 5th and 95th percentiles of the rarefied interaction coefficients overlapped with zero for 8 species. This suggests that these 8 species putative range shifts can be attributed, at least in part, to differences in survey effort. Ultimately, in this formal modelling context, I detected strong evidence of range shifts for 5 species plus moss (*Arctostaphylos uva-ursi*, *Holodiscus discolor*, *Oplopanax horridus*, moss, *Trientalis borealis*, *Vaccinium alaskaense*), and weak evidence of range shifts for 8 species (*Achillea millefolium*, *Cornus sericea*, *Luetkea pectinata*, *Menziesia ferruginea*, *Paxistima myrsinites*, *Rubus parviflorus*, *Rubus spectabilis*, *Sorbus sitchensis*). The remaining 29 species showed no evidence of climate-change-induced range shifts (Table D4).

2.3.3 Changes in cover

Year had non-zero model-averaged coefficients for all species (Table 2), suggesting that all species changed in abundance. Most species tended to decrease in cover, though a diversity of responses were observed (Fig. 6). Additionally, 11 species included a year*elevation interaction

term in their set of model-averaged coefficients. However, among the full set of focal species, explanatory power of models tended to be low and the effect of year or year*elevation was significantly or marginally significantly different from zero for only 13 species (Table D5). Seven focal species were excluded from cover analyses; see Appendix C for further detail and some additional caveats. Shrubs did not conform in the direction of their responses, but all ferns and moss showed negative responses.

Table 2. Number of species that include each coefficient in their set of model-averaged coefficients predicting cover, separated by direction of effect.

	Intercept	Year	Elevation (m)	Elevation (m^2)	Fires After 1983	Fires Before 1983	Year X Elevation	Year X Elevation^2
+	34	11	16	0	3	3	6	1
–	2	25	19	3	5	5	5	0
Total (40)	36	36	35	3	8	8	11	1

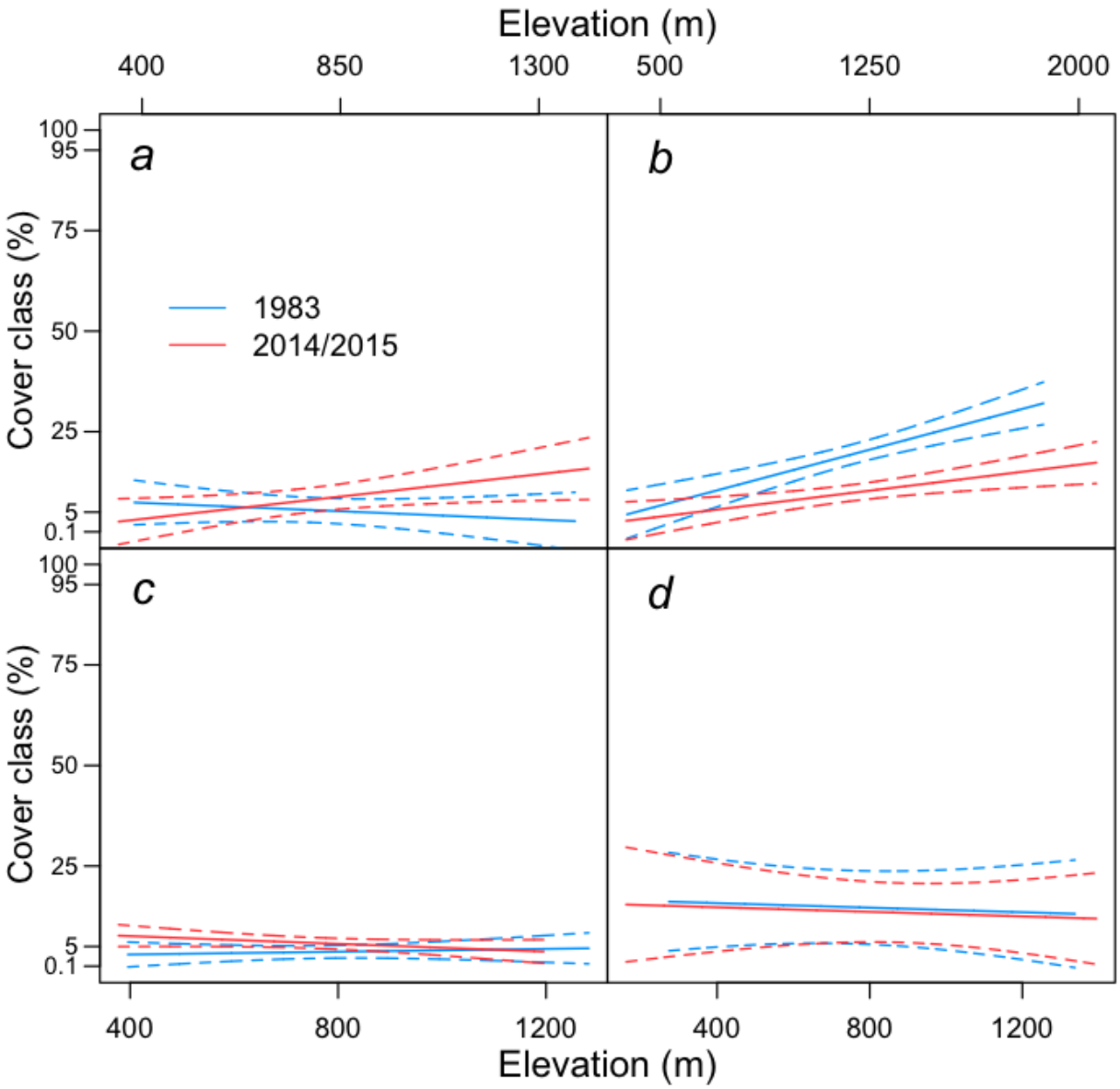

Figure 6. Cover class (%) with elevation for (a) *Alnus alnifolia*, (b) *Vaccinium membranaceum*, (c) *Linnaea borealis*, and (d) *Rubus spectabilis*. All four species include a year and/or year*elevation coefficient in their suite of model-averaged coefficients, yet show a variety of responses. Solid lines are predicted cover values with elevation and the dashed lines are model confidence intervals, with the 1983 survey indicated in blue and the 2014/2015 survey indicated in red.

2.3.4 Controlling for disturbance

Of 372 plots, 36 plots experienced fire after 1983, 23 plots experienced fire before 1983, and 313 plots did not experience fire. Plots experiencing fire either before or after 1983 were distributed relatively evenly across elevations (analysis not shown). Fires had a significant effect on cover and the likelihood of presence for some species (Table D3; Table D5). For this reason, further analyses were conducted to test for an interactive effect of survey year and fire on probability of presence and cover (Appendix B). Ultimately, only probability of presence of *C. angustifolium* was found to be confounded with fire.

2.3.5 Traits

Herbaceous species were significantly ($P < 0.05$) more likely to experience a shift in the upward direction at their modelled upper range edge (Fig. 7a). Similarly, species with fine-textured leaves were significantly ($P < 0.05$) more likely to experience an uphill shift at their modelled upper range edge (Fig. 7b). Fine-leaved species were also significantly ($P < 0.05$) more likely to experience an uphill shift in their elevation of modelled peak presence (Fig. 7c). However, patterns with leaf texture became nonsignificant when the outlier *Achillea millefolium* (raw and modelled upper-edge displacement of 669 m and 695.5 m, respectively) was removed, and growth form became marginally significant ($P < 0.1$; analysis not shown). Furthermore, a Bonferroni-corrected significance threshold level of 0.001 made all patterns nonsignificant. Traits were not significant predictors of raw shifts.

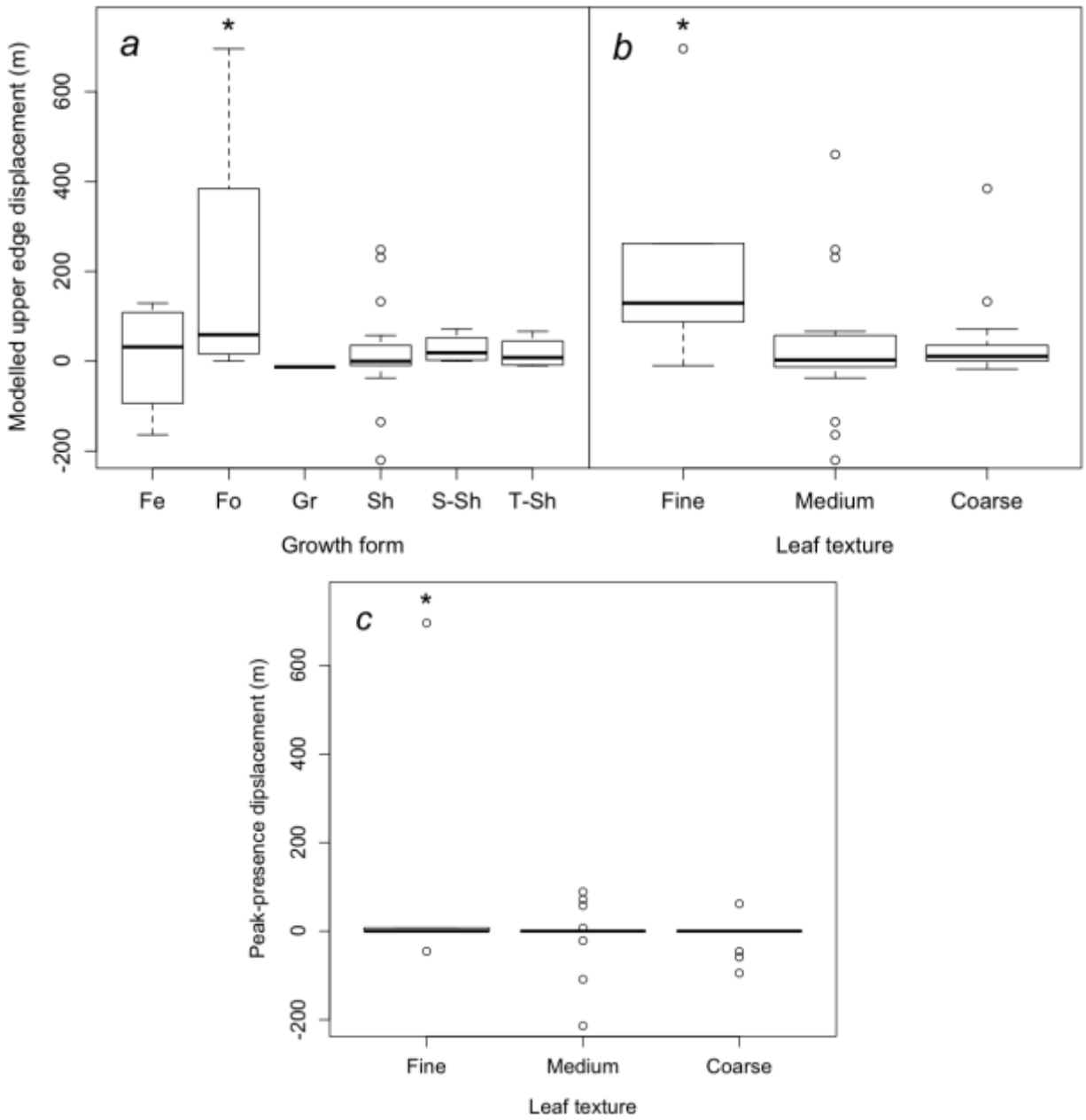

Figure 7. Association of (a) different growth forms (Fe denotes fern, Fo denotes forb, Gr denotes graminoid, Sh denotes shrub, S-Sh denotes semi-shrub, T-Sh denotes tree-like shrub) with modelled upper range edge displacement, (b) leaf texture with modelled upper edge displacement, and (c) leaf texture with modelled peak-presence displacement. For each plot, the median is the central black line, the lower edge of each box is the 25th percentile, the upper edge is the 75th percentile, and the dashed line extends between the minimum and maximum points or 1.5 interquartile ranges from the median, whichever is less. Points beyond this are indicated by open circles. Significant effect of a group ($P < 0.05$) is indicated by *. Note that these figures include data from *A. millefolium*.

Of the five traits included in the multivariate analysis, growth form, leaf texture, seed mass, and SLA were included in a top model for at least one range metric, while shade tolerance was never included in a model (Table D6). In agreement with results from univariate analyses, herbaceous plants were positively associated with uphill shift in modelled upper range edge, as evidenced by the inclusion of a positive model-averaged coefficient. Similarly, fine leaf texture was associated with an upward shift in modelled upper edge and elevation of peak presence. However, it was additionally associated with an upward shift in the modelled lower range edge and raw upper range edge, an effect not detected in univariate analyses. Model averaging also revealed that seed mass tended to positively associate with upward shifts at the raw lower and upper range edges, the modelled lower range edge, and the elevation of peak presence. Finally, SLA showed a negative relation with raw upper edge displacement, modelled lower edge displacement, and peak-presence displacement, but showed a positive relation with raw lower edge displacement. Explanatory power for models predicting raw and modelled lower edge displacement tended to be low, while it tended to be reasonably high for raw and modelled upper edge displacement as well as peak-presence displacement.

The multivariate analysis was also repeated excluding *Achillea millefolium*, yielding different results (Table D7). Shade tolerance became an important predictor for raw upper edge displacement, such that shade-intolerant species were more likely to undergo a range contraction at the upper edge. Leaf texture was no longer included in top models for raw upper edge, modelled lower edge, or modelled lower edge, remaining in the top models for peak-difference displacement only. Additionally, SLA showed a positive relation with modelled upper edge displacement, whereas before it was not included in that set of top models. Conclusions for the role of seed mass and growth form were qualitatively unchanged. Consistent with results

including *Achillea millefolium*, explanatory power for models predicting raw and modelled lower edge displacement tended to be low, while it tended to be reasonably high for raw and modelled upper edge displacement, though explanatory power for models predicting peak-presence displacement became lower. In summary, the results of multivariate trait analyses were not consistent among range metrics or with univariate analyses and changed substantially when a single outlying species was removed.

2.4 Discussion

Overall, two thirds (28/42) of species did not experience a range shift, and more than half (8/14) of the shifting species responses could be attributed to increased 2014/2015 survey effort or fire. All species showed changes in abundance between surveys, with more than two thirds of species showing a decrease in abundance, though these patterns tended to be weak. Some traits appeared to associate with one or more range shift metrics, but patterns were not consistent am ong metrics, and repeating the analysis following removal of an outlying species yielded different results.

2.4.1 Most species show range stasis

Counter to expectations given 0.8° C of warming from 1983 to 2015, two thirds of species did not exhibit a range shift. Of the remaining species which initially appeared to undergo range shifts, more than half were later shown to be artefacts of increased 2014/2015 survey effort, and one was found to be driven by patterns of fire. Ultimately, only five species, plus the functional group moss, showed strong evidence of range shifts in response to climate change. Additionally surprising was a tendency of species to move downhill at the lower edge. As NOCA was designated a protected area in only 1969, it is possible that reduced disturbance at lower

elevations altered competitive dynamics or habitat such that previously excluded species could shift downslope (Archaux 2004, Lenoir et al. 2010), although I removed plots with a suspected history of anthropogenic disturbance. However, given that species also tended to show a slight expansion at their modelled upper edge, and given also that we would expect the greater 2014/2015 survey effort to increase the likelihood of detecting range expansions on either edge, these patterns cannot be confidently categorized as a general climate change response. The trend could be investigated more robustly by repeating calculations of raw and modelled edge displacements for the rarefied dataset. In the absence of this analysis, I conservatively conclude that nearly all species showed stasis in their ranges.

Why might species fail to shift their ranges? Two disparate mechanisms may drive this pattern. First, species in NOCA may be adapting or acclimatizing to temperatures rapidly enough that fitness remains high within the historical range. The viability and frequency of this mechanism as a response to recent climate change is somewhat uncertain. Jump and Penuelas (2005) caution that even in populations with considerable standing genetic variation, the pace of climate change and its additive effects in fragmented habitats may prevent adaptation from successfully mitigating fitness consequences of climate change. Acclimatization buffers the need for adaptation and may be less capable of mitigating the fitness costs of extreme events, which are likely to increase with climate change (Jump and Penuelas 2005). Although phenotypic responses to climate change have been observed, it can be difficult to separate adaptive responses from those due to acclimatization (i.e., phenotypic plasticity; Jump and Penuelas 2005, Merilä and Hendry 2014). Genetic responses to climate change seem to be rarer than plastic responses, though robust tests are scarce (Merilä and Hendry 2014). Given that only 31-32 years has passed since the original survey, that all focal species are perennials, and that genetic

responses may occur only rarely, it is unlikely that genetic responses are driving stasis in this case. Acclimatization cannot be completely ruled out as an underlying mechanism. However, the changes in abundance observed among species suggest that acclimatization, if it is occurring, is unable to nullify all responses to the changing climate. Furthermore, acclimatization and adaptation would not limit colonization at the upper range edge, yet upper edge range expansion was rarely observed. Resistance may also lead to stasis when species have a broad thermal niche that encompasses even extreme fluctuations imposed by climate change, as has been observed in terrestrial ectotherms (Sunday et al. 2012). This mechanism cannot be confidently ruled out unless species thermal niches are quantified and compared to their degree of shift. Finally, stasis may be related to microclimate buffering of atmospheric temperatures by closed-canopy forest (De Frenne et al. 2013, Frey et al. 2016). However, focal species were fairly diverse in terms of canopy preference (inferred from shade tolerance and anecdotal observations in the field), suggesting that microclimate buffering may not fully explain the stasis I observed, especially among species that prefer open canopies.

Stasis may also be driven by time-lagged susceptibility to the fitness consequences of climate change. Time-lagged susceptibility could result from one or the combination of a number of factors. For example, species with long generation times, such as trees, could show range stasis if the pace of climate change exceeds rates of colonization of suitable habitat and population extinctions in unsuitable habitat. Susceptibility is delayed, rather than alleviated, as demography will eventually catch up with climate change and fitness consequences will become evident. Trees and other long-lived plants are generally expected to show lags in climate responses (Aitken et al. 2008). Furthermore, Perry et al. (2005) found that fish with shorter generation times are more likely to undergo range shifts. Considering that all NOCA focal

species are perennials and that some species may have cycled through only a few generations since 1983, it is possible that insufficient time has passed or intensity of warming has occurred for responses to become apparent. However, all species showed weak but detectable changes in abundance, suggesting that fitness consequences may not have been fully buffered. Given that very few species show range responses, but many species show abundance responses, dispersal limitation could be a key force in driving stasis, if stasis reflects a failure to move despite fitness consequences. This would be surprising, given that elevational range limits are not often constrained by dispersal (Hargreaves et al. 2014). However, capitalizing on newly suitable habitat above the range may require long-distance dispersal events, which are rare and often unpredictable (Nathan et al. 2008); it is therefore unlikely that sufficient time has passed for the dispersal and establishment of individuals above the historical range. Range shifts could also be impeded by prevention of successful establishment above the range due to biotic or abiotic factors (Bjorkman et al. 2016). Preliminary tests of this assertion could be evaluated by planting species above their current range in the presence of local competitors.

2.4.2 Species tend to decrease in abundance

More than two thirds of species appeared to decrease in cover, though year coefficients were often not statistically significant in top models and explanatory power of models was low. Only 11 species included an interaction coefficient in their top models, indicating that responses often appear to be occurring irrespective of location within the range. This may be especially troubling for species that tended to decrease in abundance. For example, if a population in the middle of the range decreased in abundance to a lesser degree than neighbouring populations, the healthier population could act as a seed source to support neighbours; in the absence of this interaction coefficient, populations may begin to suffer the combined effects of high extinction

rates and low immigration rates. I also expected shrubs to generally increase in cover and ferns and moss to decrease in cover (Walker et al. 2006, Elmendorf et al. 2012b). Although shrubs showed mixed directional responses, all ferns and moss decreased between surveys. The latter agrees with experimental results and, taken together, suggests that ferns and mosses may continue to decline in this region. Overall, these results suggest unfavourable outcomes for a number of species with respect to climate change, echoing the general conclusions from myriad other studies (for example, Walther et al. 2002, Parmesan 2006, Sinervo et al. 2010, Urban 2015). Again, these conclusions must be weighted in the context of poor explanatory power and nonsignificant coefficients; a more cautious interpretation suggests that just under a third of species showed changes in abundance due to climate change.

2.4.3 Traits cannot consistently explain range shifts

The ability of traits to associate with range shifts was highly inconsistent. Univariate analyses suggested that herbaceous species or those having fine-textured leaves may be more likely to undergo range expansion at the upper edge, but this pattern was driven almost entirely by the outlying *A. millefolium*. In a multivariate context, herbaceous plants were more likely to undergo a range expansion, even after the exclusion of *A. millefolium*, but only at the modelled upper edge. Similar to patterns from univariate analyses, patterns of leaf texture were driven almost entirely by *A. millefolium*. SLA shows discordant patterns at raw and modelled range edges; for example, it associated positively with raw lower edge displacement but negatively with modelled lower edge displacement. Its negative association with raw upper edge displacement was significant, even in the absence of *A. millefolium*, although this is counter both to its relation with modelled upper edge displacement and general expectations from another resurvey study (Rosbakh et al. 2014). Seed mass was consistently positively associated with

uphill shifts, except in the case of modelled upper edge displacement. Most reliably, smaller seeds were more likely to move downhill at lower range edges. This generally agrees with the expectation that smaller seeds can be dispersed more easily, and so having smaller seeds may increase the likelihood of range expansion. However, this pattern was not observed at upper edges and was observed only among the subgroup of species used for multivariate analysis; univariate analysis of the relation between seed mass and edge displacement among all species did not yield significant patterns.

Overall, the seven traits assessed here cannot be reliably used to predict traits in this system. Furthermore, vastly different conclusions could be drawn depending on the species included and the range metric used for prediction, casting concern on the validity of attempting to relate traits to these range shifts at all. The analysis also suffered from numerous drawbacks, including the fact that many Pacific Northwest flora have not been measured for a suite of traits, reducing the sample size of species available for multivariate analyses; the ability of researchers to detect trait-based relationships is only as good as the suite of traits that are included.

2.4.4 Caveats

The findings of this thesis should be interpreted in the context of several caveats. First, resurveys such as this one suffer from uncertainty in plot relocation, which may lead to inflated measurements of plot-level change through time (Vellend et al. 2013). This uncertainty can be alleviated, at least in part, by grouping plots prior to analysis (Damschen et al. 2010). I took a similar approach when I constructed elevational distributions of species among plots, rather than attempting to make paired plot comparisons between years, so I do not expect relocation error to affect my results. Furthermore, Kopecký and Macek (2015) found that measurements of temporal change were robust to relocation error.

A second caveat is that I compared change between only two time points. This could potentially exclude interesting inter-annual variation, especially when considering the substantial fluctuation in various climate variables between years (Hijmans et al. 2005). Repeat sampling at the NOCA sites in future years could help to confirm the patterns I found, but this remains a limitation within the scope of this thesis.

These analyses and interpretations also assume that all temporally varying confounding factors have been accounted for. I expected that fire and logging history were the most influential confounding factors, considering that a disturbance event associated with either may vastly alter plant communities for decades following (Agee 1994, Halpern and Spies 1995). However, infrequent disturbances such as major avalanches (which may have changed in intensity, frequency or paths since the original survey) and minor disturbances such as foot traffic from trails were not accounted for in this study. Analyses could be reassessed after incorporating data from historical satellite images describing change in avalanche regimes and trail construction. A number of plots were in avalanche chutes; these could be isolated to see if patterns in avalanche chutes differ from the park as a whole. However, as previously stated, the effect of these infrequent or minor disturbances on our conclusions is likely to be negligible.

A fourth drawback is that effect of temperature was never explicitly tested. Although temperature is known to decrease with increasing elevation, and climate change is known to have warmed the study area, species shifts along a temperature gradient could be explicitly tested using high-resolution point temperature data from ClimateWNA (Wang et al. 2012).

A caveat of using functional traits to predict shifts among species is that species may not be independent, given their phylogenetic relationships. Although a formal phylogenetic analysis was beyond the scope of this thesis, relatedness was superficially assessed by constructing

phylogenies of focal species and visually assessing trees for clustering of traits. Phylogenies were constructed using the online program Phylomatic (version 3; Webb and Donoghue 2005) and viewed as a tree using the ETE 3 online tool (Huerta-Cepas et al. 2016). Phylogenetic relations were superficially determined not to affect these results, though some groupings are worth noting: (1) shrub-like growth forms tended to cluster, especially in Eriaceae, and ferns were unsurprisingly clustered outside of vascular species; (2) all ferns showed anemochorous dispersal strategies and all *Rubus* showed endozoochorous dispersal strategies. These biases are unlikely to affect our conclusions, given that significant associations with range shifts were not observed for non-herbaceous growth forms or dispersal strategies of any kind.

Finally, this survey was restricted to only the most common species between both surveys. This was a necessary artefact of attempting to describe species ranges, but could potentially overlook interesting responses of rare or patchily distributed species. However, this restriction was also a necessary artefact of differences in effort between survey years. Any differences in effort not accounted for by rarefaction could be attributable to differences in identification effort, which could be parsed out by comparing numbers of higher-level classifications among surveys. Ideally, my focus on common, charismatic flora, for which both surveys would have a well-established search image, controls for this problem.

2.4.5 Summary and future directions

Despite warming, few species show strong evidence of range shifts, whereas most species appear to have weakly decreased in abundance across their ranges. Isolation of the primary mechanism driving this pattern depends on interpretation of the abundance results. If abundance decreases are real and indicative of fitness consequences of climate change, species may benefit from shifting their range but are limited by their ability to disperse into or establish in novel

habitat. If abundance decreases are so weak as to be ecologically irrelevant or an artefact of model selection, microclimate buffering by landscape features, slow demography, acclimatization, or some combination of all of these may be driving the absence of climate change responses. It is also possible that warming has not yet exceeded the thermal niche extremes of most species, failing to prompt a response. Finally, what little variation in range responses I observed could not be satisfyingly explained by variation in species functional traits, based on discordant conclusions among range metrics and species groupings and an overall paucity of data for ecologically relevant traits.

Predictions for future changes of NOCA flora depend whether stasis is due to resistance (acclimatization, microclimate buffering) or time-lagged susceptibility (dispersal limitation or slow demography). If resistance is driving stasis, species will likely continue to be able to resist to climate change for the foreseeable future, although the ability of phenotypic plasticity to cope with extreme climate events is uncertain (Jump and Penuelas 2005). This resistance may not be sustainable should climate warming continue on a business-as-usual trajectory. Alternatively, if time-lagged susceptibility is driving stasis, species have yet to measurably respond to climate change, and we cannot know the direction of these responses or whether they will be sufficient to avoid extinction given the rapid pace of climate change. Transplanting of tractable species above and within their existing range should be undertaken to further elucidate the causes of stasis and to provide a preliminary evaluation of the viability of assisted migration in this system (Aitken and Whitlock 2013). Furthermore, a repeat survey should be established at these sites to capture inter-annual variation and to allow for immediate detection of climate responses. Ultimately, given that abundance estimates suggest that fitness consequences may already be underway and

that traits cannot offer an informative predictive framework, the absence of range responses by Pacific Northwest flora to climate change is concerning.

Chapter 3: Conclusion

In this thesis, I aimed to describe elevation-wide climate change responses of Pacific Northwest flora. I also hoped to create a predictive, trait-based framework that could be extended to accurately predict responses in less-studied systems. I capitalized on an extensive historical survey undertaken in 1983 to use as a baseline against which to measure responses (Agee and Kertis 1987). I and my colleagues resurveyed these historical plots in 2014 and 2015. Elevational distributions were created for each time point based on species presences and absences across the full elevational range of plots. Range shifts were quantified as raw change at either boundary, change in either boundary based on modelled probability of presence, and change in point of peak presence. I also assessed temporal change in species percent cover across elevation. Fires may also impact presence and abundance, so I included fire history of each plot as a covariate in presence and cover analyses. I also accounted for greater 2014/2015 survey effort by rarefying 2014/2015 data and comparing to results from unrarefied analyses.

Given ~0.8 °C of climate warming in NOCA, I expected species to generally shift their ranges uphill, either by shifting upwards in their point of peak presence or by expanding at their upper edge and contracting at their lower edge. Though some variation in responses was observed, the majority of focal species showed stasis in their ranges, especially after accounting for the effects of survey effort and fires. This was unexpected, considering trends of upward shifts found in previous studies (for example, Lenoir et al. 2008, Moritz et al. 2008). However, others have reported either no response or a response lagging behind the pace of climate change (Bertrand et al. 2011, Forero-Medina et al. 2011, Zhu et al. 2011, Devictor et al. 2012, Ash et al. 2016). I also predicted that species abundances would respond differentially depending on their

functional group; specifically, I predicted that shrubby species would tend to increase in abundance while ferns and moss would tend to decrease in abundance. Though shrubs showed directionally variable responses in abundance, all ferns and moss tended to decrease between years, supporting expectations from experimental warming studies (Walker et al. 2006, Elmendorf et al. 2012b). Among all focal species, more than two thirds were found to decrease in abundance since the original survey, though models often had low explanatory power. Taken together, these patterns suggest that species may have experienced fitness consequences of climate change within their ranges, as evidenced by decreases in abundance, but are limited in their ability to disperse (i.e., shift their range) to mitigate these consequences. If a more conservative viewpoint is applied, most species were unaltered in their ranges and abundances, a pattern which may be driven by microclimate buffering, slow demography, and/or acclimatization (Perry et al. 2005, Jump and Penuelas 2005, De Frenne et al. 2013, Frey et al. 2016).

I also predicted that traits influencing colonization ability and/or persistence in novel habitat may associate with species magnitude or direction of range shift. I collated data describing seven traits that were hypothesized to affect these functions. Traits were assessed for the univariate and multivariate ability to predict five metrics of range shifts. Depending on the range metric used, the group of species being analyzed, and the modelling framework, different traits and directions of trait effect were associated with range shifts. Ultimately, traits could not reliably predict range shifts of species in this system.

This thesis contributes to the growing body of literature that compares contemporary data to historical data to describe recent climate change responses. Notably, I describe an overwhelming pattern of range stasis in my focal species, which is unexpected given atmospheric

warming in the region and general expectations from previous resurveys of elevational ranges. This work also acts as a voice of caution in attempting to relate functional traits to range shifts. I drew variable conclusions depending on the analytic framework used, suggesting that multiple metrics should be assessed for trait relations. Additionally, replication among systems and greater breadth of traits available for analysis is needed. However, based on this thesis and synthesis of existing literature, I do not believe that traits can be reliably used to predict responses to climate change. Even in studies that purport to show associations between traits and shifts, unexplained variation is often large or unreported, suggesting that management decisions could not be made on this basis alone.

Responses of NOCA flora to future climate change remains uncertain, with the possible exception of the five species exhibiting strong evidence of range shifts. For example, the lower-edge contraction and upper-edge expansion shown by *A. uva-ursi* may progress, moving the species generally uphill and possibly altering interspecific interactions at either edge. The tendency of species to decrease in abundance, however, suggests that the future of many NOCA flora may be grim. As such, continued research in this area is desperately needed. Species should be planted above their existing range to identify the causes of stasis and provide a preliminary evaluation of the viability of assisted migration in this system (Aitken and Whitlock 2013). Furthermore, a repeat survey should be established at these sites to capture inter-annual variation and to allow for immediate detection of climate responses in the future.

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Appendices

Appendix A Trait curation and collection

A.1 Growth form

Plants were classified as forbs, ferns, graminoids, shrubs, "semi-shrubs" (having a somewhat woody stem but growing prostrate or vine-like), or "shrub/small tree" (sometimes having a growth form characteristic of trees) based on taxonomic classifications and observations in guidebooks (Pojar and MacKinnon 1994, 2013).

A.2 Dispersal syndrome

Plants were categorized as anemochorous (wind-dispersed), endozoochorous (internally animal-dispersed), epizoochorous (externally animal-dispersed), or barochorous (passively- or gravitationally-dispersed) based on observations collected in the Fire Effects Information System (FIES) created by the US Forest Service and Department of Agriculture (Habeck 1991, 1992, Snyder 1991, 1993, Matthews 2000, Meyer 2005, Reeves 2006a, 2006b, Fryer 2010, Gucker 2012, Zouhar 2015), guidebooks (Pojar and MacKinnon 1994, 2013), published literature (Piper 1986, Moral et al. 1993, Fuller and del Moral 2003), and my qualitative assessment of their dispersal structures.

A.3 Leaf textures

Leaves were categorized qualitatively in the field as being either coarse, medium, or fine based on how easily they could be torn.

A.4 Shade tolerance

Plants were categorized as tolerant, intermediately tolerant, or intolerant of shade based on observations in guidebooks (Pojar and MacKinnon 1994, 2013) and the FIES (Snyder 1991, Habeck 1992, Howard 1993, Meyer 2005, Reeves 2006a). A fourth category, intermediate-

intolerant, was assigned to plants that were recorded as intermediately tolerant or intolerant an equal number of times in the TRY database.

A.5 SLA

Most leaf samples were pressed flat and dried at room temperature for several months, then weighed using a Mettler-Toledo AL104 microbalance. Leaves for a few species (*Holodiscus discolor*, *Goodyera oblongifolia*, *Spiraea betulifolia*, and *Trientalis borealis*) were collected shortly before lab processing and so were dried in a Shellab drying oven at 60°C for 72 hours. To calculate leaf area, photographs of leaves beside a ruler (to standardize size) were taken using an iPhone 5S (8 megapixels) and analyzed in ImageJ (version 1.51f). SLA was then calculated by dividing leaf area by mass. Additional values were taken from the literature (Antos and Zobel 1984, Antos 1988, Lange 1998, Gorzelak et al. 2012, Caplan and Yeakley 2013).

A.6 Seed mass

"Dry" infructescences (i.e., non-fleshy fruits) were stored in seed envelopes at room temperature for several months. Any dispersal-related structures were removed prior to weighing. "Wet" (i.e., fleshy fruits) infructescences were stored in a 70% ethanol solution at room temperature. These seeds were separated from fruit flesh, air-dried for 12 hours, then dried in a Shellab drying oven at 45°C for 60 hours. Seeds were then weighed using a Mettler-Toledo AL104 microbalance. Extremely small seeds were weighed in groups, then divided by the number of seeds. Only mature and putatively viable seeds were measured.

A.7 Plant height

Plant height was measured in the field as height from ground level to the tallest vegetative structure, measured with a ruler. A number of height values from TRY were assessed

to be well outside the normal range and so were removed before calculating the species' trait mean.

Appendix B Controlling for disturbance

B.1 Effect of fire on presence

Fire interacted marginally significantly ($P < 0.1$) with survey year for *C. rubescens* and *C. umbellata*, such that 2014/2015 surveys had a decreased likelihood of finding the species if the plot had burned after 1983. Fire also interacted marginally significantly ($P < 0.1$) with year for *A. millefolium* and significantly ($P < 0.05$) for *C. angustifolium* and moss, though in these cases, the 2014/2015 survey had greater probability of detection if the plot had burned after 1983. If fires were clustered near distributional edges, any putative range contractions (in the case of *C. rubescens* and *C. umbellata*) or expansions (in the case of *A. millefolium*, *C. angustifolium* and moss) shown by these groups would be confounded with the effect of fire. Fires after 1983 were spread evenly across the distributions of plots (analysis not shown), and range contractions were not observed for *C. rubescens* or *C. umbellata* (Table D3). However, *A. millefolium*, *C. angustifolium* and moss did show evidence of expansions at both range edges. To account for this, plots burned after 1983 were removed and the presence analysis was repeated for these three groups. Although *A. millefolium* and moss retained their year*elevation interaction term among top models, *C. angustifolium* no longer included a top model containing an interaction term. The possibility that this species' range expansion was driven primarily by fire cannot be excluded, and so its response cannot be exclusively attributed to climate change. As such, it was removed from the list of species showing evidence of range shifts.

B.2 Effect of fire on cover

Fire significantly ($P < 0.05$) interacted with survey year for moss, such that 2014/2015 surveys were more likely to find increased cover of moss if the plot had burned before 1983. Moss was found to decrease significantly between years, so the positive effect of the year*fire

interaction did not confound the overall pattern; furthermore, the top models describing moss cover did not change substantially when plots burned before 1983 were removed.

Appendix C Changes in cover

Acer circinatum and *A. glabrum* were excluded from cover analyses. These species were delineated as trees in the 2014 survey and so were only measured for DBH. Although the 2015 survey did measure percent cover of *A. circinatum* and *A. glabrum*, considering only the 2015 sites and their 1983 counterparts for this analysis would have been inappropriate; many 2014 occurrences of *A. circinatum* and *A. glabrum* tended to be clustered at low elevations whereas the 2015 occurrences covered only the upper half of their ranges. *Hieracium albiflorum* was also excluded, as its cover class never deviated from 1 among both surveys and so the model was unable to fit any distribution to the data. *Chimaphila umbellata*, *Goodyear oblongifolia*, and *Trientalis borealis* were not excluded from analyses; however, their cover varied insufficiently to fit all possible models. Despite being included in the presence analyses, *Gaultheria ovatifolia*, *Holodiscus discolor*, *Polystichum munitum*, and *Vaccinium alaskaense* occurred fewer than 10 times in the percent cover grouping in either or both surveys and so were excluded.

Appendix D Supplemental tables

Table D1. 43 focal species' four-letter code, latin names, common name, and functional type, including moss.

Code	Latin name	Common name	Growth form
ACCI	*Acer circinatum*	Vine maple	Tree-like shrub
ACGL	*Acer glabrum*	Douglas maple	Tree-like shrub
ACMI	*Achillea millefolium*	Yarrow	Forb
AMAL	*Amelanchier alnifolia*	Saskatoon berry	Tree-like shrub
ARUV	*Arctostaphylos uva-ursi*	Kinnikinnick	Shrub
ATFI	*Athyrium filix-femina*	Lady fern	Fern
CAME	*Cassiope mertensiana*	White mountain-heather	Shrub
CARU	*Calamagrostis rubescens*	Pinegrass	Graminoid
CEVE	*Ceanothus velutinus*	Snowbrush ceanothus	Shrub
CHAN	*Chamerion angustifolium*	Fireweed	Forb
CHUM	*Chimaphila umbellata*	Prince's pine	Forb
CLUN	*Clintonia uniflora*	Queen's cup	Forb
COCA	*Cornus canadensis*	Bunchberry	Forb
COSE	*Cornus sericea*	Red osier dogwood	Shrub
GAOV	*Gaultheria ovatifolia*	Western teaberry	Shrub
GASH	*Gaultheria shallon*	Salal	Shrub

Code	*Latin name*	Common name	Growth form
GOOB	*Goodyera oblongifolia*	Rattlesnake plantain	Forb
GYDR	*Gymnocarpium dryopteris*	Oak fern	Fern
HIAL	*Hieracium albiflorum*	White hawkweed	Forb
HODI	*Holodiscus discolor*	Oceanspray	Shrub
LIBO	*Linnaea borealis*	Twinflower	Semi-shrub
LUPE	*Luetkea pectinata*	Partridge-foot	Semi-shrub
MANE	*Mahonia nervosa*	Oregon grape	Shrub
MEFE	*Menziesia ferruginea*	False azalea	Shrub
OPHO	*Oplopanax horridus*	Devil's club	Shrub
PAMY	*Paxistima myrsinites*	Oregon falsebox	Shrub
PHEM	*Phyllodoce empetriformis*	Purple mountain-heather	Shrub
POMU	*Polystichum munitum*	Sword fern	Fern
PTAQ	*Pteridium aquilinum*	Bracken fern	Fern
RHAL	*Rhododendron albiflorum*	White-flowered rhododendron	Shrub
RULA	*Rubus lasiococcus*	Dwarf bramble	Semi-shrub
RUPA	*Rubus parviflorus*	Thimbleberry	Shrub
RUPE	*Rubus pedatus*	Five-leaved bramble	Semi-shrub
RUSP	*Rubus spectabilis*	Salmonberry	Shrub

Code	*Latin name*	Common name	Growth form
SOSI	*Sorbus sitchensis*	Sitka mountain-ash	Tree-like shrub
SPBE	*Spiraea betulifolia*	White spiraea	Shrub
TITR	*Tiarella trifoliata*	Foamflower	Forb
TRBO	*Trientalis borealis*	Starflower	Forb
VAAL	*Vaccinium alaskaense*	Alaskan bluberry	Shrub
VADE	*Vaccinium deliciosum*	Cascade blueberry	Shrub
VAME	*Vaccinium membranaceum*	Black huckleberry	Shrub
VASI	*Valeriana sitchensis*	Sitka valerian	Forb

Table D2. Generalized Variance Inflation Factors (GVIFs) and degrees of freedom for five traits entering a multivariate model. $GVIF^{(1/(2*Df))}$ allows for comparison among dimensions by standardizing based on degrees of freedom.

Trait	GVIF	DF	$GVIF^{(1/(2*Df))}$
Growth form	4.70	4	1.21
Leaf texture	2.45	2	1.25
Shade tolerance	2.32	1	1.52
Seed mass	3.77	3	1.25
SLA	3.01	1	1.73

Table D3. Species code (refer to Table D1), number of occurrences in either survey (1983 *N* and 2014/2015 *N*, where "2015 *N*" is used as shorthand for the latter), ΔAIC relative to the top model, weight based on ΔAIC (*w*), r^2, and coefficients of top models (ΔAIC < 2) predicting presence. r^2 is a pseudo-r-squared calculated by McFadden's log-likelihood method. Model-averaged coefficients appear as the last row of each species section (weighted by *w*). Annotations on the coefficients indicate significance of that coefficient in its associated model, where ~ corresponds to $P < 0.1$, * corresponds to $P < 0.05$, ** corresponds to $P < 0.01$, and *** corresponds to $P < 0.001$. An *F* annotation on the species name indicates that that species range shift is attributable to fire.

Species	1983 *N*	2015 *N*	ΔAIC	*w*	r^2	Intercept	Year	Elevation (m)	Elevation (m^2)	Fires After 1983	Fires Before 1983	Year X Elevation	Year X Elevation^2
ACCI	72	65	0.00	0.67	0.30	-2.372**	0.000	7.27E-03**	-6.30E-06***	-16.994	0.679*	0.00E+00	0.00E+00
			1.42	0.33	0.30	-2.290*	-0.167	7.28E-03**	-6.31E-06***	-16.998	0.681*	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-2.345	-0.055	7.27E-03	-6.30E-06	-16.995	0.680	0.00E+00	0.00E+00
ACGL	15	18	0.00	0.70	0.07	-4.784***	0.000	5.73E-03~	-3.53E-06*	0.000	0.000	0.00E+00	0.00E+00
			1.70	0.30	0.07	-4.887***	0.199	5.73E-03~	-3.53E-06*	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-4.815	0.060	5.73E-03	-3.53E-06	0.000	0.000	0.00E+00	0.00E+00
ACMI	10	31	0.00	0.40	0.15	-4.293***	1.293***	0.00E+00	0.00E+00	2.306***	1.599**	0.00E+00	0.00E+00
			0.81	0.27	0.16	-3.599***	-0.068	-7.12E-04	0.00E+00	2.312***	1.706**	1.29E-03	0.00E+00
			1.54	0.19	0.15	-4.570***	1.293***	2.40E-04	0.00E+00	2.298***	1.700**	0.00E+00	0.00E+00
			1.99	0.15	0.17	-6.539***	3.529	5.86E-03	-3.07E-06	2.335***	1.708**	-6.65E-03	3.65E-06
	Weighted average		NA	NA	NA	-4.492	1.262	7.22E-04	-4.55E-07	2.310	1.662	-6.42E-04	5.40E-07
AMAL	42	59	0.00	0.71	0.14	-3.283***	0.442~	4.90E-03**	-3.45E-06***	0.601	0.935**	0.00E+00	0.00E+00
			1.81	0.29	0.13	-3.042***	0.000	4.89E-03**	-3.44E-06***	0.591	0.927**	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-3.213	0.314	4.90E-03	-3.45E-06	0.598	0.933	0.00E+00	0.00E+00

Species	1983 *N*	2015 *N*	ΔAIC	*w*	r^2	Intercept	Year	Elevation (m)	Elevation (m^2)	Fires After 1983	Fires Before 1983	Year X Elevation	Year X Elevation^2
ARUV	42	32	0.00	0.13	0.04	-0.751~	-1.330*	-1.33E-03***	0.00E+00	0.558	-0.735	1.05E-03~	0.00E+00
			0.22	0.12	0.03	-0.795*	-1.335*	-1.27E-03**	0.00E+00	0.000	0.000	1.06E-03~	0.00E+00
			0.43	0.11	0.04	-2.297*	-0.662	2.18E-03	-1.68E-06	0.639~	-0.684	-6.39E-04	8.81E-07
			0.58	0.10	0.03	-2.425**	0.000	1.48E-03	-1.06E-06	0.639~	-0.678	0.00E+00	0.00E+00
			1.05	0.08	0.03	-2.241*	-0.653	2.05E-03	-1.59E-06	0.000	0.000	-6.54E-04	8.87E-07
			1.10	0.08	0.03	-1.361***	0.000	-8.34E-04**	0.00E+00	0.566	-0.723	0.00E+00	0.00E+00
			1.11	0.08	0.03	-2.285**	-0.301	1.49E-03	-1.06E-06	0.638~	-0.679	0.00E+00	0.00E+00
			1.23	0.07	0.02	-2.364**	0.000	1.35E-03	-9.69E-07	0.000	0.000	0.00E+00	0.00E+00
			1.37	0.07	0.02	-1.405***	0.000	-7.66E-04**	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.64	0.06	0.03	-1.219***	-0.301	-8.35E-04**	0.00E+00	0.564	-0.724	0.00E+00	0.00E+00
			1.74	0.06	0.02	-2.224**	-0.302	1.36E-03	-9.71E-07	0.000	0.000	0.00E+00	0.00E+00
			1.89	0.05	0.02	-1.262***	-0.301	-7.67E-04**	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-1.670	-0.534	2.98E-04	-6.18E-07	0.333	-0.390	1.46E-04	1.65E-07
ATFI	24	34	0.00	0.26	0.11	-1.596~	0.000	6.84E-04	-1.33E-06	-16.093	-0.273	0.00E+00	0.00E+00
			0.02	0.25	0.12	-1.805*	0.398	6.79E-04	-1.33E-06	-16.087	-0.274	0.00E+00	0.00E+00
			0.10	0.24	0.11	-0.526	0.000	-1.91E-03***	0.00E+00	-16.167	-0.302	0.00E+00	0.00E+00
			0.11	0.24	0.11	-0.735~	0.400	-1.92E-03***	0.00E+00	-16.162	-0.303	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-1.177	0.199	-5.88E-04	-6.80E-07	-16.126	-0.287	0.00E+00	0.00E+00

Species	1983 *N*	2015 *N*	ΔAIC	*w*	r^2	Intercept	Year	Elevation (m)	Elevation (m^2)	Fires After 1983	Fires Before 1983	Year X Elevation	Year X Elevation^2
CAME	32	34	0.00	0.53	0.43	-24.00**	0.000	2.20E-02*	-4.88E-06	-3.005**	-12.442	0.00E+00	0.00E+00
			1.32	0.27	0.43	-11.00***	0.000	5.91E-03***	0.00E+00	-3.340**	-13.170	0.00E+00	0.00E+00
			1.90	0.20	0.44	-24.05**	0.099	2.20E-02*	-4.88E-06	-3.006**	-12.442	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-20.49	0.020	1.76E-02	-3.56E-06	-3.096	-12.639	0.00E+00	0.00E+00
CARU	33	29	0.00	0.70	0.11	-5.581***	0.000	6.83E-03**	-3.42E-06***	1.964***	0.746	0.00E+00	0.00E+00
			1.74	0.30	0.11	-5.515***	-0.142	6.84E-03**	-3.42E-06***	1.964***	0.747	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-5.561	-0.042	6.84E-03	-3.42E-06	1.964	0.746	0.00E+00	0.00E+00
CEVE	26	25	0.00	0.73	0.16	-7.411***	0.000	9.82E-03***	-4.70E-06***	2.407***	-0.114	0.00E+00	0.00E+00
			1.99	0.27	0.16	-7.395***	-0.034	9.83E-03***	-4.70E-06***	2.407***	-0.114	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-7.407	-0.009	9.82E-03	-4.70E-06	2.407	-0.114	0.00E+00	0.00E+00
CHAN [F]	18	34	0.00	0.59	0.09	-9.063***	5.710*	1.17E-02*	-5.13E-06**	1.684***	-0.954	-9.89E-03*	4.31E-06*
			0.76	0.41	0.08	-5.342***	0.723*	4.39E-03*	-1.93E-06*	1.666***	-0.954	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-7.553	3.687	8.74E-03	-3.83E-06	1.677	-0.954	-5.88E-03	2.56E-06
CHUM	62	73	0.00	0.46	0.17	-3.704***	0.000	8.03E-03***	-5.24E-06***	-0.827~	0.378	0.00E+00	0.00E+00
			0.70	0.32	0.17	-3.827***	0.233	8.04E-03***	-5.24E-06***	-0.826~	0.379	0.00E+00	0.00E+00
			1.51	0.22	0.16	-3.720***	0.000	8.04E-03***	-5.25E-06***	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-3.747	0.076	8.04E-03	-5.24E-06	-0.648	0.296	0.00E+00	0.00E+00
CLUN	44	62	0.00	1.00	0.17	-6.996***	0.453*	1.33E-02***	-7.32E-06***	-1.773*	-0.734	0.00E+00	0.00E+00

Species	1983 *N*	2015 *N*	ΔAIC	*w*	r^2	Intercept	Year	Elevation (m)	Elevation (m^2)	Fires After 1983	Fires Before 1983	Year X Elevation	Year X Elevation^2
COCA	20	29	0.00	0.51	0.17	-3.036**	0.000	4.46E-03~	-3.63E-06*	-16.925	-17.655	0.00E+00	0.00E+00
			0.09	0.49	0.17	-3.267**	0.427	4.47E-03~	-3.63E-06*	-16.919	-17.656	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-3.149	0.209	4.47E-03	-3.63E-06	-16.922	-17.655	0.00E+00	0.00E+00
COSE	12	15	0.00	0.51	0.19	-7.821**	0.000	1.61E-02*	-1.13E-05*	-1.056	-15.961	0.00E+00	0.00E+00
			1.37	0.26	0.21	-5.096	-8.249	1.02E-02	-8.86E-06	-1.100	-15.921	1.87E-02	-9.27E-06
			1.63	0.23	0.19	-7.954**	0.247	1.61E-02*	-1.13E-05*	-1.053	-15.961	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-7.146	-2.078	1.46E-02	-1.07E-05	-1.067	-15.951	4.85E-03	-2.40E-06
GAOV	11	12	0.00	0.73	0.13	-11.43***	0.000	1.69E-02**	-7.78E-06**	-15.82	-16.09	0.00E+00	0.00E+00
			1.95	0.27	0.13	-11.48***	0.093	1.69E-02**	-7.78E-06**	-15.82	-16.09	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-11.45	0.025	1.69E-02	-7.78E-06	-15.82	-16.09	0.00E+00	0.00E+00
GASH	22	25	0.00	0.52	0.23	0.824~	0.000	-4.02E-03***	0.00E+00	-2.014~	-2.188*	0.00E+00	0.00E+00
			1.31	0.27	0.23	0.110	0.000	-1.93E-03	-1.35E-06	-1.983~	-2.163*	0.00E+00	0.00E+00
			1.76	0.21	0.23	0.744	0.159	-4.03E-03***	0.00E+00	-2.013~	-2.189*	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	0.615	0.034	-3.46E-03	-3.62E-07	-2.006	-2.181	0.00E+00	0.00E+00
GOOB	20	72	0.00	1.00	0.17	-3.536***	1.535***	3.89E-03*	-2.76E-06**	-0.672	-1.324*	0.00E+00	0.00E+00
GYDR	17	29	0.00	0.68	0.10	-4.193***	0.586~	4.55E-03~	-2.87E-06*	-15.72	-0.072	0.00E+00	0.00E+00
			1.48	0.32	0.09	-3.860***	0.000	4.54E-03~	-2.86E-06*	-15.73	-0.071	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-4.086	0.397	4.55E-03	-2.87E-06	-15.72	-0.072	0.00E+00	0.00E+00

Species	1983 *N*	2015 *N*	ΔAIC	*w*	r^2	Intercept	Year	Elevation (m)	Elevation (m^2)	Fires After 1983	Fires Before 1983	Year X Elevation	Year X Elevation^2
HIAL	12	14	0.00	0.50	0.08	-1.438**	0.000	-2.05E-03***	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.06	0.30	0.08	-2.422*	0.000	4.47E-04	-1.33E-06	0.000	0.000	0.00E+00	0.00E+00
			1.83	0.20	0.08	-1.525**	0.169	-2.05E-03***	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-1.747	0.034	-1.31E-03	-3.93E-07	0.000	0.000	0.00E+00	0.00E+00
HODI	17	16	0.00	0.41	0.19	-2.950*	0.000	3.43E-03	-4.22E-06	0.810	1.160*	0.00E+00	0.00E+00
			0.75	0.28	0.21	-3.194~	-3.168	3.10E-03	-3.22E-06	0.842	1.132*	1.44E-02	-1.41E-05
			1.84	0.16	0.18	-0.736	0.000	-3.08E-03***	0.00E+00	0.762	1.181*	0.00E+00	0.00E+00
			1.98	0.15	0.19	-2.922*	-0.057	3.43E-03	-4.22E-06	0.809	1.161*	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-2.656	-0.895	2.28E-03	-3.26E-06	0.811	1.156	4.03E-03	-3.93E-06
LIBO	48	74	0.00	1.00	0.25	-5.172***	0.628**	1.17E-02***	-7.84E-06***	-16.801	0.038	0.00E+00	0.00E+00
LUPE	35	46	0.00	0.48	0.47	-39.58***	0.490	4.06E-02**	-1.03E-05**	-1.980**	-13.02	0.00E+00	0.00E+00
			0.68	0.34	0.47	-39.08***	0.000	4.03E-02**	-1.03E-05**	-1.958**	-13.03	0.00E+00	0.00E+00
			1.88	0.19	0.48	-25.76*	-29.545	2.41E-02	-5.52E-06	-1.992**	-12.99	3.56E-02	-1.04E-05
	Weighted average		NA	NA	NA	-36.84	-5.267	3.74E-02	-9.42E-06	-1.975	-13.02	6.62E-03	-1.94E-06
MANE	62	68	0.00	0.68	0.31	-4.320***	0.000	1.24E-02***	-9.64E-06***	-1.660**	1.094**	0.00E+00	0.00E+00
			1.53	0.32	0.31	-4.400***	0.153	1.24E-02***	-9.65E-06***	-1.659**	1.096**	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-4.345	0.049	1.24E-02	-9.65E-06	-1.660	1.095	0.00E+00	0.00E+00

Species	1983 *N*	2015 *N*	ΔAIC	*w*	r^2	Intercept	Year	Elevation (m)	Elevation (m^2)	Fires After 1983	Fires Before 1983	Year X Elevation	Year X Elevation^2
MEFE	26	31	0.00	0.43	0.03	-5.811***	0.000	6.18E-03**	-2.49E-06**	0.000	0.000	0.00E+00	0.00E+00
			0.37	0.36	0.04	-4.224**	-3.778	2.60E-03	-8.81E-07	0.000	0.000	8.29E-03~	-3.75E-06*
			1.51	0.20	0.03	-5.913***	0.195	6.18E-03**	-2.49E-06**	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-5.258	-1.325	4.89E-03	-1.91E-06	0.000	0.000	2.99E-03	-1.36E-06
MOSS	195	328	0.00	0.41	0.18	0.848***	2.072***	-5.35E-04**	0.00E+00	-1.499***	-0.323	0.00E+00	0.00E+00
			0.93	0.26	0.18	0.262	5.022***	6.02E-04	-4.61E-07	-1.550***	-0.330	-5.46E-03*	2.17E-06*
			1.67	0.18	0.18	0.768**	2.352***	-4.64E-04*	0.00E+00	-1.494***	-0.321	-2.37E-04	0.00E+00
			1.94	0.16	0.18	0.975~	2.072***	-7.95E-04	1.10E-07	-1.508***	-0.329	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	0.703	2.879	-2.71E-04	-1.01E-07	-1.513	-0.326	-1.44E-03	5.58E-07
OPHO	29	23	0.00	0.31	0.13	-1.708~	0.000	9.24E-04	-1.69E-06	-15.91	0.243	0.00E+00	0.00E+00
			0.48	0.24	0.13	-0.463	0.000	-2.22E-03***	0.00E+00	-15.99	0.224	0.00E+00	0.00E+00
			1.21	0.17	0.14	-1.580~	-0.265	9.22E-04	-1.69E-06	-15.91	0.244	0.00E+00	0.00E+00
			1.35	0.16	0.15	-0.223	-3.787~	-2.03E-03	-3.99E-07	-15.92	0.255	7.59E-03	-3.41E-06
			1.69	0.13	0.13	-0.334	-0.266	-2.23E-03***	0.00E+00	-15.99	0.225	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-0.976	-0.669	-7.06E-04	-8.62E-07	-15.94	0.238	1.18E-03	-5.31E-07
PAMY	127	138	0.00	0.51	0.06	-1.714***	0.000	3.04E-03**	-1.70E-06***	1.188***	0.895**	0.00E+00	0.00E+00
			1.13	0.29	0.07	-1.790***	0.149	3.04E-03**	-1.70E-06***	1.191***	0.896**	0.00E+00	0.00E+00
			1.94	0.19	0.07	-2.674***	1.832~	4.68E-03**	-2.34E-06***	1.200***	0.904**	-3.13E-03	1.23E-06

	Weighted average		NA	NA	NA	-1.923	0.400	3.36E-03	-1.82E-06	1.191	0.897	-6.08E-04	2.39E-07
Species	**1983 *N***	**2015 *N***	**ΔAIC**	***w***	***r²***	**Intercept**	**Year**	**Elevation (m)**	**Elevation (m²)**	**Fires After 1983**	**Fires Before 1983**	**Year X Elevation**	**Year X Elevation²**
PHEM	61	66	0.00	0.68	0.55	-34.52***	0.000	3.68E-02***	-9.44E-06***	-2.869***	-13.41	0.00E+00	0.00E+00
			1.51	0.32	0.55	-34.67***	0.198	3.68E-02***	-9.45E-06***	-2.874***	-13.41	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-34.57	0.063	3.68E-02	-9.44E-06	-2.870	-13.41	0.00E+00	0.00E+00
POMU	20	15	0.00	0.32	0.20	0.265	0.000	-4.10E-03***	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			0.55	0.24	0.21	0.470	0.000	-4.23E-03***	0.00E+00	-1.548	-0.215	0.00E+00	0.00E+00
			1.21	0.17	0.20	0.421	-0.324	-4.10E-03***	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.65	0.14	0.20	0.728	0.000	-5.48E-03*	8.72E-07	0.000	0.000	0.00E+00	0.00E+00
			1.72	0.13	0.21	0.632	-0.333	-4.24E-03***	0.00E+00	-1.557	-0.216	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	0.454	-0.100	-4.34E-03	1.21E-07	-0.580	-0.080	0.00E+00	0.00E+00
PTAQ	47	29	0.00	0.56	0.10	-2.360**	-0.562*	2.99E-03~	-2.22E-06*	-0.886	0.490	0.00E+00	0.00E+00
			0.50	0.44	0.09	-2.367**	-0.554*	3.03E-03~	-2.26E-06*	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-2.363	-0.558	3.01E-03	-2.24E-06	-0.498	0.276	0.00E+00	0.00E+00
RHAL	24	19	0.00	0.66	0.27	-43.42***	0.000	5.31E-02***	-1.67E-05***	0.000	0.000	0.00E+00	0.00E+00
			1.30	0.34	0.28	-43.36***	-0.282	5.32E-02***	-1.67E-05***	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-43.40	-0.097	5.32E-02	-1.67E-05	0.000	0.000	0.00E+00	0.00E+00
RULA	18	20	0.00	0.72	0.19	-17.99***	0.000	2.31E-02***	-8.17E-06***	-16.48	-15.64	0.00E+00	0.00E+00
			1.88	0.28	0.19	-18.05***	0.120	2.31E-02***	-8.17E-06***	-16.48	-15.64	0.00E+00	0.00E+00

	Weighted average		NA	NA	NA	-18.01	0.034	2.31E-02	-8.17E-06	-16.48	-15.64	0.00E+00	0.00E+00
Species	**1983 *N***	**2015 *N***	**ΔAIC**	***w***	***r²***	**Intercept**	**Year**	**Elevation (m)**	**Elevation (m²)**	**Fires After 1983**	**Fires Before 1983**	**Year X Elevation**	**Year X Elevation²**
RUPA	33	26	0.00	0.30	0.09	-4.786***	0.000	7.23E-03**	-4.32E-06***	0.000	0.000	0.00E+00	0.00E+00
			0.11	0.28	0.10	-7.577***	4.692~	1.39E-02**	-7.81E-06**	0.000	0.000	-1.14E-02*	5.84E-06*
			1.09	0.17	0.09	-4.665***	-0.265	7.24E-03**	-4.32E-06***	0.000	0.000	0.00E+00	0.00E+00
			1.83	0.12	0.11	-7.882***	4.823~	1.44E-02**	-8.01E-06**	-0.160	0.654	-1.17E-02*	6.00E-06*
			1.85	0.12	0.09	-4.989***	0.000	7.47E-03**	-4.40E-06***	-0.151	0.631	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-5.956	1.869	1.00E-02	-5.76E-06	-0.037	0.154	-4.64E-03	2.38E-06
RUPE	23	30	0.00	0.62	0.07	-6.141***	0.000	6.91E-03**	-2.80E-06**	-15.966	-1.164	0.00E+00	0.00E+00
			0.97	0.38	0.07	-6.302***	0.294	6.92E-03**	-2.80E-06**	-15.963	-1.165	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-6.202	0.112	6.92E-03	-2.80E-06	-15.965	-1.164	0.00E+00	0.00E+00
RUSP	15	24	0.00	0.21	0.08	-1.679***	0.509	-1.43E-03***	0.00E+00	-15.70	0.018	0.00E+00	0.00E+00
			0.16	0.20	0.08	-2.892**	0.508	1.42E-03	-1.41E-06	-15.61	0.050	0.00E+00	0.00E+00
			0.27	0.18	0.07	-1.402***	0.000	-1.43E-03***	0.00E+00	-15.71	0.017	0.00E+00	0.00E+00
			0.43	0.17	0.08	-2.612*	0.000	1.42E-03	-1.40E-06	-15.62	0.050	0.00E+00	0.00E+00
			0.96	0.13	0.08	-1.203~	-0.247	-2.02E-03**	0.00E+00	-15.70	0.015	9.07E-04	0.00E+00
			1.35	0.11	0.09	-1.184	-2.693	-2.09E-03	3.59E-08	-15.61	0.056	6.48E-03	-2.70E-06
	Weighted average		NA	NA	NA	-1.908	-0.116	-5.37E-04	-5.10E-07	-15.66	0.033	8.16E-04	-2.91E-07

Species	1983 *N*	2015 *N*	ΔAIC	*w*	r^2	Intercept	Year	Elevation (m)	Elevation (m^2)	Fires After 1983	Fires Before 1983	Year X Elevation	Year X Elevation^2
SOSI	48	36	0.00	0.40	0.18	-11.19***	-0.364	1.38E-02***	-4.59E-06***	-1.659*	-15.52	0.00E+00	0.00E+00
			0.17	0.37	0.18	-11.33***	0.000	1.38E-02***	-4.57E-06***	-1.654*	-15.52	0.00E+00	0.00E+00
			1.11	0.23	0.18	-9.442***	-6.397	1.15E-02***	-3.86E-06**	-1.662*	-15.50	8.04E-03	-2.56E-06
	Weighted average		NA	NA	NA	-10.84	-1.619	1.33E-02	-4.41E-06	-1.658	-15.51	1.85E-03	-5.88E-07
SPBE	17	36	0.00	0.57	0.14	-4.371***	0.861**	5.45E-03*	-3.92E-06**	0.961*	0.116	0.00E+00	0.00E+00
			0.59	0.43	0.13	-4.038***	0.846**	5.02E-03*	-3.72E-06**	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-4.229	0.855	5.27E-03	-3.84E-06	0.551	0.066	0.00E+00	0.00E+00
TITR	34	46	0.00	0.51	0.07	-2.391**	0.353	2.03E-03	-1.56E-06*	-1.452*	-0.235	0.00E+00	0.00E+00
			0.12	0.49	0.06	-2.204**	0.000	2.02E-03	-1.56E-06*	-1.452*	-0.234	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-2.300	0.182	2.03E-03	-1.56E-06	-1.452	-0.234	0.00E+00	0.00E+00
TRBO	10	36	0.00	0.53	0.30	-4.336~	0.574	4.82E-03	-4.03E-06	-16.61	1.041*	6.32E-03	-6.85E-06
			0.24	0.47	0.29	-4.250**	1.516***	6.72E-03	-6.79E-0*6	-16.59	1.026*	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-4.295	1.017	5.72E-03	-5.33E-06	-16.60	1.034	3.35E-03	-3.63E-06
VAAL	11	11	0.00	0.53	0.22	-37.26**	21.604	6.61E-02**	-3.06E-05*	0.000	0.000	-3.48E-02	1.25E-05
			0.23	0.47	0.24	-36.80**	20.332	6.57E-02**	-3.06E-05*	-15.480	0.428	-3.25E-02	1.14E-05
	Weighted average		NA	NA	NA	-37.05	21.004	6.59E-02	-3.06E-05	-7.302	0.202	-3.37E-02	1.20E-05
VADE	34	73	0.00	1.00	0.54	-51.15***	1.614***	5.54E-02***	-1.50E-05***	-2.572***	1.724	0.00E+00	0.00E+00
VAME	96	152	0.00	1.00	0.13	-6.706***	0.791***	1.06E-02***	-4.23E-06***	-0.893*	-0.201	0.00E+00	0.00E+00

Species	1983 *N*	2015 *N*	ΔAIC	*w*	r^2	Intercept	Year	Elevation (m)	Elevation (m^2)	Fires After 1983	Fires Before 1983	Year X Elevation	Year X Elevation^2
VASI	24	35	0.00	0.36	0.21	-12.27***	0.459	1.16E-02**	-3.11E-06*	-1.023	-14.410	0.00E+00	0.00E+00
			0.51	0.28	0.21	-11.99***	0.000	1.16E-02**	-3.11E-06*	-1.017	-14.412	0.00E+00	0.00E+00
			1.09	0.21	0.20	-12.75***	0.454	1.22E-02***	-3.32E-06**	0.000	0.000	0.00E+00	0.00E+00
			1.58	0.16	0.20	-12.48***	0.000	1.22E-02***	-3.31E-06**	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-12.32	0.257	1.18E-02	-3.18E-06	-0.645	-9.109	0.00E+00	0.00E+00

Table D4. Species code (refer to Table D1), dataset (original vs. rarefied), number of measurements in either survey (1983 *N* and 2014/2015 N, where "2015 N" is used as shorthand for the latter), and model coefficients. The first row within each species' section is model-averaged coefficients from original, un-rarefied data (as in Table D3) and the second row is median values of coefficients from rarefaction analysis. Annotations on the rarefied coefficient indicate that the coefficient differs significantly the original coefficient (*) and/or that the coefficient does not differ significantly from zero (†) based on its 5th and 95th percentiles. An *F* annotation on the species name indicates that its range shift is attributable to fires.

Species	Dataset	1983 *N*	2015 *N*	Intercept	Year	Elevation (m)	Elevation² (m²)	Fires After 1983	Fires Before 1983	Year X Elevation	Year X Elevation²
ACCI	Original	72	65	-2.345	-0.055	7.27E-03	-6.30E-06	-17.00	0.680	0.00	0.00
	Rarefied	72	61.37	-2.291	-0.097*	7.01E-03	-6.10E-06	-16.96*	0.693	0.00†	0.00†
ACGL	Original	15	18	-4.815	0.060	5.73E-03	-3.53E-06	0.000	0.000	0.00	0.00
	Rarefied	15	13.53	-4.352*	-0.032*†	4.45E-03*	-2.98E-06*	0.000†	0.000†	0.00†	0.00†
ACMI	Original	10	31	-4.492	1.262	7.22E-04	-4.55E-07	2.310	1.662	-6.42E-04	5.40E-07
	Rarefied	10	25.03	-4.385	0.713*	7.29E-04†	-4.62E-07†	2.070*	1.777	-2.79E-04†	5.08E-07†
AMAL	Original	42	59	-3.213	0.314	4.90E-03	-3.45E-06	0.598	0.933	0.00	0.00
	Rarefied	42	47.57	-3.296	0.046*	5.05E-03	-3.50E-06	0.598	0.907	0.00†	0.00†
ARUV	Original	42	32	-1.670	-0.534	2.98E-04	-6.18E-07	0.333	-0.390	1.46E-04	1.65E-07
	Rarefied	42	29.19	-1.540	-0.861	2.24E-04†	-7.19E-07	0.390	-0.817	2.92E-04	2.59E-07
ATFI	Original	24	34	-1.177	0.199	-5.88E-04	-6.80E-07	-16.13	-0.287	0.00	0.00
	Rarefied	24	30.00	-1.674	0.069*	4.33E-04†	-1.13E-06	-16.01*	-0.162*	0.00†	0.00†
CAME	Original	32	34	-20.49	0.020	1.76E-02	-3.56E-06	-3.096	-12.639	0.00	0.00
	Rarefied	32	31.44	-19.20	0.000*†	1.57E-02	-2.91E-06	-3.109	-12.560*	0.00†	0.00†

Species	Dataset	1983 *N*	2015 *N*	Intercept	Year	Elevation (m)	Elevation^2 (m^2)	Fires After 1983	Fires Before 1983	Year X Elevation	Year X Elevation^2
CARU	Original	33	29	-5.561	-0.042	6.84E-03	-3.42E-06	1.964	0.746	0.00	0.00
	Rarefied	33	23.75	-5.522	-0.163*	6.69E-03	-3.36E-06	2.023	0.636	0.00†	0.00†
CEVE		26	25	-7.407	-0.009	9.82E-03	-4.70E-06	2.407	-0.114	0.00	0.00
	Original	26	21.83	-7.267	-0.058*	9.37E-03	-4.47E-06	2.405	-0.031*†	0.00†	0.00†
CHAN [F]	Rarefied	18	34	-7.553	3.687	8.74E-03	-3.83E-06	1.677	-0.954	-5.88E-03	2.56E-06
	Original	18	30.30	-7.816	4.364	9.29E-03	-4.07E-06	1.624	-0.902	-7.44E-03	3.24E-06
CHUM	Rarefied	62	73	-3.747	0.076	8.04E-03	-5.24E-06	-0.648	0.296	0.00	0.00
	Original	62	57.21	-3.759	-0.025*	7.81E-03	-5.14E-06	-0.262*	0.129	0.00†	0.00†
CLUN	Rarefied	44	62	-6.996	0.453	1.33E-02	-7.32E-06	-1.773	-0.734	0.00	0.00
	Original	44	54.89	-7.089	0.131	1.36E-02	-7.42E-06	-2.395	-0.637	0.00†	0.00†
COCA	Rarefied	20	29	-3.149	0.209	4.47E-03	-3.63E-06	-16.92	-17.66	0.00	0.00
	Original	20	25.43	-3.190	0.097*	4.44E-03	-3.52E-06	-16.84*	-17.56*	0.00†	0.00†
COSE	Rarefied	12	15	-7.146	-2.078	1.46E-02	-1.07E-05	-1.067	-15.95	4.85E-03	-2.40E-06
	Original	12	13.48	-7.865*	-2.078†	1.70E-02*	-1.26E-05	-0.977*	-15.92*	4.85E-03†	-2.40E-06†
GAOV	Rarefied	11	12	-11.447	0.025	1.69E-02	-7.78E-06	-15.82	-16.09	0.00	0.00
	Original	11	9.12	-12.060	-0.046*	1.75E-02	-7.90E-06	-11.68*	-11.83*	0.00†	0.00†
GASH	Rarefied	22	25	0.615	0.034	-3.46E-03	-3.62E-07	-2.006	-2.181	0.00	0.00
	Original	22	22.7	0.574	0.010*†	-3.49E-03	-3.62E-07	-1.947*	-2.124*	0.00†	0.00†

Species	Dataset	1983 *N*	2015 *N*	Intercept	Year	Elevation (m)	Elevation^2 (m^2)	Fires After 1983	Fires Before 1983	Year X Elevation	Year X Elevation^2
GOOB	Rarefied	20	72	-3.536	1.535	3.89E-03	-2.76E-06	-0.672	-1.324	0.00	0.00
	Original	20	48.29	-4.045*	1.000*	4.86E-03	-3.20E-06	-0.231	-0.385*	0.00†	0.00†
GYDR	Original	17	29	-4.086	0.397	4.55E-03	-2.87E-06	-15.72	-0.072	0.00	0.00
	Rarefied	17	24.83	-4.386	0.193*	5.11E-03	-3.10E-06	-15.61*	0.058*	0.00†	0.00†
HIAL	Original	12	14	-1.747	0.034	-1.31E-03	-3.93E-07	0.000	0.000	0.00	0.00
	Rarefied	12	11.19	-1.945*	-0.016*†	-1.21E-03	-3.75E-07	0.000†	0.000†	0.00†	0.00†
HODI	Original	17	16	-2.656	-0.895	2.28E-03	-3.26E-06	0.811	1.156	4.03E-03	-3.93E-06
	Rarefied	17	11.82	-2.437	-0.662	1.61E-03†	-2.74E-06	0.639	1.111	2.52E-03	-2.62E-06
LIBO	Original	48	74	-5.172	0.628	1.17E-02	-7.84E-06	-16.80	0.038	0.00	0.00
	Rarefied	48	69.55	-5.068	0.539*	1.15E-02	-7.73E-06	-16.75*	0.087*	0.00†	0.00†
LUPE	Original	35	46	-36.839	-5.267	3.74E-02	-9.42E-06	-1.975	-13.02	6.62E-03	-1.94E-06
	Rarefied	35	37.12	-33.319	0.026*†	3.32E-02	-8.21E-06	-1.800	-12.38	0.00*†	0.00*†
MANE	Original	62	68	-4.345	0.049	1.24E-02	-9.65E-06	-1.660	1.095	0.00	0.00
	Rarefied	62	60.35	-4.051*	-0.013*†	1.14E-02*	-9.04E-06*	-1.590*	0.864*	0.00†	0.00†
MEFE	Original	26	31	-5.258	-1.325	4.89E-03	-1.91E-06	0.000	0.000	2.99E-03	-1.36E-06
	Rarefied	26	16.12	-5.087	-1.521	4.19E-03*	-1.55E-06*	0.000†	0.000†	2.17E-03†	-9.60E-07†
MOSS	Original	195	328	0.703	2.879	-2.71E-04	-1.01E-07	-1.513	-0.326	-1.44E-03	5.58E-07
	Rarefied	195	304.0	0.299	4.859	5.61E-04†	-4.47E-07*	-1.537	-0.244	-5.81E-03	2.13E-06

Species	Dataset	1983 *N*	2015 *N*	Intercept	Year	Elevation (m)	Elevation^2 (m^2)	Fires After 1983	Fires Before 1983	Year X Elevation	Year X Elevation^2
OPHO	Original	29	23	-0.976	-0.669	-7.06E-04	-8.62E-07	-15.94	0.238	1.18E-03	-5.31E-07
	Rarefied	29	17.35	-0.223*	-5.921	-2.03E-03*	-3.99E-07*	-15.81*	0.207†	1.14E-02*	-5.19E-06*
PAMY	Original	127	138	-1.923	0.400	3.36E-03	-1.82E-06	1.191	0.897	-6.08E-04	2.39E-07
	Rarefied	127	115.8	-2.136	-0.048*	3.63E-03	-1.92E-06	1.056*	0.835	0.00*†	0.00*†
PHEM	Original	61	66	-34.57	0.063	3.68E-02	-9.44E-06	-2.870	-13.41	0.00	0.00
	Rarefied	61	55.55	-34.04	-0.080*	3.60E-02	-9.20E-06	-2.648*	-13.22*	0.00†	0.00†
POMU	Original	20	15	0.454	-0.100	-4.34E-03	1.21E-07	-0.580	-0.080	0.00	0.00
	Rarefied	20	11.04	0.386	-0.493*	-4.18E-03	7.07E-08†	-0.286*	-0.056	0.00†	0.00†
PTAQ	Original	47	29	-2.363	-0.558	3.01E-03	-2.24E-06	-0.498	0.276	0.00	0.00
	Rarefied	47	23.15	-2.506	-0.814*	3.38E-03	-2.45E-06	-0.355*	0.211	0.00†	0.00†
RHAL	Original	24	19	-43.40	-0.097	5.32E-02	-1.67E-05	0.000	0.000	0.00	0.00
	Rarefied	24	14.79	-40.57*	-0.309*	4.93E-02*	-1.54E-05*	0.000†	0.000†	0.00†	0.00†
RULA	Original	18	20	-18.01	0.034	2.31E-02	-8.17E-06	-16.48	-15.64	0.00	0.00
	Rarefied	18	13.29	-24.57*	-0.134*	3.21E-02*	-1.12E-05*	-16.25	-15.30	0.00†	0.00†
RUPA	Original	33	26	-5.956	1.869	1.00E-02	-5.76E-06	-0.037	0.154	-4.64E-03	2.38E-06
	Rarefied	33	22.14	-6.067	1.120†	1.03E-02	-5.88E-06	0.000*†	0.000*†	-3.28E-03†	1.74E-06†
RUPE	Original	23	30	-6.202	0.112	6.92E-03	-2.80E-06	-15.965	-1.164	0.00	0.00
	Rarefied	23	24.52	-6.649	0.013*†	7.61E-03	-3.09E-06	-15.825*	-1.032*	0.00	0.00

Species	Dataset	1983 *N*	2015 *N*	Intercept	Year	Elevation (m)	Elevation^2 (m^2)	Fires After 1983	Fires Before 1983	Year X Elevation	Year X Elevation^2
RUSP	Original	15	24	-1.908	-0.116	-5.37E-04	-5.10E-07	-15.663	0.033	8.16E-04	-2.91E-07
	Rarefied	15	22.35	-1.875*	0.140†	-5.84E-04	-4.81E-07	-15.621	0.055	1.09E-04†	0.00*†
SOSI	Original	48	36	-10.84	-1.619	1.33E-02	-4.41E-06	-1.658	-15.51	1.85E-03	-5.88E-07
	Rarefied	48	21.68	-10.23*	-2.871	1.25E-02*	-4.14E-06*	-1.458	-15.34*	2.41E-03†	-7.55E-07†
SPBE	Original	17	36	-4.229	0.855	5.27E-03	-3.84E-06	0.551	0.066	0.00	0.00
	Rarefied	17	33.45	-3.959	0.779*	4.66E-03*	-3.52E-06*	0.360†	0.051†	0.00†	0.00†
TITR	Original	34	46	-2.300	0.182	2.03E-03	-1.56E-06	-1.452	-0.234	0.00	0.00
	Rarefied	34	41.38	-2.381	0.070*	2.13E-03	-1.58E-06	-1.140	-0.137	0.00†	0.00†
TRBO	Original	10	36	-4.295	1.017	5.72E-03	-5.33E-06	-16.60	1.034	3.35E-03	-3.63E-06
	Rarefied	10	29.22	-4.055	1.029	5.23E-03	-5.08E-06	-16.45*	0.831	2.02E-03	-2.26E-06
VAAL	Original	11	11	-37.05	21.00	6.59E-02	-3.06E-05	-7.302	0.202	-3.37E-02	1.20E-05
	Rarefied	11	9.66	-37.08*	21.47	6.59E-02	-3.06E-05*	-7.002	0.232	-3.54E-02	1.31E-05
VADE	Original	34	73	-51.15	1.614	5.54E-02	-1.50E-05	-2.572	1.724	0.00	0.00
	Rarefied	34	67.57	-47.85	1.388*	5.17E-02	-1.40E-05	-2.772	1.722	0.00†	0.00†
VAME	Original	96	152	-6.706	0.791	1.06E-02	-4.23E-06	-0.893	-0.201	0.00	0.00
	Rarefied	96	119.9	-6.363*	0.435	9.88E-03*	-3.96E-06*	-0.402*	-0.094	0.00†	0.00†
VASI	Original	24	35	-12.32	0.257	1.18E-02	-3.18E-06	-0.645	-9.109	0.00	0.00
	Rarefied	24	28.98	-11.68*	0.073*	1.09E-02*	-2.88E-06*	-0.444*	-7.182*	0.00†	0.00†

Table D5. Species code (refer to Table D1), number of measurements in either survey (1983 *N* and 2014/2015 *N*, where "2015 *N*" is used as shorthand for the latter), ΔAIC relative to the top model, weight based on ΔAIC (*w*), r^2, and coefficients of top models (ΔAIC < 2) predicting cover. r^2 is a pseudo-r-squared calculated from the correlation between model predicted values and the midpoint of the measured cover interval. Model-averaged coefficients appear as the last row of each species section (weighted by *w*). Annotations on the coefficients indicate significance of that coefficient in its associated model, where ~ corresponds to $P < 0.1$, * corresponds to $P < 0.05$, ** corresponds to $P < 0.01$, and *** corresponds to $P < 0.001$. An *X* annotation on the species name indicates that insufficient variance was present to reliably fit one or more of that species' models.

Species	1983 *N*	2015 *N*	ΔAIC	*w*	r^2	Intercept	Year	Elevation (m)	Elevation (m^2)	Fires After 1983	Fires Before 1983	Year X Elevation	Year X Elevation^2
ACMI	10	24	0.00	0.43	0.06	5.022***	0.000	-5.14E-04	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			0.18	0.39	NA	4.410	0.000	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.76	0.18	0.07	4.948***	0.179	-5.47E-04	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	4.769	0.032	-3.18E-04	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
AMAL	42	45	0.00	0.36	0.06	9.165~	-10.82	-4.64E-03	0.00E+00	0.000	0.000	1.70E-02*	0.00E+00
			0.44	0.29	NA	6.804***	0.000	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.22	0.20	0.01	5.502***	2.529	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.67	0.16	0.01	3.928	0.000	3.64E-03	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	6.950	-3.396	-1.10E-03	0.00E+00	0.000	0.000	6.12E-03	0.00E+00
ARUV	42	29	0.00	0.31	0.12	27.16***	0.000	-9.32E-03~	0.00E+00	9.125	-11.07	0.00E+00	0.00E+00
			0.32	0.27	0.06	28.34***	0.000	-9.69E-03*	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.49	0.15	0.12	27.68***	-2.805	-8.64E-03~	0.00E+00	8.930	-11.11	0.00E+00	0.00E+00
			1.65	0.14	0.06	17.97***	0.000	0.00E+00	0.00E+00	11.14*	-7.491	0.00E+00	0.00E+00
			1.72	0.13	0.07	28.85***	-3.141	-8.89E-03~	0.00E+00	0.000	0.000	0.00E+00	0.00E+00

	Weighted average		NA	NA	NA	26.51	-0.834	-7.98E-03	0.00E+00	5.719	-6.150	0.00E+00	0.00E+00
Species	**1983 *N***	**2015 *N***	**ΔAIC**	***w***	***r²***	**Intercept**	**Year**	**Elevation (m)**	**Elevation (m²)**	**Fires After 1983**	**Fires Before 1983**	**Year X Elevation**	**Year X Elevation²**
ATFI	24	30	0.00	0.54	NA	15.66***	0.000	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.69	0.23	0.01	12.55*	0.000	3.95E-03	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.75	0.23	0.00	16.95***	-2.343	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	15.23	-0.529	9.21E-04	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
CAME	32	33	0.00	0.48	NA	19.58***	0.000	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			0.63	0.35	0.02	17.41***	4.308	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.98	0.18	0.00	17.23	0.000	1.32E-03	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	18.41	1.497	2.33E-04	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
CARU	33	26	0.00	0.26	0.04	15.89***	-6.990	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			0.29	0.23	0.07	8.674	-7.616~	7.71E-03	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			0.57	0.20	NA	12.79***	0.000	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			0.72	0.18	0.10	2.605	6.833~	1.42E-02	0.00E+00	0.000	0.000	-1.48E-02	0.00E+00
			1.38	0.13	0.02	6.407	0.000	6.57E-03	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	9.966	-2.305	5.21E-03	0.00E+00	0.000	0.000	-2.70E-03	0.00E+00
CEVE	26	20	0.00	0.50	NA	12.04***	0.000	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			0.91	0.32	0.02	10.62***	3.389	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.99	0.18	0.00	12.41*	0.000	-3.60E-04	0.00E+00	0.000	0.000	0.00E+00	0.00E+00

	Weighted average		NA	NA	NA	11.66	1.072	-6.63E-05	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
Species	**1983 *N***	**2015 *N***	**ΔAIC**	***w***	***r²***	**Intercept**	**Year**	**Elevation (m)**	**Elevation (m²)**	**Fires After 1983**	**Fires Before 1983**	**Year X Elevation**	**Year X Elevation²**
CHAN	18	30	0.00	0.57	NA	5.465***	0.000	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.91	0.22	0.00	6.131*	0.000	-5.96E-04	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			2.00	0.21	0.00	5.445***	0.030	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	5.607	0.006	-1.31E-04	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
CHUM [X]	62	60	0.00	0.51	NA	4.134	0.000	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.08	*0.30*	*0.01*	*4.464****	*0.000*	*-4.25E-04*	*0.00E+00*	*0.000*	*0.000*	*0.00E+00*	*0.00E+00*
			1.87	0.20	0.00	4.218	0.065	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	4.248	0.013	-1.26E-04	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
CLUN	44	53	0.00	0.29	0.03	6.965***	0.000	-2.44E-03	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			0.48	0.23	NA	4.763***	0.000	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			0.57	0.22	0.05	0.000[NA]	0.000	1.37E-02***	-8.67E-06***	0.000	0.000	0.00E+00	0.00E+00
			1.18	0.16	0.06	7.438***	0.000	-2.78E-03~	0.00E+00	-3.755	-2.404	0.00E+00	0.00E+00
			2.00	0.11	0.03	6.953***	0.019	-2.44E-03	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	5.026	0.002	1.58E-03	-1.88E-06	-0.602	-0.386	0.00E+00	0.00E+00
COCA	20	26	0.00	0.47	0.06	4.571	-0.478	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			0.64	0.34	NA	4.279	0.000	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.91	0.18	0.06	4.372***	-0.547	1.87E-04	0.00E+00	0.000	0.000	0.00E+00	0.00E+00

	Weighted average		NA	NA	NA	4.434	-0.326	3.40E-05	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
Species	**1983 *N***	**2015 *N***	**ΔAIC**	***w***	***r²***	**Intercept**	**Year**	**Elevation (m)**	**Elevation (m²)**	**Fires After 1983**	**Fires Before 1983**	**Year X Elevation**	**Year X Elevation²**
COSE	12	13	0.00	0.46	0.28	31.71***	-23.70**	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			0.86	0.30	0.31	13.38	-25.77***	2.76E-02	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.21	0.25	0.36	29.01***	-21.04**	0.00E+00	0.00E+00	33.488~	0.000[NA]	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	25.61	-23.66	8.17E-03	0.00E+00	8.316	0.000	0.00E+00	0.00E+00
GASH	22	23	0.00	0.36	0.35	54.71***	-18.33***	-3.81E-02**	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			0.39	0.30	0.37	65.42***	-37.96*	-5.68E-02**	0.00E+00	0.000	0.000	3.19E-02	0.00E+00
			1.38	0.18	0.39	53.20***	-17.17**	-3.76E-02**	0.00E+00	30.84	-2.510	0.00E+00	0.00E+00
			1.60	0.16	0.41	65.19***	-37.80*	-5.92E-02**	0.00E+00	31.16~	5.911	3.44E-02	0.00E+00
	Weighted average		NA	NA	NA	59.31	-27.10	-4.70E-02	0.00E+00	10.62	0.505	1.50E-02	0.00E+00
GOOB [X]	20	52	0.00	0.66	NA	4.017***	0.000	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.34	0.34	0.01	2.860	1.215	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	3.626	0.411	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
GYDR	17	24	0.00	0.28	0.10	1.803	0.000	5.18E-03~	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			0.11	0.26	0.13	2.608	-2.607	6.01E-03~	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			0.87	0.18	0.15	-1.037	3.097	1.10E-02~	0.00E+00	0.000	0.000	-7.31E-03	0.00E+00
			1.10	0.16	NA	6.191***	0.000	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.66	0.12	0.12	0.000[NA]	0.000	1.04E-02**	-3.16E-06	0.000	0.000	0.00E+00	0.00E+00

	Weighted average		NA	NA	NA	1.989	-0.130	6.25E-03	-3.83E-07	0.000	0.000	-1.31E-03	0.00E+00
Species	**1983 *N***	**2015 *N***	**ΔAIC**	***w***	***r²***	**Intercept**	**Year**	**Elevation (m)**	**Elevation (m²)**	**Fires After 1983**	**Fires Before 1983**	**Year X Elevation**	**Year X Elevation²**
LIBO	48	72	0.00	0.25	0.06	3.642***	2.212*	0.00E+00	0.00E+00	0.000	3.420*	0.00E+00	0.00E+00
			0.34	0.21	0.03	4.073***	2.175*	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.17	0.14	0.04	6.076**	2.129*	-2.59E-03	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.20	0.14	0.06	3.108	7.312~	1.23E-03	0.00E+00	0.000	0.000	-6.75E-03	0.00E+00
			1.27	0.13	0.07	5.210**	2.173*	-2.00E-03	0.00E+00	0.000	3.248*	0.00E+00	0.00E+00
			1.33	0.13	0.09	2.318	7.199~	1.73E-03	0.00E+00	0.000	3.221*	-6.55E-03	0.00E+00
	Weighted average		NA	NA	NA	4.037	3.531	-2.35E-04	0.00E+00	0.000	1.701	-1.77E-03	0.00E+00
LUPE	35	46	0.00	0.70	0.07	8.377***	-3.479*	0.00	0.00	0.000	0.000	0.00	0.00
			1.71	0.30	0.07	4.461	-3.457*	2.22E-03	0.00	0.000	0.000	0.00	0.00
	Weighted average		NA	NA	NA	7.209	-3.472	6.61E-04	0.00	0.000	0.000	0.00	0.00
MANE	62	60	0.00	0.52	0.07	16.29***	0.000	-1.04E-02**	0.00E+00	-7.961	3.827	0.00E+00	0.00E+00
			1.40	0.26	0.03	16.33***	0.000	-9.86E-03*	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.72	0.22	0.08	16.80***	-0.930	-1.04E-02*	0.00E+00	-8.446	3.706	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	16.41	-0.205	-1.03E-02	0.00E+00	-6.009	2.810	0.00E+00	0.00E+00
MEFE	26	17	0.00	0.28	0.18	-1.483	-6.375~	1.30E-02**	0.00E+00	-15.37*	-6.770	0.00E+00	0.00E+00
			0.47	0.22	NA	10.13***	0.000	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			0.51	0.22	0.05	2.759	0.000	5.99E-03*	0.00E+00	0.000	0.000	0.00E+00	0.00E+00

			1.00	0.17	0.13	-1.145	0.000	1.03E-02	0.00E+00	-10.73~	-4.842	0.00E+00	0.00E+00
			1.84	0.11	0.18	-2.809	-1.207	1.43E-02*	0.00E+00	-16.31*	-6.490	-4.27E-03	0.00E+00
	Weighted average		NA	NA	NA	1.923	-1.918	8.30E-03	0.00E+00	-7.939	-3.440	-4.75E-04	0.00E+00
Species	**1983 *N***	**2015 *N***	**ΔAIC**	***w***	***r²***	**Intercept**	**Year**	**Elevation (m)**	**Elevation (m²)**	**Fires After 1983**	**Fires Before 1983**	**Year X Elevation**	**Year X Elevation²**
MOSS	195	326	0.00	0.59	0.21	55.61***	-4.149*	-2.35E-02***	0.00E+00	-11.24**	-6.098	0.00E+00	0.00E+00
			0.70	0.41	0.21	59.05***	-9.415~	-2.67E-02***	0.00E+00	-11.60**	-6.208	4.93E-03	0.00E+00
	Weighted average		NA	NA	NA	57.03	-6.323	-2.48E-02	0.00E+00	-11.39	-6.144	2.04E-03	0.00E+00
OPHO	29	14	0.00	0.54	NA	12.26***	0.000	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.69	0.23	0.01	8.766	0.000	4.60E-03	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.77	0.22	0.01	13.02***	-2.399	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	11.62	-0.537	1.07E-03	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
PAMY	127	115	0.00	0.22	0.06	0.000[NA]	0.000[NA]	3.23E-02***	-1.57E-05***	0.000	0.000	-1.42E-02**	8.81E-06*
			0.04	0.22	0.05	19.60***	-13.93**	-5.36E-03~	0.00E+00	0.000	0.000	9.41E-03*	0.00E+00
			0.32	0.19	0.06	20.78***	-13.43*	-5.57E-03**	0.00E+00	-4.038	-3.681	8.95E-03*	0.00E+00
			1.06	0.13	0.03	14.20***	-4.506*	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.08	0.13	0.04	15.20***	-4.452*	0.00E+00	0.00E+00	-4.423~	-3.416	0.00E+00	0.00E+00
			1.61	0.10	0.03	0.000[NA]	0.000	2.57E-02***	-1.16E-05***	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	12.166	-6.820	7.59E-03	-4.69E-06	-1.353	-1.153	6.05E-04	1.98E-06

Species	1983 *N*	2015 *N*	ΔAIC	*w*	r^2	Intercept	Year	Elevation (m)	Elevation (m^2)	Fires After 1983	Fires Before 1983	Year X Elevation	Year X Elevation^2
PHEM	61	62	0.00	0.62	0.04	21.51***	-6.006*	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.00	0.38	0.05	8.880	-6.014*	7.34E-03	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	16.74	-6.009	2.77E-03	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
PTAQ	47	21	0.00	0.36	0.03	19.40***	0.000	-8.31E-03	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			0.24	0.32	NA	12.39***	0.000	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.68	0.16	0.03	19.73***	-2.158	-7.92E-03	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.70	0.16	0.01	13.26***	-2.851	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	16.23	-0.783	-4.27E-03	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
RHAL	24	18	0.00	0.48	0.07	-21.74	0.000	2.66E-02~	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			0.84	0.32	NA	20.31***	0.000	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.77	0.20	0.07	-22.96	-2.553	2.80E-02~	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	-8.621	-0.510	1.84E-02	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
RULA	18	19	0.00	1.00	0.22	27.89**	-24.96*	-1.55E-02**	0.00E+00	0.000	0.000	1.57E-02*	0.00E+00
RUPA	33	21	0.00	0.33	0.06	26.82***	0.000	-1.48E-02~	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			0.04	0.32	0.12	41.21***	-28.82*	-3.00E-02**	0.00E+00	0.000	0.000	2.98E-02*	0.00E+00
			1.13	0.19	NA	14.20***	0.000	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.47	0.16	0.06	28.23***	-3.283	-1.49E-02~	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	29.34	-9.860	-1.70E-02	0.00E+00	0.000	0.000	9.67E-03	0.00E+00

Species	1983 *N*	2015 *N*	ΔAIC	*w*	r^2	Intercept	Year	Elevation (m)	Elevation (m^2)	Fires After 1983	Fires Before 1983	Year X Elevation	Year X Elevation^2
RUPE	23	29	0.00	0.47	0.05	10.92***	-5.230~	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			0.87	0.30	NA	8.016***	0.000	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.40	0.23	0.06	15.05**	-5.544~	-3.29E-03	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	11.00	-3.724	-7.62E-04	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
RUSP	15	24	0.00	0.56	NA	13.94***	0.000	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.87	0.22	0.00	16.51*	0.000	-3.09E-03	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.95	0.21	0.00	14.77**	-1.390	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	14.69	-0.297	-6.87E-04	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
SOSI	48	24	0.00	0.53	NA	6.007***	0.000	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.58	0.24	0.01	6.388***	-1.130	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.62	0.23	0.01	8.402*	0.000	-1.67E-03	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	6.659	-0.271	-3.90E-04	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
SPBE	17	32	0.00	0.49	NA	8.073***	0.000	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			0.84	0.32	0.02	11.79**	0.000	-4.83E-03	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.98	0.18	0.00	8.298***	-0.362	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	9.318	-0.066	-1.56E-03	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
TITR	34	43	0.00	0.52	NA	7.965***	0.000	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.31	0.27	0.01	8.933***	-1.790	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00

			1.82	0.21	0.00	6.880*	0.000	1.24E-03	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	7.999	-0.483	2.60E-04	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
Species	**1983 *N***	**2015 *N***	**ΔAIC**	***w***	***r²***	**Intercept**	**Year**	**Elevation (m)**	**Elevation (m²)**	**Fires After 1983**	**Fires Before 1983**	**Year X Elevation**	**Year X Elevation²**
TRBO[X]	10	30	0.00	0.48	NA	3.955	0.000	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			0.81	0.32	0.02	1.703	2.834	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.78	0.20	0.00	4.326***	0.000	-6.65E-04	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	3.306	0.909	-1.31E-04	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
VADE	34	72	0.00	0.63	0.08	28.04***	-9.381**	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.05	0.37	0.09	43.07**	-9.607**	-8.65E-03	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	33.62	-9.465	-3.21E-03	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
VAME	96	135	0.00	1.00	0.23	-2.608	2.202	1.85E-02***	0.00E+00	0.000	0.000	-9.91E-03*	0.00E+00
VASI	24	30	0.00	0.55	NA	6.304***	0.000	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.71	0.24	0.00	3.963	0.000	1.46E-03	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
			1.91	0.21	0.00	6.044***	0.451	0.00E+00	0.00E+00	0.000	0.000	0.00E+00	0.00E+00
	Weighted average		NA	NA	NA	5.698	0.096	3.44E-04	0.00E+00	0.000	0.000	0.00E+00	0.00E+00

Table D6. Coefficients of top models (ΔAICc<2) describing the association between standardized traits and five different range metrics. Traits are growth form (GF; including S for semi-shrubs and T for tree-like shrubs), leaf texture (LT), shade tolerance (ST), seed mass (SM), and specific leaf area (SLA). The last row of each metric's section indicates the weighted average of coefficients in top models calculated from Akaike weights (*w*). Annotations on coefficients indicate significance of that coefficient in its associated model, where ~ corresponds to $P < 0.1$, * corresponds to $P < 0.05$, and ** corresponds to $P < 0.01$.

	Range metric	ΔAICc	*w*	r^2	Intercept	GF Forb	GF Shrub	GF S-Shrub	GF T-Shrub	LT Coarse	LT Fine	ST	SM	SLA
Original	Lower edge displacement	0.00	0.66	0.06	-30.55								26.77	
		1.32	0.34	0.01	-31.70									12.20
	Weighted average				-30.95								17.66	4.151
	Upper edge displacement	0.00	0.57	0.09	36.01									-64.72
		1.90	0.22	0.12	37.40								35.55	-82.55~
		1.93	0.21	0.21	11.33					-4.625	225.5~			-87.34~
	Weighted average				31.00					-0.996	48.58		7.773	-73.49
Mod	Lower edge displacement	0.00	0.35	0.02	-35.73								16.53	
		0.13	0.33	0.02	-38.53									-16.07
		1.43	0.17	0.06	-37.40								29.03	-30.63
		1.79	0.14	0.05	-57.35~					34.78	84.55			
	Weighted average				-40.06					5.009	12.18		10.85	-10.60
	Upper edge displacement	0.00	0.50	0.36	-163.8	409.9*	216.1	198.6	180.4					
		0.00	0.50	0.19	66.64					2.805	249.3*			
	Weighted average				-48.71	205.2	108.2	99.42	90.30	1.401	124.5			

	Range metric	ΔAICc	*w*	r^2	Intercept	GF Forb	GF Shrub	GF S-Shrub	GF T-Shrub	LT Coarse	LT Fine	ST	SM	SLA
Mod	Peak-difference displacement	0.00	0.60	0.35	9.985					-48.36	242.2**			-48.92~
		0.81	0.40	0.26	7.137					-15.98	212.1**			
		1.63	0.21	0.39	9.972					-53.35	265.2**		29.11	-66.71*
	Weighted average				9.081					-39.15	237.5**		6.106	-37.17

Table D7. Coefficients of top models (ΔAICc<2) describing the association between standardized traits and five different range metrics, with *Achillea millefolium* excluded. Traits are growth form (GF; including S for semi-shrubs and T for tree-like shrubs), leaf texture (LT; including C for coarse and F for fine), shade tolerance (ST; including II for intermediate-intolerant, I for intolerant, and T for tolerant), seed mass (SM), and specific leaf area (SLA). The last row of each metric's section indicates the weighted average of coefficients in top models calculated from Akaike weights (*w*). Annotations on coefficients indicate significance of that coefficient in its associated model, where ~ corresponds to $P < 0.1$ and * corresponds to $P < 0.05$.

	Range metric	ΔAICc	*w*	r^2	Int.	GF - F	GF - S	F - S	GF - T	LT - C	LT - F	ST - II	ST - I	ST - T	SM	SLA
Original	Lower edge displacement	0.00	0.65	0.05	-30.13										26.59	
		1.26	0.35	0.01	-31.03											11.90
	Weighted average				-30.44										17.36	4.132
	Upper edge displacement	0.00	0.70	0.43	82.83							44.24	-209.4*	-62.94		-68.02*
		1.69	0.30	0.47	98.07							17.25	-219.0*	-80.88	36.23	-85.70*
	Weighted average				87.42							36.10	-212.3*	-68.35	10.92	-73.35*
Mod	Lower edge displacement	0.00	0.46	0.04	-45.56*										20.65	
		0.78	0.32	0.01	-47.85*											-11.87
		1.48	0.22	0.08	-46.88*										31.89	-27.74
	Weighted average				-46.58*										16.64	-9.870
	Upper edge displacement	0.00	0.52	0.33	-163.8	345.7*	198.6	216.1~	180.4							
		1.36	0.26	0.02	70.90*										-16.03	
		1.69	0.22	0.00	72.62*											8.458
	Weighted average				-49.91	178.5	102.6	111.6	93.15						-4.196	1.877

	Range metric	ΔAICc	*w*	r^2	Int.	GF - F	GF - S	F - S	GF - T	LT - C	LT - F	ST - II	ST - I	ST - T	SM	SLA
Mod	Peak-difference displacement	0.00	0.32	0.04	0.271										5.832	
		0.31	0.27	0.03	-0.531											-5.436
		0.46	0.25	0.12	-0.226										10.06	-10.45
		1.39	0.16	0.09	7.137					-15.98	-26.14					
	Weighted average				1.016					-2.533	-4.144				4.389	-4.112