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Retreat to refugia: Severe habitat contraction projected for endemic alpine plants of the Olympic Peninsula

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By

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Accepted in Partial Completion
Of the Requirements for the Degree
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MASTER'S THESIS

Samuel Tobias Wershow
May 10, 2017

Retreat to refugia: Severe habitat contraction projected for endemic alpine plants of the Olympic Peninsula

A Thesis
Presented to
The Faculty of
Western Washington University

In Partial Completion
Of the Requirements for the Degree
Master of Science

By

Samuel Tobias Wershow
May, 2017

Abstract:

Premise of the study- The unique geography of the Olympic Peninsula has created a flora with exceptional endemism that may face high rates of extinction due to climate change. Conserving endemic taxa requires a deeper understanding of general and individual species' responses to warming in topographically complex environments. The Olympic Mountains provide an unparalleled opportunity to test predicted responses and inform conservation plans for threatened alpine taxa.

Methods- I developed Species Distribution Models (SDMs) for five endemic alpine plants of the Olympic Peninsula to estimate the potential impact of climate change on these rare taxa. First, I created high-resolution raster surfaces on the Olympic Peninsula with climatic and topographic variables for the current period and the year 2080. I used Principal Components Analysis to visualize changes in climate niche-space in the Olympic alpine and the exposure of the five endemics to changing conditions. I then constructed climate and topographic-based SDMs, to estimate changes in the distribution of habitat for each taxon. Finally, I identified potential thermal refugia as areas where suitable habitat conditions would remain by the year 2080.

Key Results- The Olympic alpine will experience novel environmental conditions in the future, with a pronounced decrease in winter snow and an increase in growing season moisture stress. Suitable habitat will be greatly reduced for all five focal taxa, with thermal refugia remaining only on the highest peaks of the eastern Olympics. Topographic SDMs suggested further decreases in the total amount of projected suitable habitat. Furthermore, I identified differences in the proportion of suitable micro-topography within each taxon's climate envelope that greatly affect the species-specific climate change prognosis.

Conclusions- The Olympic alpine endemics are stranded on ever shrinking habitat islands, and are projected to lose 85-99% of their suitable habitat by 2080. Their survival depends on their ability to persist in isolated thermal refugia on the highest peaks. Within these refugia, the distribution of micro-topography may be a critical factor in determining the long term survival prospects of threatened taxa. The Olympic Mountains and their endemic taxa are a model system illustrating the biogeographic characteristics that underpin vulnerability to climate change. Globally, taxa with narrow distributions that are already occupying the coldest locally available habitats should be considered extremely vulnerable, and may be at the forefront of climate-driven extinctions.

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For my dad, who brought me to the mountains.

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Chapter 1

Project summary

Context

This master's thesis was begun in the fall of 2014 under the direction of Dr. Eric DeChaine. Eric and I developed the conceptual basis of this project together. It was intended as an exploration of endemism in the Pacific Northwest in the context of past and future climate change. My research complements the broader objectives of Dr. DeChaine's work, understanding the evolution of North America's arctic-alpine flora. The current distribution of this flora reflects pulses of historic climate change and the coincident advance and retreat of glaciers. By similar processes, ongoing anthropogenic climate change is causing rapid shifts in the distribution and abundance of arctic-alpine plants, possibly resulting in high rates of extinction. I directed my thesis project towards one of the most pressing environmental issues of our time – the conservation of biodiversity in the face of climate change.

Background of the study

Climate change presents a growing threat to global biodiversity. Climate drives the spatial distribution of species, by determining the distribution of environmental conditions that define an organism's physiological constraints. Global warming causes habitats to move along climatic gradients – typically higher in latitude or elevation. The movement of habitat conditions necessitates a biotic response, as a population is exposed to new environmental conditions. A population can adapt to new conditions in place or move in space to track its moving habitat. When a population is unable to either adapt to new conditions or move to a new site where conditions are favorable, it will go extinct.

Species vary in their ability to respond to climate change, and also in their overall vulnerability to extinction. To conserve biodiversity in the face of climate change, managers need to predict which species are the most vulnerable, so that they can target interventions to maximize impact. Determining vulnerability for a single species is a difficult task – it requires extensive knowledge about the demographics, physiology, ecology, and genetics of the species in question. For land managers, this requirement can be prohibitively intensive – such data could take years or even decades of study to generate. There is a great need for techniques that can approximate vulnerability with a minimal amount of data.

Project Overview

In this study, I used a combination of spatial and statistical analyses to compare relative vulnerability for five plant taxa endemic to the Olympic Mountains. The Olympics harbor an exceptional number of rare, endemic, and range restricted alpine plant taxa. Olympic National Park has identified their rare alpine plants as a critical resource in need of conservation, presuming them to be highly vulnerable to climate change. I compared climate change impacts on five plants to assess their vulnerability. The comparative approach allows for inferences about the characteristics of a species' distribution that could predict vulnerability. We can then extend these inferences to other species and other mountain systems, helping guide vulnerability assessments globally. At the same time, it will provide a starting point for land managers to conserve their most threatened species.

The five focal taxa of this study – *Campanula piperi, Viola flettii, Erigeron flettii, Senecio neowebsteri, and Synthyris pinnatifida* var. *lanuginosa* – have not previously been well studied. At the outset of this project, there were not enough reliable occurrence records or distribution data to conduct any kind of climate change impact analysis. This necessitated an extensive field study to locate populations and record habitat information. During the summer of 2015, I conducted a three-month long search for populations of these species using an iterative sampling approach. First, I exhaustively surveyed known population areas to characterize each taxon’s habitat preferences. Then I used these results to guide exploratory sampling in areas where these plants had not previously been reported. This process resulted in the discovery of dozens of new populations and provided enough distribution data to construct solid Species Distribution Models (SDMs).

I also sought to tailor spatial modelling methods to the particular qualities of endemic mountain taxa. These species typically have fragmented, patchy distributions in very specialized habitats across a limited geographic range. Fine scale modelling is required to capture the distribution of microhabitat characteristics that determine the species’ distribution. The typical climate datasets that are used in SDMs are too coarse to reflect microhabitat features such as aspect, topographic exposure, and slope. To surmount this obstacle, I downscaled our climate data to reflect the local topography of the Olympic Mountains, and also modelled habitat directly based on topographic variables. Topographic modelling was based on a 10m resolution Digital Elevation Model, allowing for a much finer scale assessment of habitat requirements and more precise modelling predictions. These topographic SDMs were then combined with the climate-based SDMs to create a hierarchical, topo-climatic model that assessed both climate change impacts and micro-topographic impacts on the future distribution of habitat. This is a novel approach, one that I believe reflects best practices for modelling endemic alpine taxa. To complement the SDM approach, I also used Principal Components Analysis (PCA) to visualize how projected climate conditions compare to current conditions in the Olympic alpine, and the conditions that my focal taxa actually inhabit. These analyses corroborate the SDM results and provide additional insight into how alpine environments are changing due to warming.

Impacts

This thesis aims to increase our knowledge of how mountain systems respond to climate change, advance the field of modelling climate change impacts, and call attention to a group of critically imperiled species – the endemic alpine plants of the Olympic Mountains. It has vastly increased our knowledge of the distribution of the five focal taxa through the discovery of new populations. My results suggest that these and other similar taxa are indeed at high risk of extinction – most or all of their habitat is likely to disappear by 2080 AD. This is the first study to use hierarchical topo-climatic models to assess climate change impacts on endemic alpine plants. I believe it can be used as a guide to inform the study and conservation of similar species worldwide. This research is particularly applicable to other regional mountain systems with similar biogeographic characteristics as the Olympic Peninsula, such as Haida Gwaii and Vancouver Island.

Chapter 2

Retreat to refugia: Severe habitat contraction projected for endemic alpine plants of the Olympic Peninsula

INTRODUCTION

Consequences of a Changing Climate- Anthropogenic global warming and associated climate changes are driving the spatial reorganization of terrestrial habitats and their inhabitants (McCarty, 2001; Parmesan and Yohe, 2003; Walther et al., 2005; Parmesan, 2006). The climate-induced spatial disjunction of species and suitable habitat is accelerating declines in the distribution and abundance of many taxa (Parmesan, 2006). Climate change may surpass habitat degradation as the greatest threat to global biodiversity (Malcolm et al., 2006; Bellard et al., 2012) with extinction rates for terrestrial species approaching forty percent by 2100 AD (Thomas et al., 2004). Understanding the potential impacts of warming with the goal of conserving biodiversity requires strategic assessments of habitat loss and extinction risk (Seo et al., 2009; Dawson et al., 2011). Estimating exposure to climate change, the change in climatic conditions that a population will actually experience, is a critical first step in a general assessment of vulnerability (Dawson et al., 2011; Still et al., 2015). Vulnerability depends on exposure, but also the species' ability to respond to those changes (Thomas et al., 2004; Dawson et al., 2011; Still et al., 2015). Our current framework for estimating species responses to climate-induced range shifts relies heavily on studies of widespread species or entire communities (Kelly and Goulden, 2008; Lenoir et al., 2008; Chen et al., 2011). The potential responses of endemic alpine species have been largely overlooked (Rinnhofer et al., 2012; Jackson et al., 2015). These species likely face the highest exposure and vulnerability, so understanding the dynamics of their response is an urgent conservation imperative (Malcolm et al., 2006).

Targeting endemics for conservation protects taxa that cannot be protected elsewhere, while also conserving a high proportion of regional biodiversity (Lamoreux et al., 2006). Endemism hotspots typically include diverse microhabitats, rich in range-restricted and rare taxa, while also supporting more widespread species. As a result, endemism has been used as a surrogate for overall biodiversity in prioritizing conservation areas (Borges et al., 2000). Species that are locally or regionally rare can increase the breadth of ecosystem functions, supporting the resiliency of the entire community to disturbance (Mouillot et al., 2013; Bruchmann and Hobohm, 2014). For example, removing uncommon species from a community could promote invasion by exotic species (Lyons and Schwartz, 2001). Losing rare and endemic species from alpine ecosystems could have cascading consequences, exacerbating the ongoing extinction crisis (Bruchmann and Hobohm, 2014; Mouillot et al., 2013).

Alpine Endemism: Causes and Consequences- The rugged topography and environmental heterogeneity in alpine environments have generated exceptional rates of endemism (Myers et al., 2000; Körner, 2003; Irl et al., 2015). The alpine, defined loosely as terrain above tree-line, occurs as a geographically isolated archipelago of "sky islands," surrounded by a forested sea of unsuitable lower elevation habitats (Jackson et al., 2015). Islands of alpine tundra drive the development of patchy species distributions with small population sizes and high genetic differentiation (DeChaine and Martin, 2005). Steep environmental gradients create a mosaic of microhabitats over short distances (Dullinger et al., 2011; Scherrer and Körner, 2011), further promoting niche differentiation and speciation

(DeChaine et al., 2014). Finally, the environmental conditions experienced in the alpine tend to reduce competition, favoring slow growing, poor dispersing species (Cody and Overton, 1996; Kikvidze et al., 2005). Alpine endemics are well suited to the narrow set of local conditions in the micro-environments that they inhabit, but could have reduced ability to respond to environmental or ecological changes (Bruchmann and Hobohm, 2014).

The distributions of mountain plants in western North America reflect the legacy of climate fluctuations throughout the Quaternary Period, providing a framework for understanding the potential consequences of future environmental changes (Comes and Kadereit, 1998; Hewitt, 2000; Jackson and Overpeck, 2000; Abbott, 2008; DeChaine et al., 2014). During cold, glacial periods, alpine tundra habitats spread downslope, increasing the area and connectivity of suitable habitat (DeChaine and Martin, 2005). In warm interglacial periods, local environmental conditions in heterogeneous mountain topography become decoupled from those of the surrounding landscape (Daly et al., 2002; Scherrer and Körner, 2011) providing opportunities for cold-adapted species to retreat to *thermal refugia* – pockets of cold microhabitats that serve as sanctuaries for alpine taxa. Populations inhabiting thermal refugia may persist through periods of warming, preserving a reservoir of genetic diversity for recolonization when climatic conditions ameliorate and the distribution of suitable habitat expands once again (Hampe and Petit, 2005). Thus, the thermal refugia of mountain systems have buffered global biodiversity from extinctions during changing climates (Keppel et al., 2012).

Species response to climate change- Historically, species have displayed a suite of common responses to pulses of expansion and contraction of their habitat. They have: 1) tolerated new conditions in situ; 2) shifted their physical habitat locally to track favorable conditions; 3) migrated to suitable habitat elsewhere; 4) adapted to changing conditions; or 5) gone extinct (Dawson et al., 2011). Few of these options are available for alpine endemics. Tolerating change in situ is unlikely for endemic taxa with specialized habitat preferences. These taxa are adapted to a narrow range of environmental conditions, and have responded to past climate change by tracking habitat shifts over short-distances (Jackson and Overpeck, 2000; Broennimann et al., 2006; Jackson et al., 2009). If the magnitude of climate change is great, suitable habitat may disappear locally (Hampe and Petit, 2005; Williams et al., 2007), removing proximal habitat tracking as a possible response. Many alpine endemics are already occupying the highest elevation habitats in their range, so upslope migration is impossible. Migrating to distant sites is dependent on the dispersal capabilities and the degree of geographic isolation of a given population (Dullinger et al., 2011). Endemic alpine species face major dispersal barriers (Thomas, 2011) and are often poor dispersers (Cody and Overton, 1996), compromising their ability to migrate to distant sites. Adapting to new conditions depends primarily on the innate biological characteristics of the species – phenotypic plasticity, genetic diversity, and evolutionary capacity (Dawson et al., 2011). The small, isolated, populations common to alpine endemics are more vulnerable to extinction due to stochastic factors (Davies et al., 2004; Matthies et al., 2004). Bottlenecking of small populations can lower genetic diversity, providing limited raw material for adaptation to novel environments (Frankham, 2008). In terms of exposure, sensitivity, and adaptive capacity, endemic alpine taxa are likely to be exceptionally vulnerable to warming (Dirnböck et al., 2011; Thomas, 2011).

The current pace and magnitude of warming may overwhelm much of the alpine's capacity to harbor endemics in thermal refugia. Treelines throughout North America have moved upslope, shrinking alpine habitats (Luckman and Kavanagh, 2000; Devi et al., 2008; Flower et al., 2013). In the Canadian Rockies, average yearly temperatures have increased by 1.5°C over the past century. Warming has been more significant during winter, contributing to a 25% decline in glacial ice cover (Luckman and Kavanagh, 2000). Substantial decreases in the abundance and size of cold microsites are expected under 2°C of further warming (Williams et al., 2007) and many of the coldest microclimates may disappear entirely over the next century (Williams et al., 2007; Scherrer and Körner, 2011). Even where suitable habitat remains, increased competition and crowding is likely to negatively impact abundance (Ackerly et al., 2010).

Empirical evidence and predictive simulations from around the globe illustrate the ongoing habitat displacement and decline experienced by alpine plants due to warming, with particularly severe consequences for endemics (Pauli et al., 2003; Dirnböck et al., 2011; Lesica, 2014). In a study of 171 Western European plant species, optimum elevation increased by an average of 29m per decade, with higher rates observed in mountain species (Lenoir et al., 2008). Shifts in species composition towards warm-site adapted species has been observed across the European Alps, with the magnitude of turnover correlated with the degree of local warming (Gottfried et al., 2012). In the Rocky Mountains of North America, alpine indicator species have declined in abundance by 31-65% (Lesica et al., 2004). The pace of projected 21st century warming exceeds that of the historic record (IPCC, 2014), driving an estimated 41% decrease in species richness for the endemic flora of South Africa (Broennimann et al., 2006), the extinction of 200 native species in New Zealand (Halloy and Mark, 2003), and extensive habitat reduction for 66% of California's endemic flora (Loarie et al., 2008).

The studies above underscore the urgency of research on endemic alpine species. To mitigate biodiversity loss in sky island systems, managers need to rapidly identify vulnerable taxa. While alpine endemics as a group are highly vulnerable, each species will respond individually. By comparing climate change impacts amongst a suite of taxa, we can assess the range of individual responses and identify characteristics that predict vulnerability. We can also identify the location and characteristics of potential thermal refugia – areas that will be critical for maintaining alpine biodiversity.

Endemism and Climate Change in the Olympic Mountains- The Olympic Mountains of Washington (Figs. 1a, 1b) are an ideal system for investigating the dynamics of alpine endemic plant distributions in a rapidly changing climate. The Olympics are an isolated range with steep environmental gradients and a history as both a glacial and thermal refugium, characteristics that have promoted the development of a diverse flora with exceptional endemism (Buckingham et al., 1995; Peterson et al., 1997; Gavin, 2015). Floral distributions have been highly responsive to historic climate changes, tracking shifting habitats along environmental gradients (McLachlan and Brubaker, 1995; Gavin and Brubaker, 1999). Because the vast majority of the Olympics are protected as national park or wilderness, anthropogenic impacts on the flora through land use changes are minimal. Olympic endemics are concentrated in the highest elevation areas of Olympic National Park, they have little room to move upslope and are thought to be highly vulnerable to climate change (Halofsky et al., 2011; Gavin, 2015). Understanding the response of Olympic alpine endemics to warming will inform conservation in systems with similar biogeographic characteristics, and more broadly, to global biodiversity of mountain systems and endemism hotspots.

The Olympic flora includes nine true endemics, six shared endemics with Vancouver Island, and over 30% of Washington's state listed rare taxa (Buckingham et al., 1995, Table A1). Many of these taxa have disjunct distributions, with nearest relatives occurring hundreds or thousands of miles away in Beringia or the Rocky Mountains (Hitchcock et al., 1969; Buckingham et al., 1995; Marlowe and Hufford, 2008; Gavin, 2015). The Olympic alpine endemics currently occupy fragmented patches with very specific habitat preferences at high elevations (McLachlan and Brubaker, 1995; Peterson et al., 1997; Gavin et al., 2013). This unique flora is the result of pulses of climate change and glacial advance and retreat throughout the Quaternary Period, combined with continuous geographic isolation. During glacial maxima, the Cordilleran Ice Sheet filled the Strait of Juan de Fuca and Puget Trough, pushing up the northeastern river valleys of the Olympics and creating a huge outwash plain in the Chehalis lowlands to the south (Buckingham et al., 1995; Thackray, 2001). The Olympics, Vancouver Island, and Haida Gwaii (Fig. 1a), were all critical glacial refugia in the Pacific Northwest, acting as islands of ice-free habitat that harbored alpine-tundra species during the ice ages (Ogilvie and Ceska, 1984; Buckingham et al., 1995; Hebda and Haggerty, 1997; Byun et al., 1999; Shafer et al., 2010). Each of the three areas are unique, but host similar, insular floras, with several shared endemics between them (Buckingham et al., 1995). During warm interglacial periods, alpine-tundra habitats contracted to the highest ridges and summits, isolated by forested valleys, lowlands, or ocean from other alpine environments (Gavin and Brubaker, 2014). In response to these historic pulses of climate change, cold-adapted species have expanded and contracted their distributions locally along elevation gradients, unable to disperse to distant sites or along latitudinal gradients due to geographic isolation. Because of the similarities in the history and distribution of alpine plants throughout the region, the response of Olympic endemics can serve as a model for other glacial and thermal refugia across the North Pacific Rim.

Assessing the future of the Olympic alpine endemics- The overarching objective of this study was to evaluate the potential responses of endemic alpine plants to predicted climate change scenarios of this century. The Pacific Northwest could see up to a 3 °C increase in mean annual temperature over the next century, with more warming occurring in the winter months and a general shift towards wetter winters and drier summers (Mote and Salathe, 2010). This will likely drive changes in the distribution of suitable habitat for the Olympic alpine endemics. To assess this, we investigated exposure to climate change for five Olympic alpine endemics through Principal Components Analysis (PCA) and Species Distribution Models (SDMs). Because of the complexity of local environments and specific habitat requirements of these taxa, we used micro-topographic habitat models to refine SDM projections. This approach enabled us to address the following questions concerning general trends and individual responses of each taxon: 1) How exposed are alpine endemics to climate change driven habitat loss? We expected that future habitat conditions in the Olympic alpine will be a significant departure from the current climate envelopes these taxa inhabit, driving large reductions in suitable habitat for all five taxa. 2) How does micro-topography affect habitat loss projections? By incorporating high resolution topographic models, I hope to improve suitable habitat projections, and capture the impact of changing distributions of topographic characteristics as habitats move upslope. 3) What are the locations and characteristics of potential thermal refugia in the Olympic Mountains? Given the relatively low elevations of the Olympic Mountains, thermal refugia will likely persist only in the highest, most topographically complex habitats of the Olympics.

METHODS AND MATERIALS

Overview- This study involved four major components: 1) A field sampling study to locate sufficient occurrence data for high-resolution habitat modeling and fully characterize each taxon's distribution, 2) PCA to assess each taxon's climate envelope relative to current and projected future conditions in the Olympic alpine, 3) SDMs to project changes in the suitable habitat distribution for each taxon and identify potential thermal refugia, and 4) topographic suitability modeling to refine climate-based predictions and further investigate the influence of micro-topography on potential refugia. Unless otherwise specified, all spatial analyses were conducted in ArcMap v. 10.3.1.

Focal Taxa- Out of the nine plant taxa endemic to the Olympic alpine (Table A1), five were selected for final analysis (Fig. 2): *Campanula piperi* Howell (Campanulaceae), *Viola flettii* Piper (Violaceae), *Erigeron flettii* G.N. Jones (Asteraceae), *Senecio neowebsteri* S.F. Blake (Asteraceae), *and Synthyris pinnatifida* var. *lanuginosa* (Piper) Cronquist (Plantaginaceae). These species were selected because they have truly alpine distributions and sufficient numbers of reliable occurrence points. As a secondary consideration, we chose species that reflect the taxonomic and ecological diversity within the alpine. Four families and three distinct habitat types are represented (Table A1). Other species were excluded due to: a) taxonomic questions and the potential for misidentification; b) extreme rarity and difficulty of acquiring enough population locations; or c) relatively wide distributions throughout subalpine and montane environments. All five taxa are of conservation concern due to their habitat specificity, endemism, and high elevation. However, little is known about their ecology, demographics, or genetics.

- *Campanula piperi* (Fig. 2a), Piper's harebell, is a prostrate, spreading herb, often forming dense cushions along cracks and crevices in rock. It is an Olympic endemic, locally common on rocky exposed habitats throughout the alpine (Hitchcock et al., 1969; Pojar and Mackinnon, 2013). This species is a member of the Cordilleran clade of *Campanula* that is comprised of several narrowly endemic species in the mountains of western North America (Wendling et al. 2011).
- *Viola flettii* (Fig. 2b), Flett's violet, is a small, perennial herb, inhabiting crevices in rock outcrops in the alpine zone, and is occasionally found on talus or scree beneath outcrops (Hitchcock et al., 1969). *Viola flettii* is a sister taxon to *V. cuneata* and *V. ocellata*, within the *Viola canadensis* complex, a group of western North American endemics with diverse habitats and ecologies (McCreary, 2005). It is a rare endemic to the eastern Olympic Mountains, threatened by herbivory from introduced Mountain Goats (Pojar and Mackinnon, 2013).
- *Erigeron flettii* (Fig. 2c), Flett's fleabane, is a rare endemic, uncommon on rock outcrops in the eastern Olympic Mountains (Hitchcock et al., 1969; Pojar and Mackinnon, 2013). Few reliable historical records and almost no scientific literature exists for this taxon.
- *Senecio neowebsteri* (Fig. 2d), Olympic Mountain groundsel, is a perennial herb, inhabiting steep, loose, rocky substrates at subalpine to alpine elevations (Hitchcock et al., 1969; Pojar and Mackinnon, 2013). When present in these habitats, it can be among the most abundant of vascular plant species (personal

observation). Its putative closest relative, *S. spribillei*, is a narrow alpine endemic of the Rockies in Montana (Weber, 2002).

- *Synthyris pinnatifida* var. *lanuginosa* (Fig. 2e), Olympic Mountain synthyris, is a prostrate, cushion-forming herb, inhabiting exposed ridgetop fellfields. While locally common in its habitat, it is a rare endemic (listed as threatened by the Washington Natural Heritage Program) found only in the northeastern-most Olympic Mountains (Hitchcock et al., 1969; Pojar and Mackinnon, 2013). *Synthyris pinnatifida* var. *lanuginosa* is disjunct from sister taxa in the northern Rockies, a distribution believed to reflect glacial vicariance (Hufford and McMahon, 2004; Marlowe and Hufford, 2008).

Iterative Sampling Framework- SDMs are useful tools in locating new populations of rare taxa and targeting field sampling (Guisan et al., 2006; Williams et al., 2009; Sousa-Silva et al., 2014). To improve the quantity and precision of occurrence data, we employed an iterative modeling and sampling approach. Georeferenced herbarium records were used to generate an initial map of reliable occurrences. Because their distributions had not been characterized with enough accuracy to create high-resolution habitat models, a field study was necessary as a pre-cursor to any serious vulnerability assessment. I first sampled near known populations, and then used occurrence data to create preliminary SDMs. We identified areas of high habitat suitability where taxa have not previously been documented, targeting these areas fora second round of sampling. Occurrence data from both rounds of field sampling were combined to build final SDMs for each taxon.

Location data- Herbarium records were compiled in January 2015 from the Consortium of Pacific Northwest Herbaria (www.pnwherbaria.org), Canadensys (www.canadensys.net), the Olympic National Park Herbarium and the Royal British Columbia Museum. Duplicate records were removed. During February and March of 2015, I georeferenced every record to assess their spatial accuracy, following the SAGA protocol of Bloom et al. (in review). Where coordinates were available, latitude and longitude values were entered in Google Earth and/or Hillmap (http://www.hillmap.com/), a digital mapping program with USGS topographic layers. Locations were cross-checked for agreement with locality descriptions in the record. If latitude and longitude data were unavailable, locality information was used to approximate the location of the collection site on the map and obtain coordinates. For each record, I assigned a qualitative spatial confidence score on a 1-5 scale (Table A2). All records with a geographic uncertainty >1km (scores 4-5), were removed from further analyses.

Field Sampling- The first round of sampling was designed to comprehensively sample terrain near known populations. Three areas were targeted as having suitable habitat characteristics and reliable historical records for the focal taxa: 1. Dungeness Headwaters/Buckhorn Wilderness; 2. Hurricane Ridge/Klahane Ridge; and 3. Skokomish Wilderness/Mt. Ellinor (Fig. 1b). These areas were sampled between June 21st and July 21st, 2015. Search transects were established near known occurrence locations across gradients in elevation, aspect, and topographic position. Sampling circles of 10m radii were established at every 100m change in elevation along each transect. Ten meters was intended to be large enough to capture rare, patchily distributed species, while remaining manageable for one person to search. The area within this circle was searched to confirm presence or absence of target taxa. For all sites, I recorded latitude and longitude coordinates, GPS uncertainty, elevation, aspect, substrate, community associations, and qualitative site descriptions. Any target taxon encountered along the transect between search circles was recorded as a presence along with a complete site record. Areas of obvious unsuitability (e.g. forest cover, ice) were recorded as absences without a search.

Occurrence data generated in the first sampling round were used to construct basic SDMs for each taxon in ArcMap. I extracted PRISM climate data to occurrence locations to establish climate envelopes for each variable, and then generated habitat suitability rasters based on the number of variables that fell within the range of observed values for each taxon. The northern Bailey Range and the ridge complex between Grand Pass and Hayden Pass in the central Olympics were identified as areas of highly suitable habitat for a majority of taxa that did not have historical occurrence records (Fig. 1b). Selected areas were sampled in August and September of 2015 using the same field protocol described above. Occurrence records from both rounds of sampling were combined to create a master dataset of presences and absences for final analysis.

Predictor Variable Generation- Species Distribution Modeling and PCA were based on a selected set of environmental predictor variables, combined with the occurrence data described above. All variables were based on a 10m Digital Elevation Model (DEM) of the Olympic Peninsula. The DEM tiles were downloaded from the University of Washington (https://wagda.lib.washington.edu/data/geography/wa_state/#elevation) in ASCII raster format and joined together into a single mosaic raster in ArcMap. The mosaic DEM was then clipped to include only terrain over 800m in elevation, thus defining the extent of all spatial analyses. The DEM was resampled to 30m for use in downscaling. Downscaling is a critical step in habitat modelling for mountain taxa, reflecting the intense local effects of topography and elevation on microclimate (Flower et al., 2013; Irl et al., 2015). Twenty-four annual bioclimatic variables from the PRISM dataset (Daly et al., 2002), for the Normal Period (1961-1990) were downscaled to 30m resolution in ClimateWNAv4.62, downloaded from the University of British Columbia Center for Forest Conservation Genetics (cfcg.forestry.ubc.ca/projects/climatedata/climatebcwna/#ClimateWNA) in August 2015. The same 24 variables were downscaled for the 2080 ensemble averages of the 23 CMIP3 Global Circulation Models (GCMs) available in ClimateWNA with the A2 emissions scenario. Given the current trajectory and demonstrated emissions since this generation of models was developed, A2 was the most realistic of the available scenarios (Peters et al., 2013).

The following topographic variable rasters were calculated in ArcMap based on the 10m DEM: slope angle, aspect, Topographic Position Index (TPI), and solar radiation. The aspect raster was transformed into variables representing Northness (-cos(aspect*PI/180), Eastness (sin(aspect*PI/180), and Northeastness (sin((aspect*PI/180)+PI/4)) on a scale of -1 to 1, with 1 being due north, east, or northeast, respectively. TPI is a measure of the relative elevation of a point to its surroundings, representing the degree of exposure of a point, and the concavity/convexity of the terrain. I calculated TPI as *elevation-focal mean,* where elevation is the elevation at the point of interest and the focal mean is the average elevation of each grid cell in the defined focal radius, at focal radii of 20m, 30m, 50m, 100m, 300m, and 500m. Solar radiation combines slope, aspect, and latitude measurements to calculate the intensity of solar radiation experienced at a given point. I calculated the annual mean and daily average solar radiation intensity (in Watts/m^2) at each solstice.

Variable selection- I reviewed high elevation and rare plant niche modeling studies, (Guisan et al., 1998; Guisan and Theurillat, 2000; Guisan et al., 2006; Hijmans and Graham, 2006; Williams et al., 2009; Austin and Van Niel, 2011; Gogol-Prokurat, 2011; Brenna R Forester, 2013; Flower et al., 2013; Alfaro-Saiz et al., 2014; Barbet-Massin and Jetz, 2014; Sousa-Silva et al., 2014; Oke and Thompson, 2015) and studies of alpine plant ecology (Körner, 2003; Kikvidze et al., 2005; Löffler, 2007; Rixen et al., 2014; Wehn et al., 2014), selecting ClimateWNA variables that were commonly used and deemed ecologically relevant. The remaining nine predictor variables were clipped to the study extent and extracted as latitude-longitude coordinate point tables. To eliminate correlated predictor variables, which can diminish model realism (Franklin, 2010), I assessed a PCA (Table A3) and correlation matrix (Table A4) generated in R v.3.2.2. I selected five variables for final consideration, choosing 1-2 variables that loaded heavily on each of the first five principle component axes (Table A3). When multiple variables were highly correlated and had similar PC loadings, preference was given to the variable with greater ecological relevance. Two of the remaining variables, Mean Annual Temperature (MAT) and Mean Warmest Month Temperature (MWMT), were highly correlated, so I compared their performance in pairs of candidate SDMs (Table A5). SDMs were assessed in Maxent v. 3.3.3k ((https://www.cs.princeton.edu/~schapire/maxent), and in a Logistic Regression Generalized Linear Model (GLM) using randomly generated pseudo-absences in R. The GLM formula was $logit = (\beta 0 + \beta 1X1 + \beta 2X2 \ldots)$ where X represents the predictor variables and β are the model coefficients. Area Under Curve (AUC) and the Minimum Predicted Area to achieve 95% commission (MPA_{95}) scores were calculated in Maxent. Aikake's Information Criterion (AIC) scores were generated for the GLMs. Maxent performance metrics were somewhat equivocal, but AIC scores for models using MAT were significantly lower (more likely) than models using MWMT for four out of five taxa (Table A5). For consistency across models, final climate models for all taxa used Climatic Moisture Deficit (CMD), Continentality (TD), Precipitation As Snow (PAS), and MAT.

Topographic candidate models were compared using presence-absence data and logistic regression in R. AIC scores were used to select the most likely model and classification tables were used to assess discrimination ability. Models using TPI at 20m focal radius (TPI20), Slope, and Annual Solar Radiation (ASR) minimized AIC and maximized correct classification of presence/absence.

Principal Components Analysis **–** The PCA had two purposes: 1) to characterize the breadth of climate conditions experienced across each taxon's range relative to the entire range of climatic conditions present in the Olympic alpine and 2) to estimate the degree of exposure by visualizing the disjunction of future alpine climate conditions with current conditions. PCA was conducted in R on a scaled, centered data matrix of 1848 points and their extracted climate values for the four bioclimatic predictor variables. One hundred ninety-two points encompassed the presence locations for all five taxa. 828 points were randomly generated from the extent of terrain in the Olympic Mountains above 1400 m to represent current climatic conditions in the Olympic alpine. 1400 m is an approximation of the average position of treeline in the eastern Olympic Mountains, discerned using satellite imagery in Google Earth. Future bioclimatic predictor values were calculated for the same 828 points to represent future alpine conditions.

Species Distribution Modeling Framework- Rather than combining topographic and climatic variables into one predictive model, I built independent climate and topographic SDMs at different spatial resolutions, combining them into a hierarchical topo-climatic model. Hierarchical modeling has been proposed as a way to improve the realism and accuracy of SDMs (MacKey and Lindenmayer, 2001; Trivedi et al., 2008). Climate variables influence species distributions at a broader scale, are interpolated from coarse native datasets, and discriminate well between suitable habitat and the background conditions of the study extent. Topographic variables better reflect microhabitat characteristics, discriminate well between actual presence and absence sites, and can be generated at much finer resolution (MacKey and Lindenmayer, 2001). I generated climate SDMs in Maxent to define the climate envelope, the general extent of habitat suitability. Within this extent, we applied a topographic-only, presence-absence SDM using logistic regression in R to predict probability of occurrence at fine spatial scales and assess changes in topographic suitability between current and future climate envelopes.

Model Refinement and Validation- Final climate models were run in Maxent with 10-fold cross validation to assess model stability and uncertainty. Cross validation is a preferred method where small sample sizes prevent the use of independent training and test data (Pearce and Ferrier, 2000), as in the case of the focal taxa. Prevalence was set individually for each species as the proportion of presences within total sampling points. Maxent logistic outputs were projected into ArcGIS as rasters of continuous habitat suitability values from 0 to 1. A binomial threshold value for suitability was established for each species to achieve 95% commission (the proportion of presence sites designated as suitable by the model). The resulting climate suitability raster was then used to define the extent of projection for the topographic model. Habitat suitability was classified based on Maxent suitability scores as Unsuitable (<0.01), Low (0.01-0.1), Moderate (0.1-0.34), or High (>0.34).

Output from topographic models were transformed into rasters representing the probability of occurrence at each grid cell, scaled between 0 and 1. This is calculated by the formula: $\frac{1}{1+e^{-logit}}$,where the logit is the response variable for the logistic GLM equation: $logit = (\beta 0 + \beta 1X1 + \beta 2X2 \ldots)$ where X represents the predictor variables and β are the model coefficients. A binomial suitability threshold was established to maximize model discrimination success for each species. Topographic suitability rasters were then clipped to the extent of suitable habitat defined by both the current and future climate SDM projections. I calculated the proportion of suitable topography within each SDM time period, and then calculated the percent habitat reduction for both climate-only SDMs and the combined topo-climatic SDMs as:

$$\frac{Area\ of\ currently\ suitable\ habitat - area\ of\ future\ suitable\ habitat}{Area\ of\ currently\ suitable\ habitat} \times 100$$

RESULTS

Field Sampling- I sampled a total of 260 sites over two rounds, including the discovery of 40 new occurrences in areas where the focal taxa had not previously been recorded (Table 1), expanding our understanding of the habitat preferences and distributions of these taxa. *Campanula piperi* was encountered on rocky outcrops, cliffs, talus, and scree, usually above 1500 m, in all study areas. *Viola flettii* occurred infrequently, in all study areas, typically in small, isolated patches on ledges, cliffs, and outcrops above 1500 m. *Erigeron flettii* occurred throughout the eastern Olympics, from Royal Basin south to Mt. Ellinor, in small (often less than 10 individuals), isolated populations on ledges and cliffs above 1400 m. The three aforementioned taxa were also occasionally discovered on outcrops and boulders in drainages at slightly lower elevations. *Senecio neowebsteri* inhabited all study areas north of the Dosewallips River, usually at elevations over 1700 m. It was strictly limited to steep slopes on unstable substrates ranging from gravel to talus. When found, *S. neowebsteri* was often locally common. *Synthyris pinnatifida* var. *lanuginosa* was found only east of the Elwha and north of the Dosewallips, usually over 1700 m. Therein it was limited to high, exposed ridgetop fellfields, and was at times locally common in those habitats.

Principal Components Analysis- The PCA defined the breadth of climate conditions experienced by each taxon and visualized the magnitude of future habitat changes in the alpine. A scatterplot of the first two principal components (Fig. 3) showed well defined climate space for current and future alpine conditions and individual taxa. Climatic Moisture Deficit (CMD) and Continentality (TD) loaded heavily on PC1, which accounted for 43% of observed variance, while PC2 was primarily driven by PAS and MAT, accounting for 35% of variance (Table 2). A high value for PC1 represents a climate with lower seasonal temperature differences and less droughty conditions in the summer, conditions that characterize the milder, more maritime climate of the western Olympics. Higher values for PC2 describe a colder climate with more precipitation falling as snow, conditions which currently predominate at the highest elevations of the Olympic alpine. Future climate space is projected to be a significant departure from current alpine conditions, with little overlap between the two time periods. Future points are lower on the PC2 axis, indicating that increasing temperature and decreasing winter snowpack could be major drivers in habitat changes. CMD and TD are both projected to increase, driving a smaller translocation of climate space along the PC1 axis (Fig. 3).

All five taxa currently occupy a colder, drier, snowier subset of the Olympic alpine climate conditions. Their distributions are centered in the northeastern or eastern Olympics, on the drier, leeward side of the peninsula. We projected minimal overlap between each taxon's climate envelope and future conditions, suggesting severe disjunction of current populations with their future suitable habitat envelopes. Overlap was the smallest for *E. flettii* and *S. pinnatifida* var. *lanuginosa*, which experienced the narrowest range of climate conditions at field sites. *Campanula piperi*, *V. flettii*, and *S. neowebsteri* occupied comparatively broader climate envelopes (Fig. 3), but still projected low overlap with future conditions.

Species Distribution Modeling- Maxent produced discriminant, stable, and robust predictions of suitable habitat for all five taxa. Mean AUC scores over 10 cross-validated runs all exceeded 0.95 (st.dev. < 0.02), indicating stable models and sufficient sample sizes to characterize habitat (Table 3). Suitable habitat aligned well with known distribution ranges, and the most highly suitable habitats occurred in areas known to be centers of abundance for each taxon. Models did not project suitable habitat in high alpine regions where taxa have not been reported, further supporting their discriminating power (Fig. 4). The following are descriptions of projected suitable habitat for the present and future (2080 AD), for each taxon, presented in order of total areal extent of suitable habitat.

- For *C. piperi* under current conditions, models predicted a continuous network of highly suitable habitat throughout the high ridge complexes of the northern and eastern mountains, from Klahane Ridge to Mount Constance. Significant patches with moderate and high suitability were also found in the Skokomish Wilderness and northern Bailey Range. Generally, habitat suitability increased along with elevation (Fig. 4a). Suitable habitat for *C. piperi* contracted by 86% by the year 2080 (Table 3) across the current range, with the most extensive losses in the northern Olympics. The Bailey Range and Hurricane Ridge/Klahane Ridge areas will lose nearly all of their suitable habitat. Suitable habitat remained only on the high peaks and ridges of the eastern Olympics, at elevations above 1900m (Fig 4a).

- The distribution of currently suitable habitat was similar for *V. fletti*, although there was considerably less moderately and highly suitable habitat (Fig. 4b). *Viola flettii* lost 89% of its suitable habitat (Table 3), including nearly all the habitat around its northern populations in the Bailey Range and Hurricane Ridge areas. Suitable habitat remained in fragmented patches on peaks along the Dosewallips-Dungeness divide, at Mt. Constance and around Mt. Stone in the Skokomish Wilderness (Fig. 4b).
- For *E. flettii*, low to moderately suitable habitat was distributed widely throughout the eastern Olympics (Fig. 4c). Patches of high habitat suitability occurred on northeastern peaks and in a significant patch around Mt. Stone and Mt. Skokomish in the southern Olympics (Fig. 4c). In the future, only tiny fragments of low habitat suitability remained on Mt. Constance and a few nearby peaks. Overall reduction was 99% (Table 3).
- Currently suitable habitat for *S. neowebsteri* was restricted to the northeastern Olympics, from Klahane Ridge to Mt. Constance, with other significant patches in the Northern Baileys, and a few patches south of the Dosewallips (Fig. 4d). High habitat suitability occurred primarily on the high, northeastern ridges, from Marmot Pass to Elk Mountain. Habitat was reduced by 99% (Table 3), with remaining fragments on Mt. Constance and along the Dosewallips-Dungeness divide (Fig. 4d).
- Finally, currently suitable habitat for *S. pinnatifida* was limited to the high ridges of the northeastern Olympics, from Klahane Ridge to Mt. Constance. Habitat contracted by 99%, to small fragments on Mt. Constance and nearby peaks to the west (Fig. 4e).

All taxa projected massive habitat contraction throughout their ranges, with near total loss around northern populations in the Bailey Range, Mt. Angeles, and Hurricane Ridge areas. Highly suitable habitat patches became smaller and more fragmented. Taxa with higher elevation ranges, lower prevalence (Table 1), and narrower climate envelopes (Fig. 2), experienced higher habitat loss, greater fragmentation, and lower suitability within potential refugia (Fig. 3). Mt. Constance, the peaks of the upper Dosewallips, Mt. Stone, and The Brothers were identified as potential thermal refugia (Fig. 5). In these areas, habitat suitability was maintained or occasionally even increased in the future (Fig. 4).

Topographic Suitability Modeling- Topographic suitability modeling showed promising ability to predict presence and absence at high spatial resolution (Fig. 6). The thresholds used to define suitable habitat ranged from 0.11 to 0.35, and closely approximated the field prevalence of the taxon. The area and proportion classified as suitable/unsuitable and the correct percentage of presences/absences were highly sensitive to the choice of threshold (Table 4).

Models for four of five taxa correctly predicted more than 70% of presences. The model for *E. flettii*, which was the least prevalent of the five taxa, had no significant predictor variables and correctly predicted only 56% of presences. The model for *S. pinnatifida* var. *lanuginosa*, which correctly predicted 85% of presence locations, was the only model to predict less than 50% of absences. Models for all five taxa had positive slope coefficients, indicating that they were more likely to be found on steeper slopes. Slope coefficients were significant predictors for *C. piperi* and *V. flettii.* ASR coefficients were positive for all taxa except *E. flettii*, although they were significant only for *S. pinnatifida* var. *lanuginosa* and *S. neowebsteri*. TPI was a significant predictor only for *C. piperi* (Table 4).

When topographic models were projected within the current and future climate envelope models, overall areas classified as suitable were greatly reduced. The coupled models also portrayed suitable habitat as highly fragmented and sensitive to subtle differences in local topography (Fig. 6a). While the amount of projected suitable topography was sensitive to the choice of threshold, the change in proportional suitable topography between current and future climate envelopes was consistent for each taxon, regardless of threshold. The future climate envelopes of *C. piperi* and *V. flettii* contain higher proportions of suitable habitat than the current envelope. Therefore, the projected habitat loss for the coupled topo-climatic model is reduced relative to the climate-only model (Fig. 6b). *E. flettii, S. neowebsteri, and S. pinnatifida* var. lanuginose were projected to lose more than 99% of their climatically defined suitable habitat, leaving only tiny fragments within which to evaluate topography. Inclusion of topographic models did not appreciably alter the projected habitat reduction for these taxa.

DISCUSSION

Field study – My sampling efforts greatly increased the knowledge of the distributions of five threatened endemic taxa (Table 1). By utilizing an iterative sampling and modelling approach, I was able to locate new populations of each taxon, improving my ability to model habitat accurately and aiding future research and conservation efforts. I recommend this approach whenever habitat modelling is undertaken with rare or cryptic species. SDMs and other correlative niche models have great potential for streamlining field sampling and locating unreported populations. Field sampling confirmed that *C. piperi, V. flettii, E. flettii, S. neowebsteri*, and *S. pinnatifida* var. *lanuginosa* are habitat specialists within a narrow range of environmental conditions – generally, the rocky terrain of the high alpine. While elevation is a broadly limiting factor, micro-topography appears to be critical in structuring the distributions of these taxa at fine spatial scales.

***The changing climate of the Olympic alpine* –** The PCA scatterplot visualized two important trends for the plants of the Olympic alpine. First, future conditions in the Olympic alpine will be a radical departure from the current climate; under the A2 scenario temperatures will be hotter, growing season moisture deficits will increase, and winter snow will be greatly reduced (Fig. 2, Mote and Salathe, 2010). This portends a dramatic restructuring of alpine plant communities. Second, the five endemics that I studied already occupy narrow climate envelopes at the cold, snowy edge of current climate space in the Olympic alpine (Fig. 3). As temperatures warm and precipitation at high elevations shifts from snow to rain, these climate conditions will cease to exist. The endemics have essentially topped out – they are already occupying the highest and coldest available terrain, and there is no colder climate space available for their distributions to shift into as climate warms. This corroborates the growing body of literature suggesting that high elevation taxa, especially those inhabiting the cold edge of available climate space, are the most exposed and possibly most vulnerable to climate change (Guisan and Theurillat, 2000; Fagre et al., 2003; Halloy and Mark, 2003; Lenoir et al., 2008; Dullinger et al., 2011; Rixen et al., 2014; Wehn et al., 2014; Dobrowski and Parks, 2016). Amongst the five endemics, the taxa with more restricted geographic ranges and more specialized habitat preferences have narrower climate envelopes (Table 1, Fig. 3). Their climate space is less likely to overlap with future conditions, constituting higher exposure than more broadly distributed alpine taxa.

My results strongly support the expected trend of contraction of suitable habitat to the highest available elevations, with coincident fragmentation and isolation of remaining refugia. All five taxa have distributions centered in the highest locally available terrain, so as warmer conditions drive the climate envelope upslope, total suitable habitat area is greatly reduced (Fig. 4). The similarities in patterns of reduction indicate that these taxa share the same climatic niche. Furthermore, the shared signal of complete habitat loss in northeastern Olympics indicates that this area – the driest region of the Olympics, may be close to environmental thresholds that constrain alpine plant life (Fig. 4). This region may thus experience the greatest extent and pace of vegetation turnover, as nearly all of its precipitation as snow shifts to rain, compounding increased summer moisture deficits. The shared distributions of thermal refugia indicate common characteristics that define the best habitat for all of these taxa. Thermal refugia are clustered on the highest peaks of the eastern Olympics, but not on the high peaks of the Bailey Range and Mt. Olympus Massif (Fig. 5). While the northeastern mountains may be too dry, the western peaks could be too wet. The Mt. Constance area represents an optimal combination of elevation, projected temperatures, and precipitation, where favorable habitats could persist for all five taxa well into the 21st century.

Differences amongst taxa* -** Differences in climate SDM projections between taxa were mostly a matter of extent, not pattern. I found that a taxon's degree of rarity corresponded to its projected habitat loss. While a number of studies have suggested that endemic taxa are disproportionally vulnerable (Broennimann et al., 2006; Malcolm et al., 2006; Loarie et al., 2008; Dirnböck et al., 2011), specific characteristics of these taxa's distributions seem to correlate with habitat loss: 1) ***Geographic range – *C. piperi* and *V. flettii* were more broadly distributed and had more modeled suitable habitat while *S. neowebsteri* and *S. pinnatifida* var. *lanuginosa* have narrower ranges and had higher projected habitat reduction (Figs. 3 and 4). Populations of the more narrowly distributed taxa were also likely to be further from projected thermal refugia (Fig. 5); 2) ***Prevalence*** - the most common taxon, *C. piperi*, had the least habitat loss while the least common, *S. pinnatifida* var. *lanuginosa* and *E. flettii*, experienced the greatest habitat loss and highest exposure (Tables 1 and 3, Figs. 3 and 4); and 3) ***Elevation*** – The highly exposed *S. pinnatifida* var. *lanuginosa* and *S. neowebsteri* have both the narrowest elevation ranges and the highest mean elevations (Table 1). They are narrowly adapted to the coldest habitats, conditions that may disappear entirely from the Olympic alpine (Fig. 3).

***General patterns of topographic suitability models* -** More realistic projections of suitable habitat and habitat loss were attained through the addition of nested topographic suitability models. Because these topographic models are a subset of climate envelope models, the total area of suitable habitat is necessarily reduced when the models are combined (Fig. 6a). We believe including topographic models greatly enhances the realism of SDMs and more accurately estimates the distribution of both current and future suitable habitat. A climate envelope based model alone will overestimate the amount and connectivity of suitable habitat, especially for taxa with specialized habitat requirements. Further, assessing vulnerability based only on the change in climate envelopes misses an important associated factor – the change in the distribution of topography. While topography itself will not change appreciably over the next 100 years, as climate envelopes shift upslope, they may encompass different distributions of topographic characteristics (Scherrer and Körner, 2011). For example, there may be higher slope angles, different substrate types, or more exposed terrain within the higher elevations of the future climate envelope. This changing proportion of suitable topography could alter projections of habitat changes under warming.

In the example of *C. piperi* and *V. flettii*, I found a higher proportion of suitable topography within the future climate envelope compared to the present (Fig. 6b). Therefore, the percent reduction in suitable habitat was less for the combined topo-climatic model than for the climate only model. This illustrates the potential buffering effect of rugged, high elevation terrain, a phenomenon that has made mountains refugia for biodiversity during times of rapid climate change. High peaks can contain a higher density of favorable microsites for taxa like *C. piperi* and *V. fletti* - topographic specialists adapted to harsh conditions. Even though their habitat may be greatly reduced overall, it is possible that higher elevation habitats may be able to support higher population densities, allowing the embattled species to persist until conditions ameliorate (Daly et al., 2010; Dobrowski, 2011; Scherrer and Körner, 2011; Keppel et al., 2012).

Assessing vulnerability and potential responses of endemic alpine plants **-** The dramatic reduction in suitable habitat threatens current populations of alpine endemics. Most of their current range will become unsuitable and they will experience novel environmental conditions. These findings corroborate other studies suggesting that alpine plants will face earlier snowmelt and longer, hotter summers (Mote and Salathe, 2010), conditions that could expose plants to spring freezes, increase moisture stress during the growing season, and disrupt phenology, pollinator interactions, and disturbance regimes (Kearns and Inouye, 1997; Körner, 2003; Inouye, 2008; Kelly and Goulden, 2008; Beaubien and Hamann, 2011). They will also experience increased competition as milder temperatures facilitate the establishment of taxa from lower elevations (Kikvidze et al., 2005). All of these factors could lower survival and reproductive output, causing population declines, unless these taxa can acclimate or adapt to the new conditions.

The Olympic alpine endemics appear ill-equipped to respond to warming. Their suitable habitat is contracting rather than shifting - future suitability is limited primarily to the summits of currently suitable mountains, so proximal habitat tracking will not be an option. Escape via long distance dispersal is also unlikely; the fact of their endemism suggests that they lack the capacity to disperse to and colonize the mountains of Vancouver Island or the North Cascades. They are confined to shrinking islands of alpine habitat, with significant dispersal barriers and great distances separating them from the nearest potential habitats in other ranges. Only small pockets of suitable habitat – thermal microrefugia, will remain on the highest peaks and ridges. For both *C. piperi* and *V. flettii*, the topographic characteristics of potential refugia appear favorable for survival. As specialists of steep, rocky, outcrops, *C. piperi* and *V. flettii* will encounter a relatively high density of suitable topography within projected refugia. Consequently, they may be capable of maintaining robust populations. Rock outcrops may also be difficult for lower elevation taxa to colonize, thus limiting competition within projected refugia.

For the other three taxa, the signal of habitat loss was so strong that the suitability of topography within potential thermal refugia is irrelevant (Figs. 4 and 6). *Erigeron flettii's* habitat and ecology are similar to those of *C. piperi* and *V. flettii* (Gavin 2015, personal observation), so it too may fare well in refugia if its climate envelope does not disappear completely. *Senecio neowebsteri* and *S. pinnatifida* illustrate the vulnerability of "trailing edge" populations, those that are near the lower elevational or latitudinal boundary of their climate envelope (Hampe and Petit, 2005). Such populations will experience the most rapid and severe exposure to climate change. Trailing edge populations may also be subject to "extinction debt," in which the current distribution lags behind changes in climate and habitat that have already occurred, resulting in disequilibrium of the population with its habitat requirements (Araújo and Pearson, 2005; Dullinger et al., 2012; Norberg et al., 2012). Those populations may already be marginal, with depressed reproductive output and fitness (Walck et al., 2011). While mountain topography has buffered arctic-alpine communities from extinction during past periods of warming, the pace and magnitude of current warming could overwhelm the refugial capacity of mountains and cause high rates of extinction amongst arctic-alpine taxa (Williams et al., 2007).

Some alpine plants may be able to persist in warmer climates through adaptation. Assessing adaptive capacity requires a great deal of specific knowledge on the genetics, reproductive biology, and physiology of a species, information that is unavailable for these and most endemic taxa. Nevertheless, the shared biogeographic history of the Olympic endemics suggests that they have poor adaptive capacity. They are thought to be relict populations, isolated first to glacial refugia and then confined to higher elevations during Holocene warming rather than adapting to and competing in new habitats (Buckingham, 1995; Gavin and Brubaker 2015; Gavin, 2015). This process can result in bottlenecking, diminishing the genetic diversity that is required for adaptation and favoring populations that are well adapted only to a very specific set of environmental conditions (Davies et al., 2004; Mathies et al., 2004; Still et al., 2015). In general, endemics are also poor competitors and dispersers (Cody and Overton, 1996; Bruchmann and Hobohm, 2014).

Given the lack of other options, the survival of the endemics will probably depend on their ability to persist in thermal micro-refugia. Thus, their proximity to future refugia could be a critical determinant of their vulnerability. The size and connectivity of refugia will depend on the magnitude of climate change (Hannah et al, 2014), and are therefore subject to the inherent uncertainties of future climate projections. While the size of refugia may be uncertain, relative patterns of suitability hold regardless of climate change magnitude, so we can identify the most likely locations of refugia. The projected refugia of the eastern Olympics (Fig. 5) may harbor the few remaining populations of the alpine endemics in the future - critical sources of propagules and genetic variation if climate conditions allow distributions to expand once again.

The SDMs and PCA estimated the exposure of each taxon to climate change driven habitat loss, but fall short of a full vulnerability assessment. To make robust conclusions about vulnerability amongst these taxa, projections of exposure and habitat loss must be combined with the other chief components of vulnerability: demographics, sensitivity, and adaptive capacity. We cannot make a thorough assessment of these components without much more detailed data and knowledge on the demographics, physiology, ecology, and genetics of these organisms. Nevertheless, their extreme exposure, combined with their endemic status and relative rarity put all of these taxa at risk of severe habitat loss and possible extinction due to warming.

***Modeling Caveats* -** I have projected a strong, consistent signal of high exposure and upslope habitat contraction for the Olympic alpine endemics. But, climate-based habitat models assume climate is the primary limiting component of the species' distribution. At the fine spatial scales necessary for modeling endemic taxa, substrate characteristics or ecological interactions may also be important, or the distribution may not be at equilibrium with its climate envelope. While SDMs may align well with known distributions, this may be because climatic conditions are correlated with other habitat variables (bedrock or soil type, for instance) that are strong drivers of plant distributions (Araújo and Pearson, 2005; Pearson and Dawson, 2005). As the climate envelope shifts, it may become decoupled from some drivers of the current distribution, leading to erroneous future habitat projections. SDMs provide a good approximation of likely changes, but real time monitoring of populations is crucial for understanding the dynamic response of plants to climate change.

By downscaling with a high resolution DEM and incorporating topographic habitat models, I've attempted to create the most realistic models possible given available data. However, total habitat area estimates and binary assignations of suitable/unsuitable habitat at precise locations are both highly sensitive to the choice of threshold – the suitability value at which habitat is defined as suitable or unsuitable. While these thresholds were designed to maximize the model's accuracy predicting presences and absences, and generally performed well, they do not represent a meaningful biological or environmental threshold. SDM model output is better interpreted as a continuous representation of relative habitat suitability and probability of occurrence.

Applying the results to inform conservation planning- The degree of endemism and rarity as inferred from a species' distribution, combined with habitat suitability forecasting, can approximate overall vulnerability well (Still et al., 2015). This allows land managers to prioritize vulnerable areas and taxa for conservation attention with relatively little data or technical sophistication. But, because of the uncertainties inherent in SDMs, they should not be considered predictions of future presence or absence; actions that rely on a precise magnitude or location of change should be avoided (Lawler et al., 2010; Schwartz, 2012). Model predictions that do not depend on a specific outcome at a specific place, such as relative patterns of vulnerability amongst taxa (e.g., *C. piperi* vs. *S. pinnatifida* var. *lanuginosa*) or areas (e.g. the Bailey Range vs. Mt. Constance), are more reliable. In the early stages of monitoring and assessment, low-risk, broad-benefit actions should be targeted to areas where they will have the greatest impact. In the Olympics, projected thermal refugia offer the best chances of species survival, so mitigation of non-climate impacts could be targeted there. Limiting impacts from hikers and non-native mountain goats (Houston et al., 1994) would help preserve refugial areas by reducing threats that are independent of the direct effects of climate change.

Regional and global implications- Endemic mountain taxa are urgently threatened by the warming climate. Using the Olympic endemics as a model system, we can identify other areas and specific taxa that are vulnerable to habitat loss or extinction. Generally, distributional and demographic characteristics such as geographic range, rarity, habitat fidelity, and niche breadth, can all inform relative vulnerability. Taxa with small ranges, specific habitat requirements, high elevations, and narrow climate envelopes are likely to be the most vulnerable to local extirpation. For example, another Olympic endemic *Astragalus australis var. cottonii* (M.E. Jones) S.L. Welsh (Fabaceae) appears highly vulnerable, based on its extremely limited geographic range and narrow elevation distribution (Kaye, 1999). Similarly, *Micranthes tischii* (Skelly) Brouillet & Gornall (Saxifragaceae), an endemic shared between the Olympic Mountains and the Vancouver Island Range, is known only from small, isolated populations within a very high, narrow elevation range (Samuel Wershow, Olympic National Park, unpublished data). It is thus likely to be extremely vulnerable to climate change driven habitat loss. Other endemics, such as *Petrophytum hendersonii* (Canby) Rydb. (Rosaceae) and *Eucephalus paucicapitatus* (B.L. Rob.) Greene (Asteraceae), inhabit a broader range of elevations and climatic conditions, and are considerably less rare (Samuel Wershow, Olympic National Park, unpublished data). Like *C.*

piperi, they are less exposed to and better suited to respond to climate change than the narrowly endemic taxa.

The nearby mountainous islands of Haida Gwaii and Vancouver Island (Fig. 1a) are also rich with endemism, sharing a history as isolated glacial refugia and similar physiographic characteristics (Taylor and Mulligan, 1968; Warner et al., 1982; Ogilvie and Ceska, 1984; Buckingham et al., 1995; Byun et al., 1999; Shafer et al., 2010). Thus, our study of the Olympic alpine endemics provides context for the response of these floras to climate change. The Queen Charlotte range of Haida Gwaii is considerably lower (800-1500m) than the Olympics, spans a smaller area, and contains only small patches of alpine habitat. Moist, rocky cliffs and runnels at mid to high elevations harbor most of the Haida Gwaii endemics (Taylor and Mulligan, 1968; Ogilvie and Ceska, 1984). Under a strict climate-driven view, the outlook for Haida Gwaii endemics appears even more bleak than that of the Olympics. Even widespread alpine taxa like *Rhodiola integrifolia* Raf. (Crassulaceae) are expected to experience almost complete loss of suitable habitat therein (Forester et al., 2013). Though their distributions have been poorly studied, the Haida Gwaii endemics may already be occupying all the suitable micro-topography within the limited extent of the alpine. Thus, their future may rely on the degree to which the rugged terrain buffers them from the tempo and magnitude of climate change.

A much smaller Pacific Northwest glacial refugium existed on the Brooks Peninsula of Vancouver Island (Fig. 1a), where only a few peaks of the Refugia Range avoided glaciation (Haggarty and Hebda, 1997). As in Haida Gwaii, alpine conditions are defined less by elevation (alpine occurs at ~600-800m) than by micro-topography, and endemic plants tend to be restricted to cold, wet, microhabitats in chasms that split vertical cliff walls (Haggarty and Hebda, 1997). Brooks Peninsula endemics must rely on the buffering effects of the chasms, but are probably the most vulnerable of the three island-peninsula refugia due to the extremely limited amount and low elevation of alpine habitat. The mountains of Haida Gwaii and the Brooks Peninsula represent windows into the future of the Olympic endemic flora: alpine habitats have largely disappeared already, and the endemic flora survive in presumed thermal microrefugia. All three of these endemism hotspots have played pivotal roles in the maintenance of regional biodiversity during periods of climate change, yet face high rates of extinction in the future.

Conversely, mountain ranges that span larger latitudinal and elevational gradients, such as the Rocky Mountains of North America, provide greater opportunities for habitat tracking in response to warming (Forester et al., 2013). In such ranges, fragmentation of alpine habitats could also drive differentiation in widespread taxa. In the cordilleran clade of *Campanula*, of which *C. piperi* is a member, the complex topography and large latitudinal gradient of the Rockies have driven rapid radiations during past periods of climate change (Wendling et al., 2011; DeChaine et al., 2014). Alpine habitats became more fragmented during interglacial periods, limiting gene flow, providing an opportunity for divergence, and promoting endemism within the clade. Regardless of location, all mountain taxa are in danger of isolation via habitat fragmentation due to the pace and magnitude of projected climate change (Jump and Penuelas, 2005; Dobrowski and Parks, 2016). Their migration to suitable sites must outpace the velocity of warming and so depends on their dispersal capabilities. Should seeds arrive at a new site, they still face competition and other barriers to establishment, even where habitat is suitable (Norberg et al., 2012).

***Next steps* -** The connection between endemism and exposure to climate change has not been explicitly tested. My results suggest that exposure and modeled habitat loss correspond with the degree of endemism exhibited by each taxon's distribution. This could be tested by modelling habitat loss with a larger data set of plants spanning an endemism index – defined by characteristics such as rarity, habitat fidelity, niche breadth, or geographic range size. This research also highlights the need for greater basic biological knowledge of rare and threatened plants. To fully understand vulnerability and be able to model population level changes, we need to unlock the genetics, ecology, physiology and demographics of these poorly studied taxa. To constrain uncertainty, SDMs should ideally be run across multiple emissions scenarios, and a range of individual GCMs as opposed to an ensemble average.

***Conclusions* -** Insular, high elevation taxa such as the Olympic alpine endemics are at once exceptionally vulnerable, of great conservation importance, and difficult to study. As their habitats contract upslope, they will be increasingly confined to isolated thermal refugia. Survival in refugia will depend on the innate adaptability of the species, the pace and magnitude of climate change, and the distribution of suitable topography within refugia. High-resolution topographic modelling is essential for predicting habitat reduction in these taxa and other range-restricted habitat specialists. For some taxa, beneficial topography of high elevation refugia may provide a buffer against habitat reduction. For others, their climate envelope may disappear entirely, overwhelming the buffering capacity of high, rugged terrain. They may be at the forefront of climate-driven extinctions. Ultimately, the pace and magnitude of warming will be critical; changes in our emissions trajectory could be the difference between survival and extinction.

If endemic species are lost we also lose the opportunity to learn from their biogeographic and evolutionary histories, which contain crucial clues into the links between climate, topography, and the spread and diversification of species. We know these species and others like them are highly exposed to climate change – the habitats they are adapted to will largely disappear. How they will respond remains uncertain. Monitoring and testing this response presents a tremendous opportunity for applied research and conservation in one of the jewels of the U. S. National Park system. The Olympics could become a model for understanding and mitigating climate driven habitat loss for threatened alpine taxa around the world.

Tables

Table 1. Summary of field sampling results. New populations refers to the number of field recorded occurrences at locations where the taxon had not previously been documented. Elevation range is the range of the 5th and 95th percentile elevation values recorded for each taxon's field occurrences. Prevalence is the proportion of total sampled sites where the taxon was present.

Taxon	**Herbaria records**	**Field occurrence**	**New populations**	**Elevation mean (m)**	**Elevation range (m)**	**Sampling prevalence**
C. piperi	22	71	12	1833	1533-2104	0.37
V. flettii	7	34	7	1812	1589-1980	0.16
E. flettii	4	27	6	1773	1488-1989	0.12
S. neowebsteri	9	34	12	1853	1719-2008	0.17
S. pinnatifida* var. *lanuginosa	9	27	3	1922	1764-2049	0.13

Table 2. Principle Components Analysis. The relative loadings of each climatic predictor variable on each of the first two principle components (PC1 and PC2) are shown, as well as the proportion of variance accounted for by each principle component. CMD = Climatic Moisture Deficit- the difference between precipitation and potential evapotranspiration. PAS = Precipitation as Snow- precipitation falling as snow during the winter months. TD = Continentality- the difference between the mean warmest and coldest month temperatures. MAT = Mean Annual Temperature.

	PC1	**PC2**
CMD loading	-0.71	-0.09
PAS loading	0.39	0.67
TD loading	-0.52	0.3
MAT loading	0.25	-0.67
Proportion of Variance	0.43	0.35

Table 3. Maxent SDM r*esults based on four climatic predictor variables.* **Mean test AUC** = Area Under Curve of the receiver operating characteristic, a metric of the models discriminating power. **StDevAUC** = the standard deviation of the AUC values from 10 cross-validated trials. Binomial threshold was calculated as the threshold value of logistic habitat suitability output, scaled from 0 to 1, that achieved 95% commission (classified 95% of presence points as suitable). % habitat reduction was the difference in area classified as suitable based on the binomial threshold between the Normal Period and 2080 AD projections.

Taxon	**Mean test AUC**	**StDev$_{\text{AUC}}$**	**Binomial threshold**	**% habitat reduction**
C. piperi	0.953	0.019	0.05	86
V. flettii	0.966	0.019	0.014	89
E. flettii	0.961	0.013	0.008	99
S. neowebsteri	0.959	0.015	0.015	99
S. pinnatifida* var. *lanuginosa	0.984	0.006	0.008	99

Table 4. Topographic SDM results. Topographic suitability modelling was conducted in R using logistic regression. Binomial thresholds were chosen to maximize discrimination of presences and absences. Correct presence is the proportion of field presence sites classified as suitable by the model, and correct absence is the proportion of field absence sites classified as unsuitable. Coefficients are listed for each predictor variable, and significant variables (p<0.05), are indicated by *. TPI (Topographic Position Index), the difference between the elevation of a point and the mean elevation of surrounding points within a 20m radius. ASR (Annual Solar Radiation) is the annual solar radiation experienced at a site, and Slope is the slope angle.

Taxon	***Binomial threshold***	***Correct Presence***	***Correct Absence***	***TPI Coefficient***	***ASR Coefficient***	***Slope Coefficient***
C. piperi	0.35	0.71	0.63	0.09*	0.0000007	0.069*
V. flettii	0.17	0.74	0.64	0.048	0.000001	0.078*
E. flettii	0.12	0.56	0.61	0.092	-0.0000008	0.014
S. neowebseri	0.14	0.74	0.58	0.086	0.000004*	0.020
S. pinnatifida* var *lanuginosa	0.11	0.85	0.46	-0.113	0.000004*	-0.02

Figures

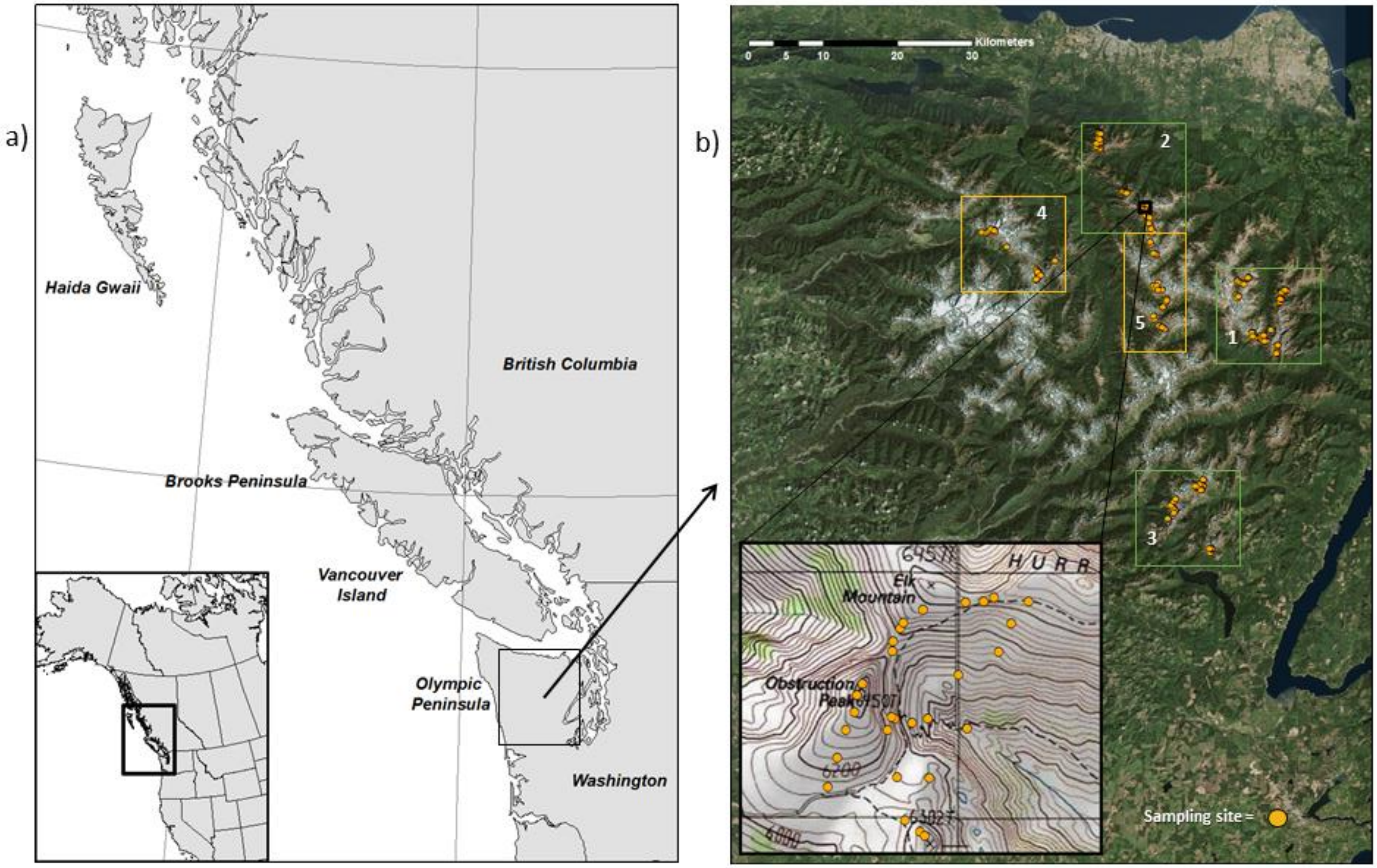
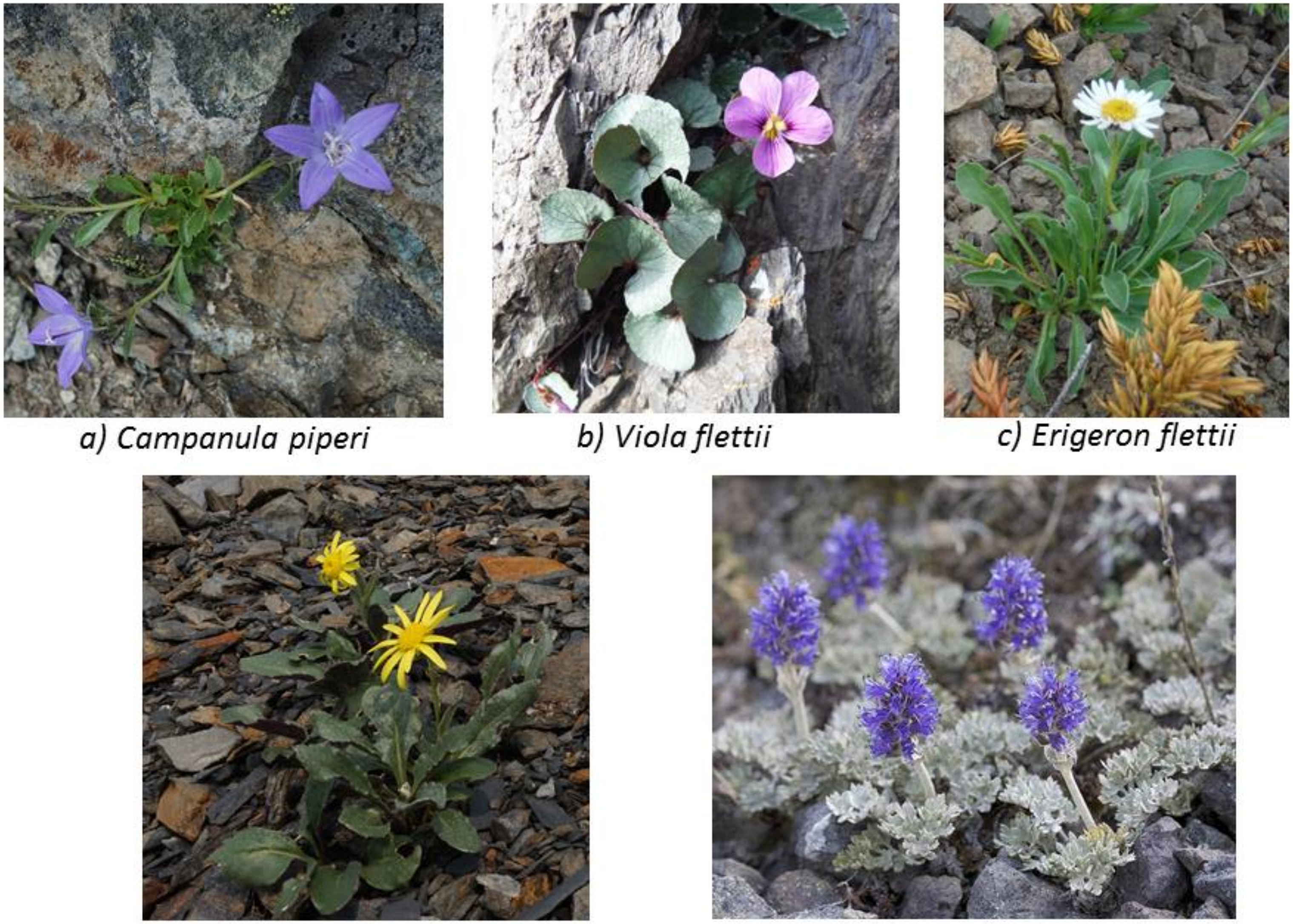


Figure 1. Reference maps. **Fig. 1a.** Reference map of the Pacific Northwest, detailing locations pertinent to this study. The Olympic Peninsula, Vancouver Island, and Haida Gwaii are all hotspots of endemism and Pleistocene glacial refugia. Olympic Mountains are indicated as the field study area.

Fig. 1b. Map of field study locations. First round sampling areas (green boxes), are as follows: 1. Dungeness Headwaters/Buckhorn Wilderness; 2. Hurricane Ridge/Klahane Ridge; 3. Skokomish Wilderness/Mt. Ellinor. Second round exploratory sampling areas (yellow boxes): 4. Bailey Range; 5. Grand Pass to Hayden Pass. Inset map details layout of field sampling sites.



a) Campanula piperi *b) Viola flettii* *c) Erigeron flettii*

d) Senecio neowebsteri *e) Synthyris pinnatifida* var. lanuginosa

Figure 2. The five alpine taxa endemic to the Olympic Mountains that were used in this study. Photo credits for figs. 2a-d: Sam Wershow. Photo credit for Fig. 2e: Rod Gilbert.

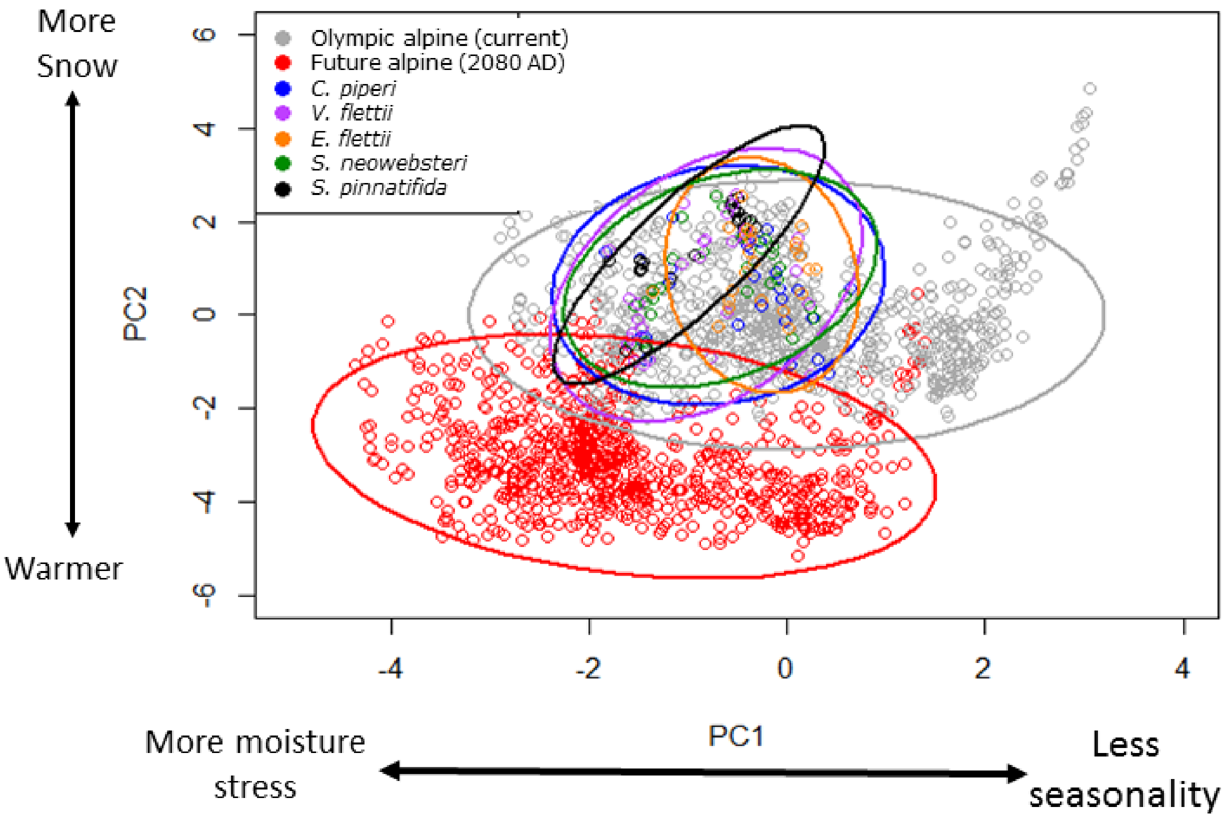


Figure 3. Principle Components Analysis. Scatterplots of first two principle components of climate conditions at each presence site, and the current and future conditions at randomly sampled sites representing the Olympic alpine (terrain over 1400m in elevation). Ellipses represent the 5th-95th percentile range of each group's multivariate climate envelope. Climate conditions were represented by four variables: Climatic Moisture Deficit (CMD), Mean Annual Temperature (MAT), Precipitation as Snow (PAS), and Continentality (TD). TD and CMD had strong negative loadings on PC1. Negative values along the PC1 axis represent more extreme seasonal differences and increased moisture stress. Mean annual temperature loaded negatively on PC2, while PAS loaded positively. Negative values along the PC2 axis represent warmer conditions with less winter snow.

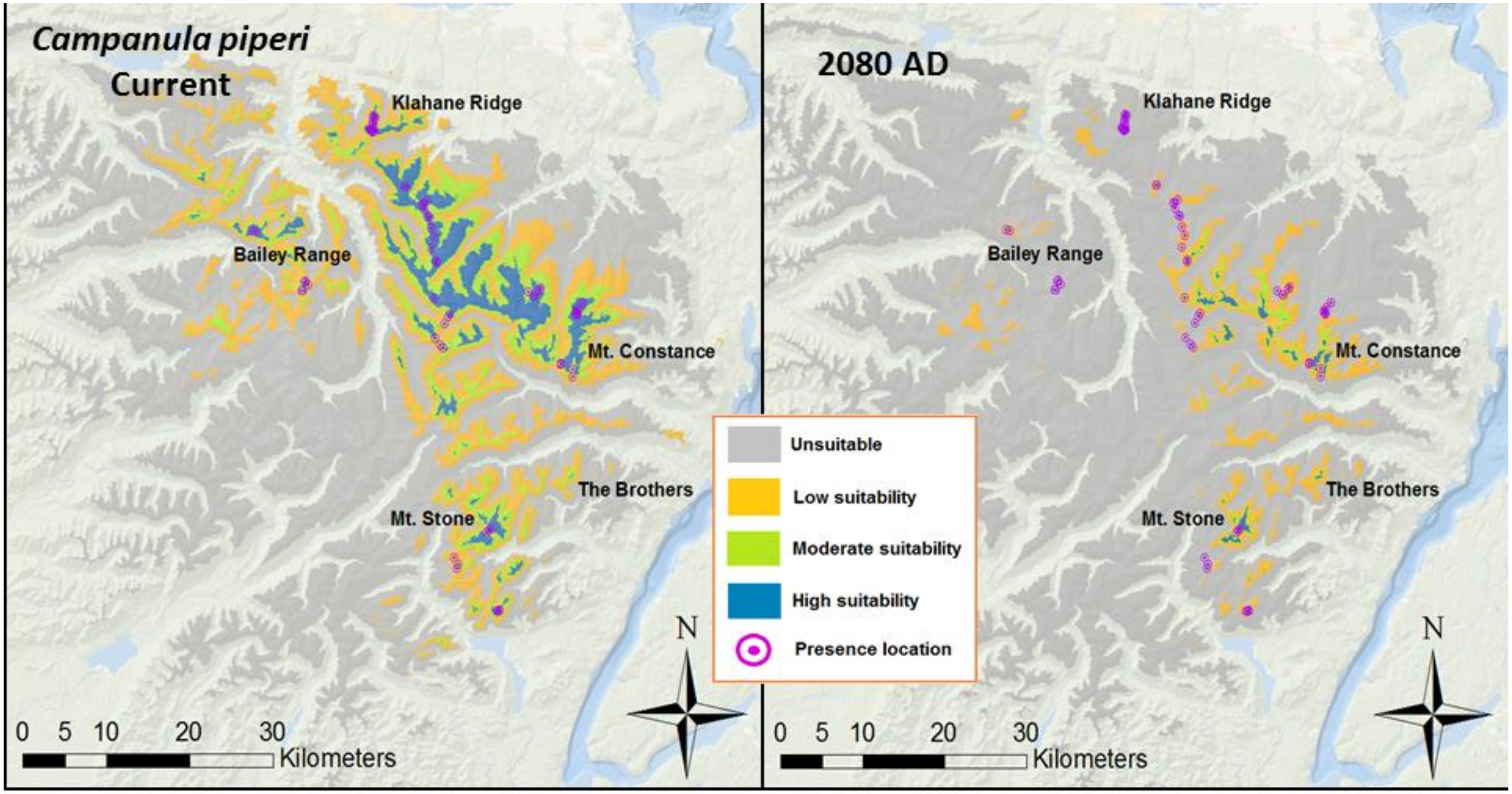


Figure 4. Species distribution models for the current (normal period) and future (2080AD,) based on Maxent logistic output. Model extent is defined as the Olympic Peninsula over 800 meters of elevation. Four predictor variables were used in habitat modelling: Climatic Moisture Deficit, Continentality, Mean Annual Temperature, and Precipitation as snow. Presence data was obtained from field sampling during the summer of 2015. Habitat suitability is classified based on Maxent suitability scores as Unsuitable (<0.01), Low (0.01-.1), Moderate (0.1-0.34), or High (>0.34). **Figure 4a.** SDMs for *C. piperi.*

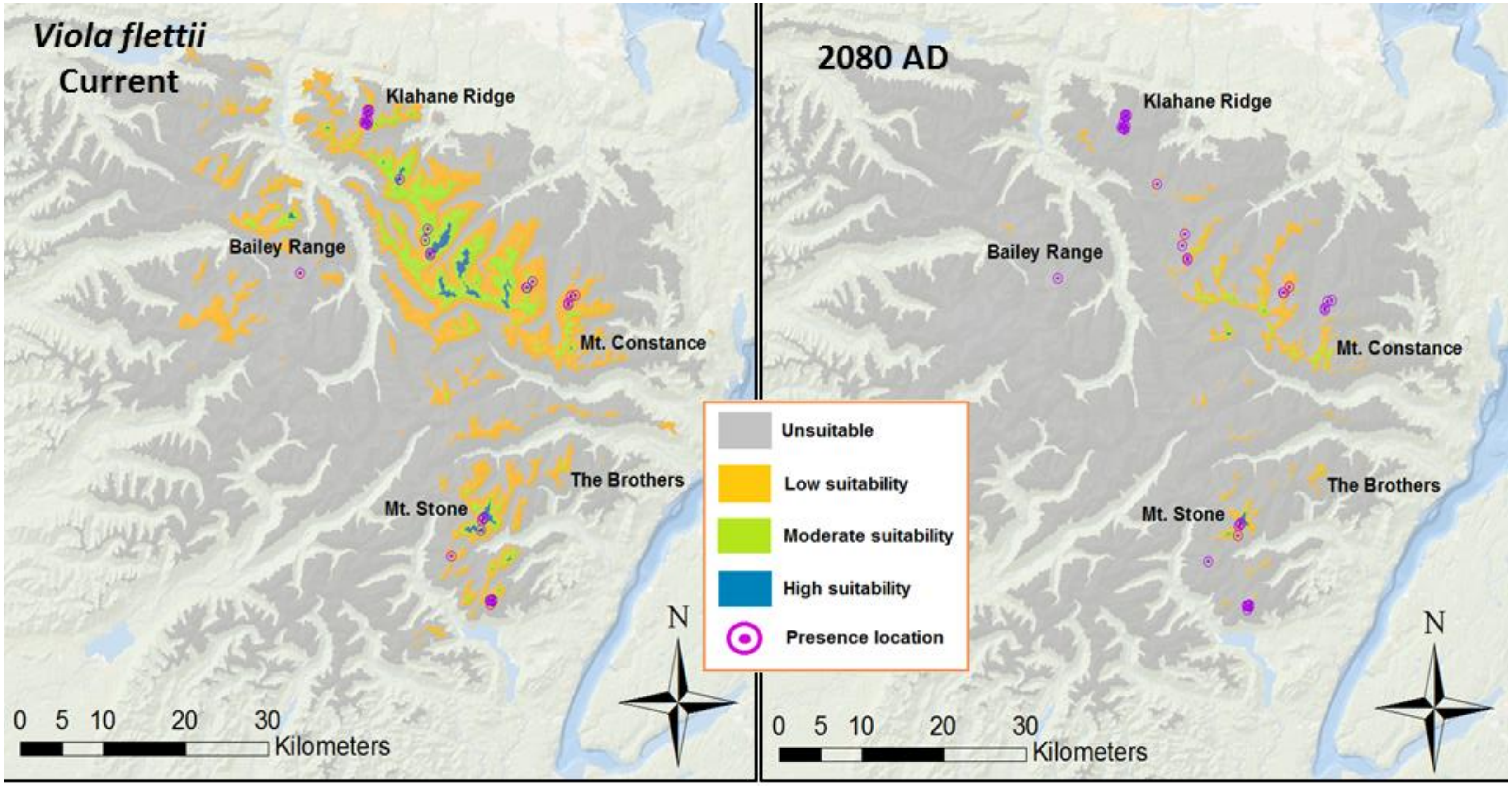


Figure 4b. SDMs for *V. flettii* for current (normal period) and future (2080AD).

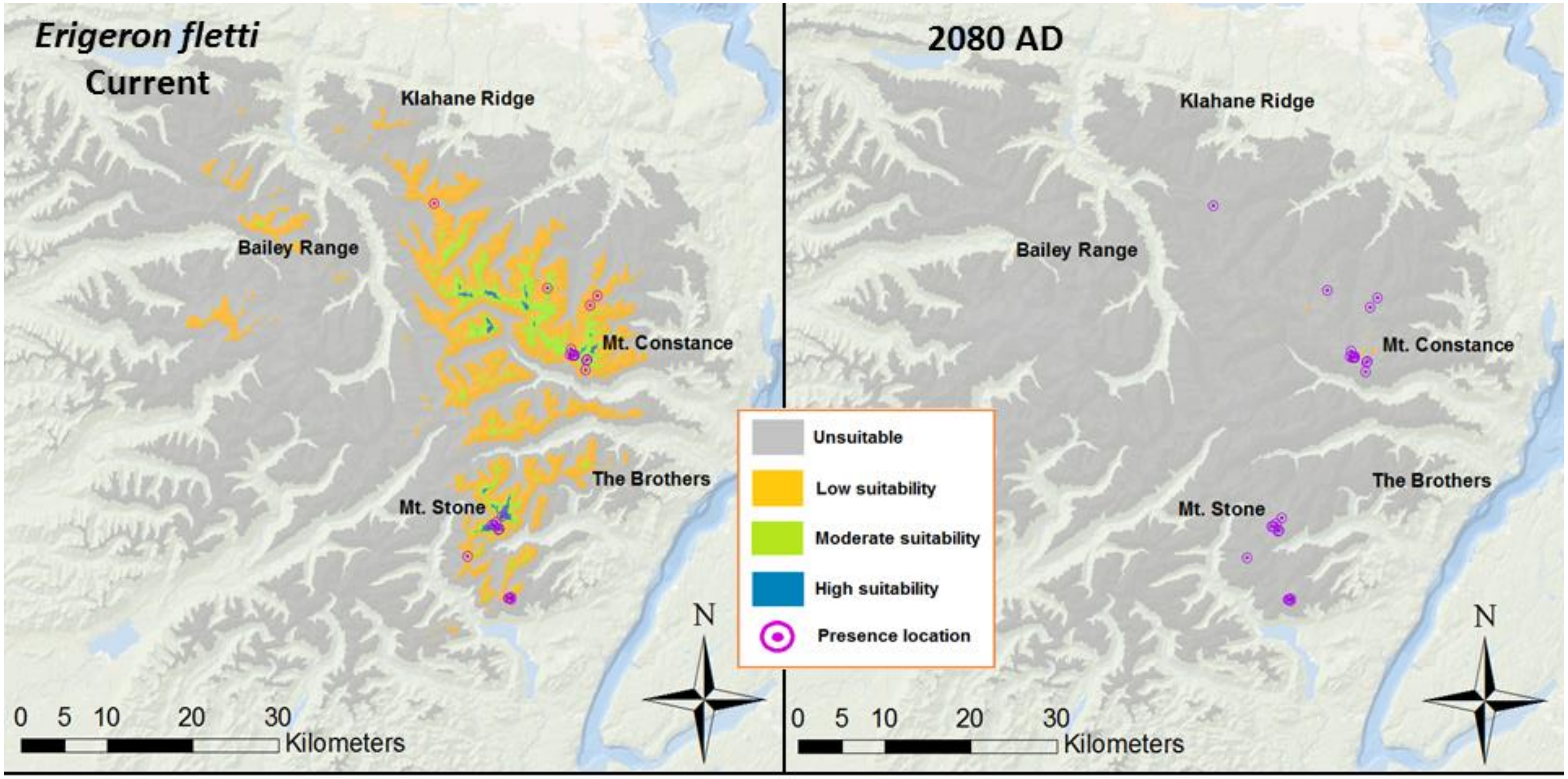


Figure 4c. SDMs for *E. flettii* for current (normal period) and future (2080AD).

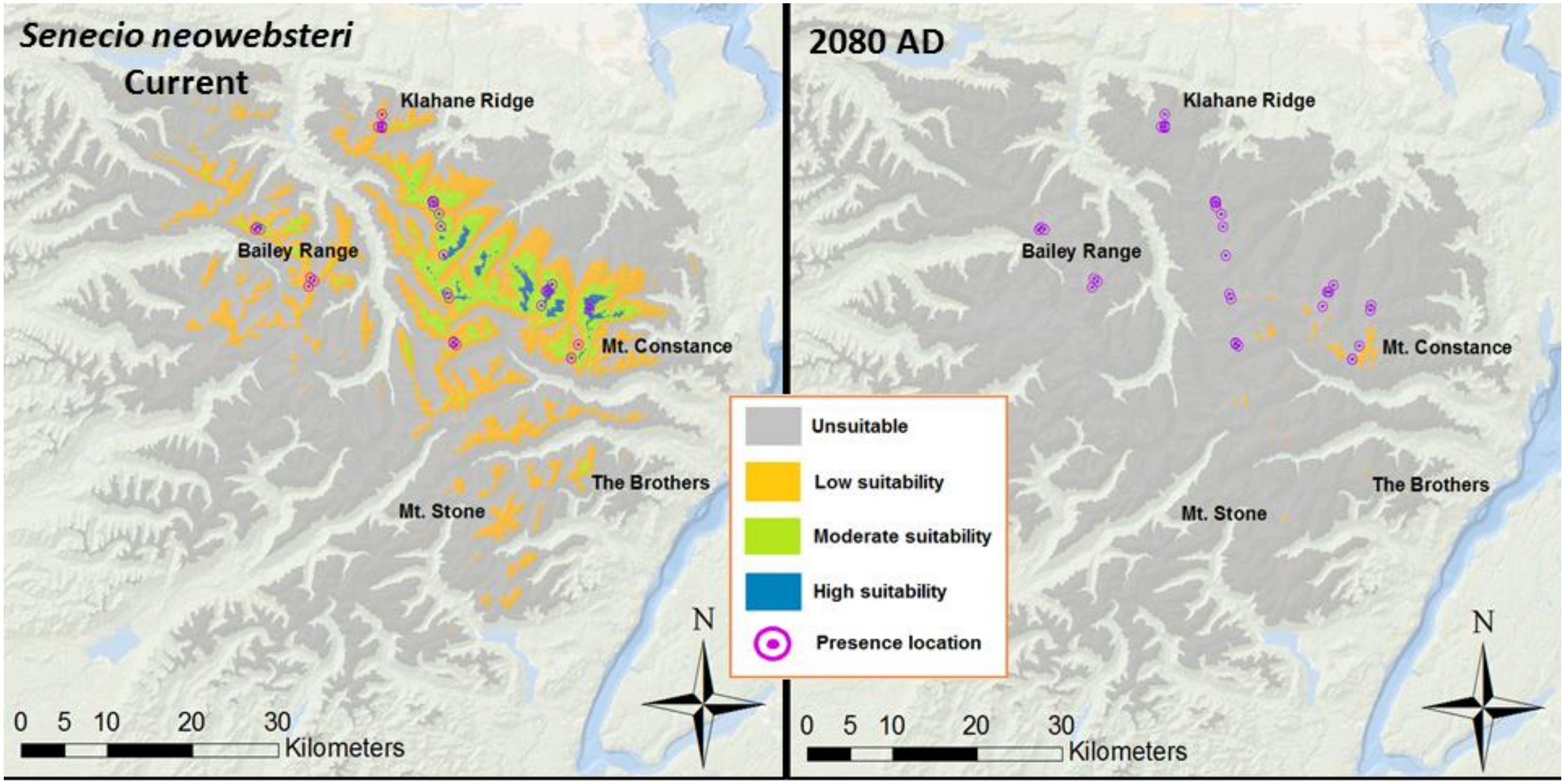


Figure 4d. SDMs for *S. neowebsteri* for current (normal period) and future (2080AD).

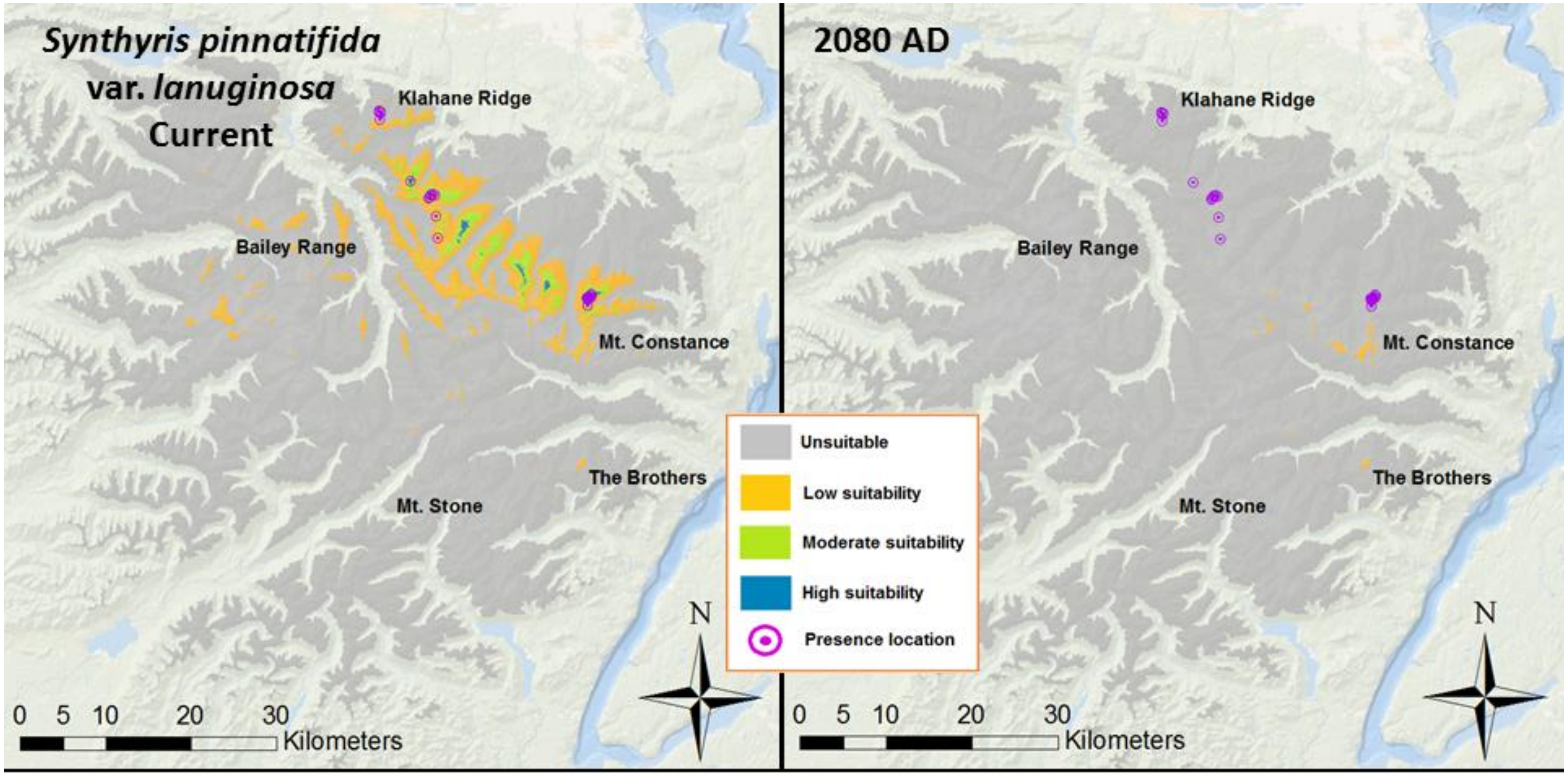


Figure 4e. SDMs for *S. pinnatifida* var. *lanuginosa* for current (normal period) and future (2080AD).

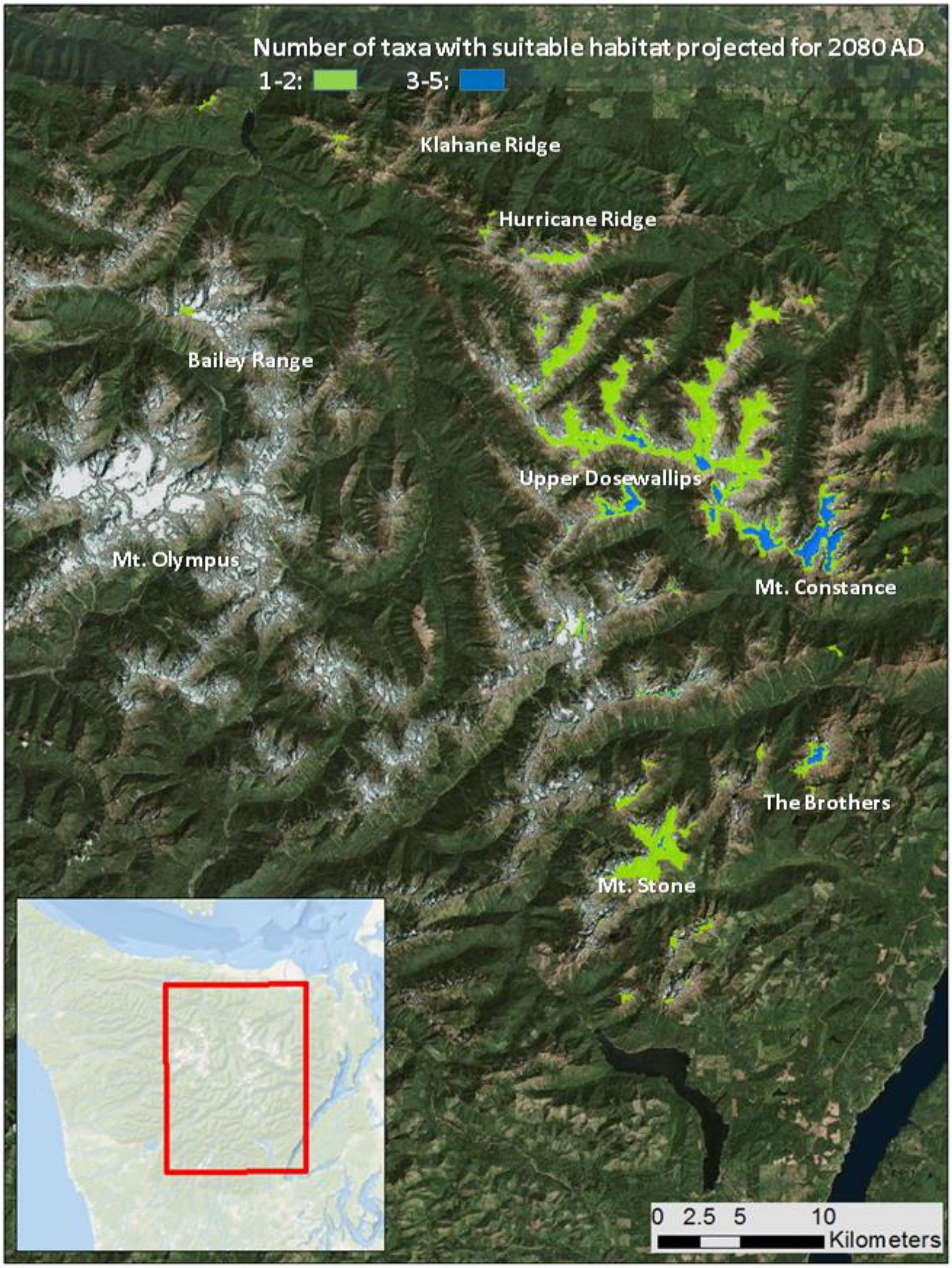


Figure 5. Map of potential refugia, generated from the intersection of future (2080 AD) suitable habitat projections of all five taxa. Habitat suitability projections were based on Maxent logistic output, thresholded to achieve 95% commission.

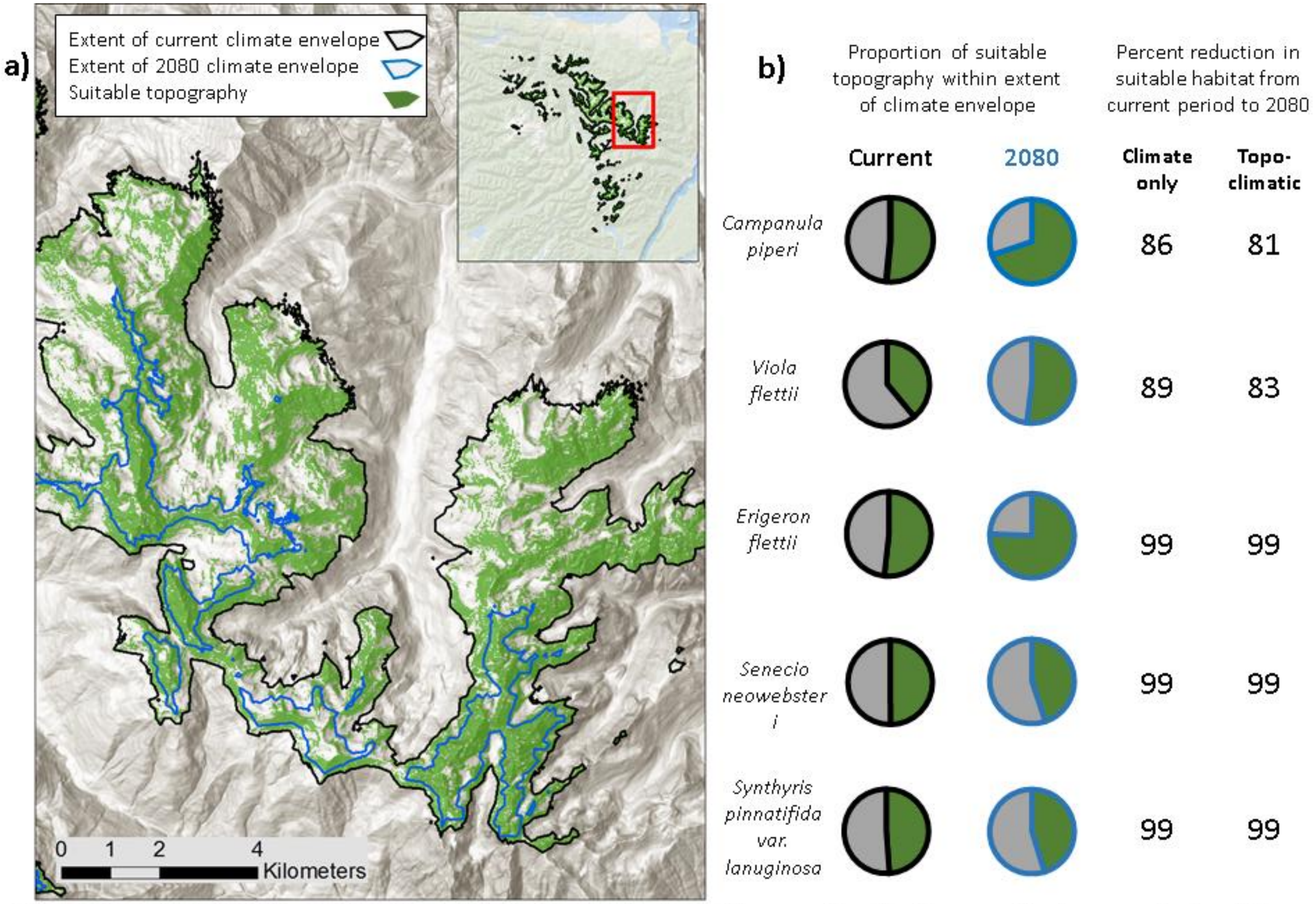


Figure 6. Topo-climatic SDM. **Fig. 6a.** Topo-climatic SDM for *C. piperi*, showing suitable topography within the extents of both current and projected future climate envelopes. **Fig. 6b.** The proportion of suitable topography within the extent of current and future climate envelopes for each taxon. These proportions were used to calculate the total percent habitat reduction projected by the topo-climatic models, which is compared to percent habitat reduction projected by the climate only models.

APPENDIX

Table A1. Plant taxa endemic to the Olympic Peninsula and Vancouver Island. Taxa in bold were selected for this study. (Buckingham et al., 1995; Camp et al., 2011; Hitchcock et al., 1969; Pojar and MacKinnon, 2013).

Taxon	Range	Habitat	Microhabitat	Family
Campanula piperi	Olympics	Alpine	Rock outcrops/scree	Campanulaceae
Viola flettii	Olympics	Alpine	Rock outcrops	Violaceae
Erigeron flettii	Olympics	Alpine	Rock outcrops	Asteraceae
Senecio neowebsteri	Olympics	Alpine	Loose steep scree	Asteraceae
Syntheris pinnatifida* var. *lanuginosa	Olympics	Alpine	Ridgetop fellfields	Scrophulariaceae
Petrophytum hendersonii	Olympics	Subalpine/Alpine	Rock Outcrops	Rosaceae
Erigeron peregrinus	Olympics	Coastal	Sphagnum bogs	Asteraceae
Astralagus cottonii	Olympics	Alpine	Scree/gravel/sand	Fabaceae
Taraxacum olympicum	Olympics	Subalpine/Alpine		Asteraceae
Abronia umbellata ssp. *Acutalata*	Olympics/V.I.	Coastal	Beach	Nyctaginaceae
Eucephalus paucicapitatus	Olympics/V.I.	Montane to Alpine	Meadows/scree slopes	Asteraceae
Castilleja parviflora var. *olympica*	Olympics/V.I.	Subalpine/Alpine	Meadows/slopes	Orobanchaceae
Claytonia multiscapa ssp. *Pacifica*	Olympics/V.I.	Subalpine/Alpine	Meadows	Portulacaceae
Pedicularis bracteosa var. *atosanguinea*	Olympics/V.I.	Subalpine/Alpine	Meadows	Scrophulariaceae
Micranthes tischii	Olympics/V.I.	Alpine	Boulders/crags	Saxifragaceae

Table A2. Georeferencing spatial confidence score table. Adapted from Bloom et al., 2017.

1	Accurate within 10m from coordinates. Population can be easily located using coordinates.
2	Accurate between 10 and 100m of coordinates. Population can be located based on coordinates and site/location descriptions
3	Accurate between 100m and 1km of coordinates. Requires searching in the field to locate population.
4	Not reliable within 1km. Population may be present in the general area but will require extensive search.
5	Coordinates unreliable or absent and true location impossible to determine based on information contained in record.

Table A3. PCA of potential climate predictor variables. One to two variables were selected from each of the first five principle component axes. PCA was calculated on a scaled, centered matrix of random points throughout the study area.

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**
MAT	-0.4191037	-0.07901231	0.03609391	0.10748236	0.05883887	-0.28933492
MWMT	-0.3973317	-0.15844767	0.25429879	0.11154206	-0.07649498	-0.12350845
MCMT	-0.4057652	0.08007905	-0.25882489	0.16888081	-0.12098696	-0.11504833
TD	0.1618074	-0.35295758	0.79136800	-0.14029995	0.10513891	0.03117096
MAP	-0.1798255	0.56408545	0.26949676	0.32212960	0.66520166	0.12641789
DD.5	0.3981312	-0.17950091	0.19314450	0.12892523	-0.16003744	-0.34942948
NFFD	-0.4148733	0.04521156	0.12456036	-0.06046271	-0.32904456	0.81787364
PAS	0.3112979	0.37312603	0.27408304	0.57190793	-0.58094886	-0.10332927
CMD	0.1256212	-0.58820030	-0.20051338	0.69041835	0.22609143	0.26295731

Table A4. Correlation matrix of Pearson's coefficients between potential climate predictor variables. Pearson's coefficients >0.8 are highlighted.

	MAT	**MWMT**	**MCMT**	**TD**	**MAP**	**DD.5**	**NFFD**	**PAS**	**CMD**
MAT	1	0.9661	0.9278	-0.292	0.3358	0.9717	0.9564	-0.772	-0.182
MWMT	0.9661	1	0.8156	-0.052	0.264	0.9915	0.9271	-0.743	-0.101
MCMT	0.9278	0.8156	1	-0.621	0.4512	0.8265	0.913	-0.678	-0.321
TD	-0.292	-0.052	-0.621	1	-0.421	-0.083	-0.319	0.1637	0.4167
MAP	0.3358	0.264	0.4512	-0.421	1	0.2219	0.493	0.2483	-0.868
DD.5	0.9717	0.9915	0.8265	-0.083	0.2219	1	0.9172	-0.773	-0.063
NFFD	0.9564	0.9271	0.913	-0.319	0.493	0.9172	1	-0.651	-0.378
PAS	-0.772	-0.743	-0.678	0.1637	0.2483	-0.773	-0.651	1	-0.253
CMD	-0.182	-0.101	-0.321	0.4167	-0.868	-0.063	-0.378	-0.253	1

Table A5. Performance of final candidate models in logistic regression and Maxent. AIC=Aikake's Information Criterion (logistic regression). AUC= Area Under Curve (Maxent). MPA$_{95=}$Minimum Predicted Area for 95% commission (Maxent).

Species	**Variables**	**AIC**	**AUC**	**MPA$_{95}$**
CP	TD,PAS,CMD,MAT	783.8	0.961	0.178
CP	TD,PAS,CMD,MWMT	795.05	0.963	0.176
EF	TD,PAS,CMD,MAT	325.63	0.968	0.176
EF	TD,PAS,CMD,MWMT	313.58	0.969	0.167
SN	TD,PAS,CMD,MAT	436.55	0.968	0.171
SN	TD,PAS,CMD,MWMT	442.82	0.968	0.177
SP	TD,PAS,CMD,MAT	325.63	0.989	0.085
SP	TD,PAS,CMD,MWMT	327.99	0.987	0.101
VF	TD,PAS,CMD,MAT	403.64	0.975	0.149
VF	TD,PAS,CMD,MWMT	407.72	0.978	0.146

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