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Dendrochronology of Seaside Juniper (Juniperus maritima)

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Dendrochronology of Seaside Juniper (*Juniperus maritima*)

By

Dustin Gleaves

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of the Requirements for the Degree
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Master's Thesis

Dustin Gleaves

July 27th, 2018

Dendrochronology of Seaside Juniper (*Juniperus maritima*)

A Thesis
Presented to
The Faculty of
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In Partial Fulfillment
Of the Requirements for the Degree
Master of Arts

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ABSTRACT

Seaside juniper (*Juniperus maritima*) is a recently discovered tree species endemic to the Salish Sea region and is an as yet unutilized dendrochronological resource. This study reports the first dendrochronological investigation of the species. We sought to determine if Seaside junipers are capable of crossdating, a requirement for consideration as a dendrochronology study species, and to identify correlations between instrumental climate records and radial growth to determine climate-growth response. We collected tree core samples from Seaside juniper in five sites throughout the San Juan Islands and nearby mainland. Samples collected from one of five sites successfully crossdated. Bootstrapped correlation function analysis found the dominant growth-limiting factor of Seaside junipers is growing season minimum temperatures in the prior year (r = 0.547) and in the current year (r = 0.524), potentially indicating a common growth-limiting factor of either temperature or solar irradiance. Understanding this climate-growth relationship will aid in development of a conservation strategy for this rare and endemic species.

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Table of Contents

List of Tables and Figures

Literature Review

Juniperus maritima

Juniperus maritima in Washington Park, *Anacortes*, *WA*

Seaside juniper (*Juniperus maritima*) is a recently discovered species of juniper tree endemic to the Salish Sea region. Prior to discovery in 2007, Seaside juniper was believed to be Rocky Mountain juniper (*J. scopulorum*) due to cryptic speciation (Adam, 2007). Seaside juniper belongs to Virginiana group, classified as new world smooth leafed junipers along with Rocky Mountain juniper, Eastern redcedar (*J. virginiana*), and Creeping juniper (*J. horizontalis*)

(Adams, 2014). The habitat range of Seaside juniper is presently constrained to the Salish Sea basin (Fig. 1) which minimally overlaps the distribution of Common juniper (*J. communis*) and one population of hybridized Rocky Mountain and Seaside juniper in the Okanogan Highlands, on the margins of both species' native range (Adams, 2015; Fig. 2.). The species is morphologically distinguished by frequently exserted seeds and the maturation of cones in 14-16 months compared to 24 months in Rocky Mountain junipers (Adams, 2014). The largest individual presently known is located on Skagit Island, WA and measures 118 cm in diameter (Adams, 2014). The justification for speciation by (Adams, 2007) is that all 3 criteria of the Ownbey species concept are fulfilled (Ownbey, 1950). Seaside juniper and Rocky Mountain juniper populations are genetically distinct to nearly the same degree as Eastern redcedar and Rocky Mountain juniper, although Seaside juniper is less morphologically distinct Adams (2007). These geographically isolated genetic variations are believed to be the result of allopatric speciation caused by late Pleistocene glaciation (Adams et al., 2010). However, several populations on the margins of the Rocky Mountain juniper and Seaside juniper territories show signs of genetic hybridization (Adams, 2014). Since Adams (2015) has identified that hybridization of the two populations is taking place, free gene exchange is occurring, and the original justification for speciation may be jeopardized. Hybridization between flora species is normal and does not indicate that the two parent plants are the same species (Baack and Rieseberg, 2007). Hybridization by allopatric introgression is also known to occur between Rocky Mountain juniper and many other North American juniper species (Scher, 2002) especially Eastern redcedar (Flake et al., 1978) as determined by leaf terpenoid composition, further supporting Seaside Juniper speciation. All known Seaside juniper and Rocky Mountain juniper hybrids are exclusively located east of the Cascade Mountains (Adams, 2014) and do not constitute a known risk of species confusion to any research conducted in the San Juan Islands.

Paleoecological History

Adams et al. (2010) hypothesizes that the origin of Seaside juniper is allopatric speciation caused by a subpopulation of ancestral Rocky Mountain junipers becoming geographically isolated from the general population by the Vashon Glaciation resulting in a Pleistocene glacial refugium in the Olympic Mountains (Fig. 3). As junipers typically expand downslope (Weisberg et al., 2007), individuals located at high elevations of the Olympic Mountains would be expected to expand to the northwest. The modern day geographic distribution of Seaside juniper shows a spatial distribution consistent with an origin point in the Olympic Mountains west of the maximum extent of the Vashon Glaciation’s Puget Lobe (Booth et al., 2003; Adams, 2010; Fig. 3) and subsequent dispersal following glacial retreat northward. This supports the hypothesis of a glacial refugium within the Olympic Mountains that retained a sub-population of ancestral Rocky Mountain juniper. Stands of mixed juniper species are currently present on the Tibetan Plateau at an elevation of 4900 meters above sea level (Hampe and Petit, 2010), greater than twice the elevation of Mt. Olympus, which is the highest point in the Olympic Range, and gene flow modeling of Tibetan Plateau populations reveal that juniper species are capable of survival in montane climates for millennia (Opgenoorth et al., 2010), further supporting the Seaside juniper glacial refugium hypothesis. The absence of Seaside juniper on islands in the Puget Sound (Fig. 4) causes individuals located on the north face of the Olympic Mountains to be greater than 58 km from the next nearest known living Seaside juniper. No genetic differentiation between Olympic and Puget Sound populations exists (Adams et al., 2010; Adams, 2014) indicating that these populations separated recently relative to the separation of

Seaside juniper and Rocky Mountain juniper populations. Far more stands of Seaside juniper exist in the San Juan Islands and near-shore mainland sites than exist in the Olympic Mountains (Adams, 2014; Fig. 4), indicating that the latter sites are atypical of the species despite being situated closer to the hypothesized glacial refugium location.

If a glacial refugium in the Olympic Mountains is the origin site of Seaside juniper as a species, then dispersal has been directed generally northward and downslope at a rate of approximately 240 total kilometers (the distance from Mt. Olympus to the northmost known living Seaside juniper) over 10,000 to 25,000 years (approximate beginning of Holocene deglaciation). This is a rapid rate of tree migration especially if Seaside juniper shares Rocky Mountain juniper's traits of optimal seed production at age 50 to 200 years (Herman, 1958) and pollination via wind dispersal (Noble, 1990). Cone dispersal is accomplished via both gravity and zoochory (Adams, 2014), which could account for both the rapid migration and the geographic separation of stands if distribution occurred in the late Holocene. Distribution via migratory birds can potentially transport viable seeds at distances greater than the present habitat expanse of Seaside juniper (McCaughey et al., 1986) and typically results in a latitudinal distribution along avian migration routes (Cain et al., 1998) which is consistent with the modern distribution of Seaside juniper. This is also consistent with the non-contiguous distribution of the species as zoochory dispersed seeds may simply pass over the south Puget Sound islands without colonizing. Alternatively to, or in conjunction with, recent dispersal, the current distribution of Seaside juniper throughout the San Juan Islands and Gulf Islands could be the result of cone dispersal via gravity alone during the Hypsithermal when land in the Puget Sound was more contiguous, followed by transformation to an island network caused by rising sea-level. Rocky Mountain juniper, Utah juniper, and Western juniper (*J. occidentalis*) have been observed to generally expand downslope or at equal elevation (Weisberg et al., 2007) and to establish in deep soils (Burkhardt, and Tisdale, 1969) such as those located at the margins of glacial retreat (Booth et al., 2003).

The Genus Juniperus

Junipers grow natively throughout North America, Europe, Asia, Eastern Africa, and numerous Atlantic Islands (Adams, 2014). Common juniper has the greatest range of any juniper species and is the only juniper species found in both the eastern and western hemisphere (Adams, 2014). Of the 75 presently identified juniper species worldwide, North America is home to 33, and of those only Seaside juniper, Common juniper, and a small population of hybridized Rocky Mountain juniper and Seaside juniper grow within the Salish Sea Basin (Fig. 2).

The recent discovery of a juniper species through genome analysis is not limited to Seaside junipers. As with Rocky Mountain juniper, Mountain juniper (*J. monticola*) was previously believed to be a single species endemic to Northeastern Mexico with specific populations expressing stunted growth due to regional canopy cover (Adams et al., 2007). The former Mountain juniper and its presumed compact form are now known to be three distinct species (Adams et al., 2007; Adams et al., 2010). In another pattern similar to Seaside juniper and Rocky Mountain juniper, differences in leaf terpenoids between the three species in northeastern Mexico were identified decades' prior (Zanoni and Adams, 1975; Zanoni and Adams, 1976) but this conclusion was not able to define the species by itself. The species were taxonomically distinguished when Compact Mountain juniper (*J. compacta*) was identified and distinguished from Mountain juniper (Adams et al., 2007) and later Zanoni junpier (*J. zanonii*) was likewise distinguished from Compact Mountain juniper (Adams et al., 2010). Unfortunately, neither Zanoni juniper nor Compact Mountain juniper are optimal candidates for dendrochronology as both are shrub-like in morphology (Zanoni and Adams, 1975; Zanoni and Adams, 1976) and their nearest taxonomic relatives (Adams, 2014) have not been successfully used in tree-ring research (Grissino-Mayer, 1993).

Several publications by Adams and various associates identifying new juniper species over the last 10 years follow the same pattern of events: cryptic speciation caused initial misidentification of Compact Mountain juniper, Zanonii juniper, and Seaside juniper. Each were erroneously regarded as members of a different, but geographically proximate species due to taxonomy being defined generally by morphology prior to technological advancements making DNA analysis possible. Initial large-scale sampling of leaf terpenoids were conducted and analyzed by Principal Coordinate Ordination. Frequently, the results were inconsistent with existing taxonomic classification, and would separate the single species into multiple terpenoid composition groups that were also separated geographically. Following the advent of DNA analysis methods, genomic studies were used to evaluate if these chemical differences were indicative of genetic differences. As DNA analysis is costlier than leaf terpenoid analysis, smaller scale genomic studies of SNPs (Single Nucleotide Polymorphisms) were used to identify variations in relevant DNA sequences of a population. These SNP groupings were generally consistent with chemical and geographic groupings (Adams, 2007), validating the hypothesis that observed chemical differences are tantamount to genetic differences that are conclusive of speciation.

Furthermore, these genomic studies have also produced a suggested reclassification of genera which would ordain the genus *Hesperocyparis* for many western hemisphere originated juniper species including Seaside juniper (Adams et al., 2009). This revision also appears to lessen the perceived genetic distance between Seaside juniper and Alaska yellow cedar

(*Callitropsis nootkatensis*) which is known to be climate sensitive in multiple sites in the Cascade Mountains (Robertson, 2011) and which are likely comparable to the Olympic Mountain populations of Seaside juniper suggesting potential for exhibition of climate sensitivity by Seaside juniper.

Limiting Factors and Future Threats to Seaside Juniper

The high-salinity soils associated with Seaside junipers are comparable to the soil conditions of the pinyon-juniper woodlands of the American Southwest, but not to the deep limestone soils preferred by Eastern redcedar of the American Midwest (Adams, 2007). The coastal environments of Seaside juniper are also subject to salt spray. Coastal conifers exhibit damage, stunted growth, and krummholz growth when exposed to the dual stressors of salt spray and mechanical stress from coastal winds (Wells and Shunk, 1938). Research on salt spray damage primarily focuses on economic damage to timber harvest species (Gustafsson and Franzén, 1996) and does not presently include substantial research on the effect of salt-spray on Juniper species in a natural environment. Rocky Mountain juniper and Eastern redcedar are known to be at least moderately salt sensitive in lab experiments, exhibiting folial damage when sprayed with water containing 350ppm sodium chloride (Miyamoto et al., 2004) which is a lower concentration than the typical ocean salt spray concentration in the near-shore environment occupied by Seaside juniper (Barbour, 1978). If the finding of salt sensitivity in Rocky Mountain juniper is accurate, then this may indicate an adaptation of Seaside juniper towards salt tolerance, as Rocky Mountain juniper would presumably struggle to successfully establish in a salt spray rich environment.

Climate change may also alter natural disturbance regimes such as drought periods which are known to increase the propensity for fire and pest insect outbreaks (Flower et al., 2014).

Several studies have concluded that insects are not a contributing factor to juniper mortality (Floyd et al., 2009; Gaylord et al., 2013). Localized mortality events of juniper species as a result of disturbance events have been identified, but did not directly indicate the cause, which were determined to potentially be insect outbreak or fire events (Huffman et al., 2008). If Seaside junipers in the Pacific Northwest share the mortality dynamics of other juniper species in other regions, then predicted drought and the associated increased likelihood of fire pose a greater direct threat to Seaside juniper than insect outbreak or inclement annual climate conditions.

Seaside juniper exhibits a high level of phenotypic plasticity and ability to adapt to a wide envelope of environmental conditions, given its presence in the highly varied climates of near-shore islands, the montane environment of the Olympic Mountains, and the evident former high-elevation glacial refugium (Adams, 2011). Soil characteristics of juniper sites vary from the deep soils preferred by young Rocky Mountain junipers to the moderate to thin soils typical of both Western juniper and Rocky Mountain juniper trees in climax succession stage forests (Burkhardt and Tisdale, 1969).

Necessity for Revision of Prior Misidentifications in Literature

It is possible that prior misidentification of Seaside juniper as Rocky Mountain juniper may cause necessary revision of prior research on juniper species of the Pacific Northwest. Fortunately, aside from the work of Robert Adams, few publications have made conclusions reliant on the presence of Rocky Mountain juniper in the Pacific Northwest to a degree that necessitates revision. The International Tree Ring Data Bank (ITRDB) is a centralized databank of chronologies made available for public free use (Grissino-Mayer and Fritts, 1997). At present there are no ITRDB records of any juniper species within the Seaside juniper habitat range described by Adams et al. (2010) indicating no studies on junipers have been contaminated by errors in ITRDB data. Adams (1983) initially identified the spread of Rocky Mountain juniper as a result of glacial refugia which created two geographically separated populations of Rocky Mountain juniper. Following the discovery of Seaside juniper by (Adams, 2007) an update was published to account for this new information (Adams et al., 2010) indicating that the change is at least accounted for in source literature by the original author. The USDA Forest Service presently displays data available for public and inter-office use which states the range of Rocky Mountain juniper includes Vancouver Island and other Puget Sound islands, as well as the surrounding mainland (Scher, 2002) which is evidently in reference to Seaside juniper populations (Adams 2010). As this report is a publicly available resource published by a trusted government agency, it may lead to future misidentifications if not revised. Kruckeberg (1964) serves as a guide for plant identification, and references an observed population of Rocky Mountain Juniper on the Twin Sisters Mountains in Whatcom County, which is unlikely to be accurate, but also is not pertinent to the content of Krukeberg's article and is an immaterial nominal error. Detling (1948) provides a biogeographic method for modeling climate extremes based on model species, but incorrectly defines areas of the Pacific Northwest as being dominated by Rocky Mountain juniper stands. If no difference in climate response is identified between Rocky Mountain juniper and Seaside juniper, then this will be an immaterial error however if a difference is discovered then this may necessitate revision of the model.

Dendrochronology Performed on The Genus Juniperus

"Crossdating" is defined as synchronous variations in ring growth between individual trees (Fritts, 2012). It is essential to dendrochronology as it indicates that multiple individual trees exhibit a common response to external environmental factors such as climate and provides a method for confirming proper placements of ring years in the presence of missing or false rings

(Fritts, 2012). At least fifteen species of the genus *Juniperus* are known to crossdate effectively, including Rocky Mountain juniper (Grissino-Mayer, 1993). The prior successful crossdating of other species within the genus, if these are considered valid model species, indicates the potential for climate sensitivity and crossdatability in Seaside junipers as well. Rocky Mountain juniper, Utah juniper, and Eastern redcedar have all exhibited climate sensitivity (Grissino-Mayer, 1993); however, these studies may not be relevant to Seaside junipers in the Pacific Northwest for either biological or environmental factors.

Rocky Mountain juniper, being the nearest genetic relative and nearest geographic neighbor to Seaside juniper (Adams, 2010) is likely the most representative model species. Rocky Mountain juniper has been shown to crossdate confidently and to be sensitive to monthly total precipitation, total water year precipitation, and monthly Palmer Drought Severity Index (PDSI) (Spond et al., 2014). However, this study was performed on individuals located in New Mexico, which is arid relative to the Pacific Northwest and may suffer drought stress to a severity not experienced by Seaside junipers. Utah juniper has been shown to crossdate well and exhibit sensitivity to temperature and precipitation but suffers a reputation for poor crossdating which has caused a setback in Utah juniper dendrochronological research for much of the 20th century (Derose et al., 2016). Western juniper has been shown to crossdate successfully and has shown sensitivity to regional seasonal drought (Pohl et al., 2002). Eastern redcedar has been shown to crossdate well (Lewis et al., 2009), has shown sensitivity to seasonal temperature and precipitation (Guyette et al., 2007), and has been shown to produce false-rings in response to temporary hot and dry conditions occurring during the normal growing season (Edmondson, 2010). Eastern redcedar is not as closely related to Seaside juniper as Rocky Mountain juniper and their habitat range is separated by hundreds to thousands of miles causing genetic, climactic, and geographic differences that make comparison dubious. However, in combination with Rocky Mountain juniper, Western juniper, and Utah juniper’s sensitivity, this additional case of sensitivity in a *Juniperus* species does further support the potential for crossdating and climate sensitivity in Seaside juniper. While specific examples of successful crossdating of these juniper species exist, these do not represent all locations, individuals, or species. Regardless of species, junipers in the Mojave Desert area frequently do not crossdate successfully due to a high frequency of missing and false rings due to erratic growth patterns of arid-climate junipers (Towner et al., 2001).

Tree ring chronologies available on the ITRDB for use as paleoclimate proxies in Northwest Washington State are generally limited to high elevation sites and protected old growth forest. To date, no chronologies for the San Juan Islands are available and chronologies in the Olympic Mountains do not include any juniper species. This absence of juniper species data, despite available samples and known climate sensitivity of other juniper species represents an opportunity to expand paleoclimate data to at least the time span of presently living Seaside juniper species.

Disturbance Regime Disruption in Western Juniper

Despite environmental differences, understanding how Western juniper colonizes new territory in the pinyon-juniper woodlands may help to describe the expansion pattern of Seaside juniper throughout the Pacific Northwest during the Holocene. The pinyon-juniper woodlands biome of the American Southwest extends from Central Oregon through the four corners region and is named for the landscapes dominated by Western juniper and/or pinyon pine (*Pinus edulis*) (Wiese, 2013). Western juniper is a pioneer species that has been observed to be an early successional shrub in disturbed sites (Cottam and Stewart, 1940) as is Eastern redcedar

(Holthuijzen et al., 1987). Expansion of Western juniper beyond pre-Columbian boundaries at the cost of sagebrush, grasslands, and aspen stands has been a subject of ecological concern in the region and the cause has been debated in literature for more than 5 decades (Baker and Shinneman, 2004). In some sites, juniper cover has nearly doubled over the course of only 30 years (Soulé et al., 2004). If ecological parallels can be identified, then these findings may be relevant as a model towards explaining the apparent rapid expansion of Seaside juniper throughout the Salish Sea region.

Dendrochronological investigations of Western juniper have revealed several conclusions. First, periods of aggressive juniper invasion coincide with favorable climatic conditions for juniper reproduction, especially during the late 1880s (Miller and Rose, 1995). Second, Western juniper expansion appears to be restricted by fire events in the grassland, which have decreased in frequency from the 1600s to present (Young and Evan, 1981). Third, grasslands which have been reduced by livestock grazing experience suppressed fires and weakened native grass populations, but the phenomena of juniper expansion pre-dates widespread livestock grazing (West and Young, 2000). Fourth, individual trees that survive exposure to fire increase reproductive activity in the two following years (Miller and Rose, 1999). Finally, juniper expansion is most aggressive in areas with the least topographic relief, with most population increase taking the form of increased density of the existing range and occurring episodically following disturbance events (Weisburg et al., 2007). The narrative drawn by these findings is that Western juniper expansion in the Pinyon-juniper Woodlands is controlled via natural fire regimes. However, immediately following fire events, remaining individuals rapidly expand into the disturbance zone, which is evidently paramount to their lifecycle as fire exposure triggers a physiological response of increased cone production. Historic fire events in the grasslands pushed back against juniper expansion, keeping the two regions in equilibrium. However, fire suppression in grasslands because of livestock grazing and climatic variability have disrupted this equilibrium and encouraged spatial expansion of Western juniper. The expansion of Seaside juniper from glacial refugia in the Olympic Mountains may mirror this activity. The glacial till exposed by glacial retreat of the Puget lobe would be open to colonization by pioneer species in a dynamic alike the exposed topsoil of fire disturbance sites. While the soil profiled of these two scenarios would be very different, the soil composition of juniper sites is described very broadly, including serpentine soils, bare rock, and deep nutrient rich soils (Adams, 2014), which suggests a strategy of colonization which is indiscriminate of soil composition. Growth restricting fires were less frequent and severe at the margin of the Cordilleran Ice Sheet (Power et al., 2008) further encouraging rapid juniper expansion.

Dendrochronology of the Pacific Northwest

The chronologies of the greatest temporal expanse in the Pacific Northwest from any species extend to around 800 years before present (Robertson, 2011) and are limited to moderate and high elevation mountain locations as these locations are more prone to growth limiting climatic factors and legal protection from logging. Chronologies from lowlands can still be used to reconstruct climate as well as provide insight to factors remote to the study area such as chronologies built in the Columbia River basin correlating to upstream hydrology more accurately than to local climate (Littell et al., 2016). Dendrochronology in wet environments like the Pacific Northwest is often limited to samples from living trees because dateable dead wood is rare as the would-be samples to tend rot under exposure. Tree ring dating of remnant wood has been performed on preserved wooden artifacts of the Pacific Northwest to determine dendroprovenance of the wood sample based on existing chronologies (Mobley and Eldridge, 1992). The rings of remnant wood samples found underwater can sometimes be quantifiably measured and while sunken logs of the pacific northwest have rarely been utilized for this purpose (Pitman, 2011), they have provided approximate dates of mortality through radiocarbon dating (Karlin et al., 2004). Coarse woody debris (CWD) from Western red cedar (*Thuja plicata*) which had low levels of decay and which were selected for dendrochronological applicability have been successfully used to determine the death date of logs and snags in old growth forests of British Columbia (Daniels et al., 1997), some with death dates greater than 270 years prior to measurement. This suggests the potential for use of remnant wood in dendrochronological studies of Seaside juniper in the Salish Sea basin if conditions are such that the trees are not intentionally cleared or burned and that the state of decay is minimal enough to obtain viable tree core samples.

Existing chronologies in the Olympic Mountains were primarily developed to reconstruct temperature and precipitation variables (Peterson and Peterson, 2001). Multiple studies have found that climate factors, and therefore climate-growth response of trees, in subregional climates of the Olympic mountains vary greatly over relatively small distances (Peterson, et al., 1997; Peterson, et al., 2002) indicating that conclusions from chronologies of any one region may not extrapolate well onto neighboring regions despite proximity. The common practice of referencing regional master chronologies is limited in spatial expanse in the Pacific Northwest compared to more environmentally homogenous locations, requiring a greater density of sample sites to create a comprehensive dendrochronological record. Paleoclimate publications for the San Juan Islands and nearby Gulf Islands is presently limited to marine factors such as sea level (Fedje et al., 2009). The gap in literature on terrestrial paleoclimate data for the San Juan Islands constitutes a major deficiency in sub-regional climate knowledge.

A common trend among Pacific Northwest species is sensitivity to climatic oscillations such as the El Niño Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) (Knapp et al., 2002; Robertson, 2011). PDO has been shown to be more extreme in oscillatory frequency and magnitude over the last 100 years than in the 300 years prior (Gedalof and Smith, 2001) influencing the natural fire regimes of the Pacific Northwest, but is countered by human land use (Hessl et al., 2004). Known patterns of PDO oscillations over the last 400 years permits an opportunity to identify oscillatory response in Seaside juniper, which is a novel field of research as much of the range of Rocky Mountain juniper exists in regions where climate is not well correlated to PDO and ENSO oscillations (Allen, 2013; Adams, 2014).

Conclusion

The present state of dendrochronology research on the species Seaside juniper is that it is non-existent. Our understanding of the genetic relations of species within the family *Cupressaceae* has been revised by several recent studies, calling into question the preconceived notions of similarity between juniper species and making some interspecies comparisons dubious although none of these revisions give cause to suspect that Seaside juniper is not ecologically comparable to other juniper species in western North America as model species. Paleoclimate reconstructions of the Pacific Northwest are growing in spatial and temporal comprehensiveness annually, however locations including Seaside juniper stands have not yet been the subject of any study at stand level spatial resolution. Studies of climate proxies throughout the Olympic Mountains exist, but no dendrochronological reconstructions of climate presently in literature can be applied to the San Juan Islands without interpolation from sites which are too remote to be reliable. Climate change may pose a risk to Seaside juniper in the form of altered climatic factors and disturbance regimes beyond survival tolerances. Much of the Seaside juniper population is located on islands and therefore cannot migrate in response to such changes, potentially resulting in extirpation of island populations. Individuals not located on islands may still not be capable of migrating at a rate consistent with climate change, though this prediction is based on the range dynamics of other juniper species and not confirmed by direct observation of Seaside juniper. These trees, in this location, are a valuable and unutilized source of potential dendrochronological research in the fields of biology, ecology, and climatology. A chronology built from the core samples of Seaside juniper will contribute to the body of knowledge by expanding understanding of the biological niche of Seaside juniper, the suitability of Seaside juniper for future dendrochronological research, and potentially the climate history of the San Juan Islands and Olympic Mountains.

Dendrochronology of Seaside Juniper

Introduction

Seaside juniper (*Juniperus maritima*) is a recently discovered species of tree endemic to the Salish Sea region (Adams, 2007; Fig. 1). Prior to discovery in 2007, Seaside juniper was believed to be Rocky Mountain juniper (*J. scopulorum*) due to cryptic speciation (Adams, 2007). The presence of Seaside juniper within the Salish Sea basin tends to be restricted to low-elevation, arid sites with shallow soils and south aspects (Fig 4; Appendix A) that are relatively xeric compared to the remainder of the Salish Sea region (Peel et al., 2007; Table 1), which is consistent with the generally xeric habitats of other juniper species (Adams, 2014). The geographic and environmental limitations of this habitat present a risk to the long-term survival of the species as the environmental niche is narrowly defined and natural migration is rare due to small, disjunct, and frequently island-locked populations. The Nature Conservancy presently ranks the conservation status of Seaside juniper as vulnerable due to the potential for low recruitment, human development, and storm exposure at specific sites and Douglas fir (*Pseudotsuga menziesii*) intrusion at most sites (NatureServe, 2017). Future climate change may exacerbate this species' vulnerability via direct climatic influences on the growth and reproduction (Ibáñez et al., 2007) as well as indirect effects related to increased competitive pressure from Douglas-fir intrusion (Aitken et al., 2008). Due to the recent discovery of this formerly cryptic species, little is known about the environmental controls on its distribution and growth. Understanding the habitat dynamics of this rare endemic is a crucial first step in any conservation efforts.

Dendrochronological methods can elucidate the relationship between annual variability in climate and the annual radial growth of trees. No dendrochronological analyses of Seaside juniper have thus far been published, so the suitability of this coastal species for crossdating and further dendrochronological analysis remains unknown. Prior studies have succeeded in correlating precipitation and temperature with the radial growth of Utah juniper (*J. osteosperma*) (Derose et al., 2016) and Rocky Mountain juniper growth (Spond et al., 2014), and regional seasonal drought has been correlated with Western juniper (Pohl et al., 2002). All of these juniper species are close relatives to Seaside juniper (Adams, 2014) indicating a potential for climate sensitivity in Seaside juniper. Understanding the climate-growth response of Seaside juniper will increase our understanding of the environmental niche of the species and aid in the development of a conservation strategy.

We therefore set out to determine if Seaside juniper is capable of crossdating, and, if so, to identify the relationship between climate and this species' annual radial growth. We also aimed to compile a comprehensive dataset of all known locations of Seaside junipers to expand our knowledge of the full geographic range and climate envelope of this recently discovered and as of yet minimally surveyed species. This work is novel as no dendrochronological chronology of Seaside juniper presently exists and no comprehensive dataset of known presence sites is presently available in literature.

Study Species

Seaside juniper is found exclusively throughout the islands and nearby mainland of the Salish Sea (Fig 1; Fig. 4). It is distinct in appearance, typically expressing lobate radial growth. The trunk typically grows upright and winding, often splitting into multiple trunks between zero and three meters from the ground. However, Seaside juniper also displays a high degree of phenotypic plasticity, with some individuals growing shrublike, to a height of approximately one meter with multiple diffuse trunks. Some individuals, if growing in highly stressful conditions, will grow in a carpet-like ground cover such as in the case of the Deception Pass State Park population (Adams, 2014) or exhibit Krumholz growth as observed in some individuals growing in Olympic National Park (Adams, 2014).

Study Sites

We sampled at five field sites throughout the San Juan Islands and nearby mainland. All study sites were located within the Salish Sea drainage basin. The Salish Sea is the body of water composed of the Puget Sound, The Strait of Georgia, and The Strait of Juan de Fuca (Fig. 1). The coastal mainland and islands of the Salish Sea exhibit a warm-summer Mediterranean climate, Koppen climate classification Csb, characterized by warm, low precipitation summers and cool, high precipitation winters (Peel et al., 2007). Sites where Seaside junipers presently grow are atypically arid in comparison to the rest of the Salish Sea basin (Table 1). The 1981 to 2010 climate normal for Washington Park, Anacortes, WA (our primary research site) reports a mean annual temperature of 10.9°C and a mean annual precipitation of 706.3 mm (Hamann et al., 2013). All field site elevations were less than 100 meters above sea level (Table 2). Soil depths range from exposed bedrock to moderate depth based on subjective categorization of the softness of the soil and the degree of root and bedrock exposure (Table 2), with some, but not all, sites containing serpentine soils.

The five field sites in this study (Fig. 5) from south to north are as follows:

Hope Island – A 0.73 km^2 island located in Skagit Bay. It is a Washington State Park open to the public since 1990 and was previously a private island. All samples were obtained from the south aspect exposed hillside of the southwestern quarter of the island.

Washington Park – A 0.88 km^2 park located in Anacortes, Washington. It is a city park with paved walking paths, unpaved trails, and social trails throughout the juniper stand. We found junipers growing predominately on the south aspect of the park.

Shaw Island – All samples were obtained from Cedar Rock Preserve, a 1.50 km^2 nature preserve owned and maintained by the University of Washington. It is located on the southern central shore of Shaw Island. The preserve was previously private agricultural land and was partially logged for conversion to pasture as recently as 1880 (Mills, 2008).

Orcas Island – The 2nd largest of the San Juan Islands. All samples were obtained from private properties (with permission of the owner) along the Fishing Bay waterfront in the town of Eastsound. Several trees had been excessively pruned or were presently being intentionally irrigated and were omitted from sample collection. No junipers were observed to be present anywhere on Orcas Island other than Eastsound.

Sucia Island – A 2.59 km^2 island located two miles north of Orcas Island making it the 2nd northmost San Juan Island. It has been a Washington state park since 1960. Samples were collected on the south face of the Ev Henry, Wiggins Head, and Lawson Bluff trails. Most samples collected from Sucia Island were too disintegrated to accurately measure.

Location scouting revealed the absence of Seaside juniper, defined here as the directly observed non-presence of Seaside juniper of any size, shape, or age, at Clinton ferry landing, Camano Island State Park, Cama Beach State Park, Juniper Beach, Coupeville, WDFW Skagit

Wildlife Area, Fish Town, Flagstaff Point, Kukutali Preserve, all of Lopez Island other than upright head, Samish Island, Larrabee State Park, Obstruction Pass State Park, Lummi Island, Portage Island, Lummi peninsula, Lake Terrell, and Birch Bay (Fig. 6).

Methods

Climate Envelope Model

Climate Envelope Modeling is a habitat modeling method which determines habitat suitability based on a multi-criteria analysis of climate variables over a specified geographic range. The present day climate envelope of Seaside juniper (Fig. 7) was determined from 145 known presence sites of both Seaside juniper and presumably misidentified Rocky Mountain juniper. Presence sites (Appendix A) were obtained through field collection (Fig. 5; Table 2), from literature (Sprenger and Dunwiddie, 2011; Adams, 2014), and from the Burke Museum Online Herbarium (Burke Museum, 2017). Climate data of presence locations were obtained from a 1 km raster of 1961-1990 climate normal from ClimateWNA v.5.51 (Hamann et al., 2013). The Salish Sea basin boundary (Freelan, 2009) is described as the hydrologic source boundary of Salish Sea waters as inferred from topography. All data were projected to North America Lambert conformal conic projection with bilinear resampling prior to analysis unless already projected as such in the source data. In ArcMap, redundant presence locations within the same 1km cell were manually identified and removed using the editor toolbar. The elevations of any presence sites that were not supplied with elevation measurements in their source were determined using the USGS 30 arc-second DEM and the ArcMap raster to point tool. Presence locations and elevations were input to ClimateWNA v5.40 and output to an excel spreadsheet.

Climate variable rasters were clipped to the extent of the Salish Sea basin boundary. Statistical analysis to determine inhabitable ranges of climatic variables was performed in Excel to produce the mean of the present range +/- 1.96 standard deviations to include the expected median 95 percentiles of each variable.

Climate envelope modeling was performed using ESRI Arcmap 10.5.1. The evaluated climate variables of growing season (April through September) mean minimum temperatures and total summer (July through September) precipitation were selected iteratively through exploration of the location of known presence sites and analysis of the relationship between annual radial growth and climate. As discussed in the results section, we found that radial growth of Seaside junipers in Washington Park strongly correlates with growing season minimum temperatures (Table 3) and the current geographical extent of Seaside juniper is restricted to areas of low precipitation (Table 1).

To define the relationship between average climate conditions and the geographic distribution of Seaside juniper, we used ESRI ArcMap 10.5.1 to extract the minimum, lower quartile, mean, upper quartile, and maximum values of climate variables from a 1km raster of 1961-1990 climate normal obtained from ClimateWNA v.5.51 (Hamann et al., 2013) of all cells within the Salish Sea basin boundary (Freelan, 2009) and for cells containing known presence sites (Fig 3.). These values were exported in .csv format and imported into R 3.3.3 (R core team, 2013), then visualized using box-plots (Fig. 8; Fig. 9; Fig. 10).

Site selection

We collected tree core samples from five sites throughout the San Juan Islands and the nearby mainland (Fig. 5; Table 2). We selected sites for accessibility and the presence of a sufficient quantity of mature Seaside juniper trees from known juniper locations documented by Adams (2014), known individual sites documented in the Burke Museum online herbarium (Burke Museum, 2017), and from predictive habitat modeling (Fig. 7) followed by in-situ identification.

Field methods

We collected tree core samples using an increment borer by extracting either one or two cores from the largest trunk of live trees at breast height and at positions parallel to aspect. Where possible, we took two cores from each tree, but this was not always possible due to many trees being inaccessible on one side. For trees where two cores were collected, each was collected from opposing sides of the tree (Speer, 2010). For each sampled tree, we recorded location using a Garmin GPSMAP 64. We also recorded DBH, categorical soil depth, slope, the height of the first trunk split, and the proportion of foliated canopy to total canopy (Table 2).

Laboratory methods

Samples were dried and then glued to wooden core mounts. We sanded cores using a belt sander with 320 grit sandpaper and then hand sanded the cores to a fine polish using 400 and 600 grit sandpaper. Sanded cores were scanned using an HP Scanjet 8300 at 1800 DPI resolution and measured to the nearest micrometer using CDendro and CooRecorder (Cybis Elektronik, 2010). Statistical crossdating was completed using Cdendro (Cybis Elektronik, 2010). Based on the results of our statistical crossdating, we inserted records to correct for missing rings. Cores that could not be successfully crossdated were omitted from further analysis. Minimum age of trees not cored to the center ring were estimated geometrically (Duncan, 1989).

Measurements from the crossdated cores were exported in Tucson decadal format and imported into R 3.3.3 (R core team, 2013). Statistical analysis was performed in R using the dplR (Bunn, 2008) and TREECLIM (Zang and Biondi, 2015) packages. Raw measurements were converted to Ring Width Index (RWI), a unitless growth index. We independently detrended each series by fitting either a modified negative exponential function or straight horizontal line to eliminate age related growth trends from the series and independently prewhitened each series using an AR1 model prior to averaging into a single chronology (Bunn, 2008). The final chronology was constructed by averaging together annual index values of each detrended series. Mean interseries correlation was calculated by dplR (Bunn, 2008) as the mean Pearson's r correlation coefficient of each series' tested against the mean chronology (Fritts, 2012). Mean sensitivity was calculated by dplR (Bunn, 2008) and is a measure of difference in consecutive year measurements with higher values indicative of reactive growth, which is potentially favorable to dendrochronological study (Fritts, 2012).

Statistical analysis

To quantify the relationship between internal climate variability and annual radial growth rates, we compared the ring-width chronology with instrumental climate records obtained from PRISM (PRISM climate group, 2018) and West Wide Drought Tracker (Abatzoglou et al., 2018) for the 4km cell which includes all sampled trees in Washington Park. We used a bootstrapped correlation function analysis with 1000 resampling iterations (Zang and Biondi, 2015) to assess the statistical significance of our correlation results.

Results

Climate Envelope Model

Our climate envelope parameters of mean value +/- 1.96 standard deviations produced a growing season minimum temperature range of 5.8°C to 9.9°C and a summer precipitation range of 24 mm to 183 mm. Climate Envelope Model parameters correctly classified suitable habitat in 97.9% of known presence sites (142 out of 145) indicating that the model is consistent with the actual distribution of the species (Fig. 7). However, 23 out of the 28 field sites we visited within the area classified as suitable did not contain Seaside juniper trees (Fig. 6). The majority of potential habitat is located on the interior coastal region of the Salish Sea. Uninhabitable areas are typically inland and at higher elevations.

Dendrochronology

We collected a total of 131 tree core samples from 72 mature trees at 5 sites (Fig. 5) throughout the San Juan Islands and nearby mainland (Table 2). At Hope Island we collected 19 cores from 12 trees. The oldest individual sampled at Hope Island had an innermost ring formed in 1933, and the site-wide median aged individual’s innermost ring was formed in 1950. At Washington Park we collected 41 cores from 21 trees. The oldest individual sampled at Washington Park had an innermost ring formed in 1739, and the site-wide median aged individual’s innermost ring was formed in 1853. At Shaw Island we collected 22 cores from 11 trees. The oldest individual sampled at Shaw Island had and innermost ring formed in 1821, and the site-wide median aged individual’s innermost ring was formed in 1948. At Orcas Island, we collected 36 cores from 21 trees. The oldest individual sampled at Orcas Island had an innermost ring formed in 1875, and the site-wide median aged individual’s innermost ring formed in 1933.

At Sucia Island we collected 13 cores from 7 trees. The oldest individual sampled at Orcas Island had an innermost ring formed in 1720, and the site-wide median aged individual's innermost ring formed in 1860.

We developed a master chronology only for the Washington Park site. We did not develop master chronologies for our other sites due to the low number of old trees and extensive structural failures in samples from these locations. We collected 41 cores from 21 trees in Washington Park (Table 2) with the final chronology being composed of 23 cores from 15 trees due to omission of non-correlating or undatable cores. The chronology was truncated to a sample depth of 5 which resulted in a total chronology range of years 1788 to 2016. The Washington Park chronology successfully crossdated (mean interseries correlation $r = 0.39$, $p < 0.001$, mean sensitivity 0.261) (Fig. 11).

The Washington Park chronology positively correlates to several current and prior year temperature variables (Table 3), especially to monthly minimum temperature, and especially across the April through September growing season (Fig. 13). We found the strongest correlations with prior year growing season minimum temperatures ($r = 0.55$, $p<0.01$) and current year growing season minimum temperatures ($r = 0.52$, $p<0.01$) (Table 3). The strongest single-month correlation found was to prior July mean minimum temperature ($r = 0.51$, $p<0.05$) (Fig. 13). A strong negative correlation was found with current year growing season diurnal temperature range ($r = -0.47$, $p<0.01$). We did not find any significant correlations with precipitation (Fig. 14) or PDSI (Table 4) despite climate envelope modeling finding distribution consistent with low precipitation (Table 1; Fig. 7).

Discussion

The habitat range defined by the climate envelope model is consistent with the Koppen climate classification of warm-summer Mediterranean (Csb) climate (Peel et al., 2007) which, during the growing seasons, is similar in precipitation patterns to the xeric habitats observed to be preferred by other juniper species (Adams, 2014). Areas of potential presence not presently known include the interior of south Vancouver Island, southern coastal British Columbia, most Gulf Islands south of Texada Island, and low elevation sites throughout the south Puget Sound. The climate envelope model identifies a contiguous corridor of habitat within the Elwha river basin which connects the current range of known presence with the proposed glacial refugium in the high elevation Olympic Mountains (Adams et al., 2010; Fig. 2) supporting the glacial refugium hypothesis if this present-day climate corridor is representative of a similar corridor prior to the northward expansion of the species. The climate envelope model also indicates a corridor between the current range of known presence and the recently discovered population of hybridized Seaside and Rocky Mountain junipers near Ross Lake National Recreation Area (Adams, 2015) providing a potential route for introgression by Rocky Mountain juniper and/or expansion beyond the boundary of the Salish Sea basin for Seaside juniper. However, it is essential to recognize the limitation of the climate envelope model as an indicator of where Seaside juniper may not be excluded due to climate, it is not an indication of guaranteed presence as exemplified by the frequent absences discovered by our scouting throughout the area defined as climatically suitable according to our climate envelope analysis (Fig 5). The absence of Seaside juniper in areas with suitable climate points to other limiting factors on its distribution.

Dispersal limitations, competition abilities, and human land use history are likely factors restricting the range of this species. Little is known about Seaside juniper's dispersal abilities, but its close relative Rocky Mountain juniper is known to have optimal seed production at age 50 to 200 years (Herman, 1958), with cone dispersal accomplished via both gravity and zoochory (Adams, 2014) and pollination via wind dispersal (Noble, 1990). If Seaside juniper shares these traits, then dispersal is limited to approximately 50 year generational divides at distances constrained by wind pollination and a lack of migratory birds known to feed on juniper cones (Adams, 2014). The only avian species known to consume the cones of Rocky Mountain juniper is the Bohemian Waxwing (*Bombycilla garrulus*) (Adam, 2014). However, the Bohemian Waxwing's range does not include the Salish Sea basin. Canada Grouse (*Falcipennis canadensis*), American Crow (*Corvus brachyryhnchos*), Willow Flycatcher (*Empidonax traillii*), Plumed Mountain Quail (*Oreortyx p. plumifer*), and Sharp-tailed Grouse (*Pediocetes phasianellus*) are known to consume cones from juniper species in general (Adams, 2014). Of these five species, only Willow flycatcher has a range including the Salish Sea basin (Sogge et al., 1997). While the American Crow does not have a coinciding range with the Salish Sea basin, their consumption of juniper cones may indicate juniper cone consumption by the closely related and potentially conspecific Northwestern crow (*Corvus caurinus*) (Hebert et al., 2004) which does inhabit the Salish Sea Basin. The Willow Flycatcher and Northwestern Crow are unlikely to be a vector of single-event long-distance cone dispersal as the Northwestern crow is non-migratory at the latitudes of the Salish Sea (BirdLife International, 2016) and the Willow Flycatcher is present only for nesting during the summer (Sogge et al., 1997) when juniper cones are not yet mature (Poddar and Lederer, 1982; Adams, 2014). The northwest crow is potentially capable of inter-island distribution in the modern geography of San Juan Islands and Gulf Islands occurring in a series of short distance cone dispersals as the American crow's maximum gut passage time of approximately four hours (VerCauteren et al., 2012) would likely be sufficient for inter-island travel so long as the flight range of non-migratory individuals is equal to or greater than the inter-island distances.

Absence sites within the habitable zones of the climate envelope model are typically in the areas of greatest and most recent land use conversion (Fig. 6) which may represent several already realized extirpations due to human development consistent with the Nature Conservancy's description of risk from human development (NatureServe, 2017). Major logging and pasture conversion of the Pacific Northwest began in earnest during the mid-19th century (Rienstra et al., 2001), at which time juniper was considered low value timber according to personal accounts by settlers (Mills, 2008). Juniper species have little to no economic use except in desert climates where few other trees grow (Adams, 2014). As a result, the cutting of juniper worldwide and especially in mountainous and forested regions is usually performed for land conversion rather than timber harvest (Adams, 2014).

Many undeveloped absence locations, including Iceberg Point and Point Colville on Lopez Island, appear to be optimal habitat based on their microclimatic characteristics. Presuming that Seaside juniper was previously present in Iceberg Point, the specific cause for the present day absence may be due to deliberate fire activity by Native Americans performing meadowland burning as maintenance for camas (*Camassia spp.*) beds (Murphy, 2005). Fire suppression has been implemented in the Pacific Northwest for the majority of the 20th century (Spies, 2010). Site specific studies have found that fire scars of Douglas fir indicate a maximum regional fire-free interval of 11 years at Iceberg Point over the past several centuries compared to the present day fire-free period of 103 years (Spurbeck and Kennum, 2003) indicating a recent cessation of previously regimented burning. However, several Seaside juniper presence sites also show evidence of deliberate fire ignition in the pre-settlement period (Sprenger and Dunwiddie, 2011) indicating that if fire caused extirpations exist, they are not universal among burn sites. Juniper species are known to be fire sensitive (Young and Evans, 1981) and climate adaptive (Adams, 2014), suggesting that fire is the more likely culprit of extirpation. Seaside juniper in the Pacific Northwest may experience some benefit from fire suppression due to a reduction in injury or mortality from burning similarly to the Western juniper is the juniper-pinon Woodlands (Young and Evan, 1981). However, the net effect to Seaside juniper is likely to be negative because unlike Western juniper, Seaside juniper tends to grow near stands of other potentially competitive tree species (Adams, 2014). Fire suppression in the Pacific Northwest often results in encroachment by competitive species such as Douglas fir or invasive weeds (Agee, 1996), allowing their intrusion into Seaside juniper territories and eventually outcompeting Seaside juniper for canopy. This scenario would be detrimental to new seedling establishment considering the already strained recruitment rate of Seaside juniper (NatureServe, 2018). Absence sites in apparently suitable habitat may be considered for facilitated introduction of Seaside juniper as a species conservation measure.

The moderately strong interseries correlation of the Washington Park chronology shows that crossdating is possible and indicates that Seaside juniper exhibits a consistent climatic response within the stand. Seaside juniper is therefore a potential resource for dendrochronological study, made even more valuable by a lack of other regional tree-ring records in this coastal area.

We found that annual radial growth rates were positively correlated with growing season minimum temperatures, and negatively correlated with diurnal temperature range (Table 3).

These results indicate heat-limited growth and/or solar irradiance stressed growth. This interpretation is supported by the fact that Seaside juniper was generally restricted to southerly aspects at all our sites, indicating microsite preference for maximized heat and irradiance. Diurnal temperature range is negatively correlated to cloud cover (Dai et al., 1999), which transitively indicates a positive correlation between Seaside juniper growth and cloud cover. This potentially indicates solar stressed growth caused by photoinhibition (Larcher, 2003) rather than a temperature related growth response, as maximum temperatures were not found to influence growth (Table 4) as would be expected in a heat-limited growth scenario. The lack of a precipitation signal in radial growth despite inhabiting a climate envelope containing atypically low precipitation for the region potentially indicates an establishment relationship to precipitation which is relevant to recruitment, but not to adult growth.

Seaside juniper's apparent habitat preference for maximized solar irradiance despite solar stressed growth indicates competition avoidance by colonizing habitats with microclimates that are uninhabitable by other species, which is a strategy observed in many other juniper species (Adams, 2014). This contradiction of climate and habitat is consistent with other juniper species' general habitat preference of hot and arid climates (Adams, 2014) despite frequently exhibiting heat stressed and water limited growth (Spond et al., 2014; DeRose et al., 2016). In addition, the soil depth of Seaside juniper stands are generally low to moderate depth but range from deep to near-absent (Table 2). Soil compositions range from the glaciomarine deposits and spodosols typical of the Pacific Northwest (Rocchio et al., 2016) to ultramafic (Kruckeberg, 1967). This may indicate that while Seaside juniper occupies a narrow climate envelope, they are relatively indiscriminate of soil characteristics. This further suggests a habitat exclusion strategy of occupying soils which chemically exclude tree species which would otherwise outcompete the

Seaside juniper for canopy, such as Douglas fir, similarly to the soil exclusion strategy observed in Bristlecone Pine (*Pinus longaeva*) (Fryer, 2004).

Seaside juniper has proven to be a challenging species for dendrochronological study. The low population of adult trees, the frequent breakage of cores, the inaccessibility of many individuals, and a propensity for missing rings all create challenging but surmountable barriers to dendrochronological research on the species. The few reliable records of mature stand locations caused site selection to require scouting and in-situ species identification. As is common among juniper species (Speer, 2010; Adams, 2014), Seaside juniper exhibits lobate growth which creates periods of increased or decreased growth localized to one portion of the trunk, thereby producing a growth signal in that portion of the tree which is unrelated to climate and may not be representative of the individual's total radial growth of that year. Also in common with other juniper species, Seaside junipers exhibit frequent missing rings on generally inconsistent years, which required re-measurement of most cores. This complicated the interpretation of ring widths throughout the chronology and increased the frequency of omitted samples. Despite these challenges, we found that it is possible to create a viable site chronology and that crossdating is possible for collections with a great enough sample depth, great enough age of samples, and for which cores remain intact enough to accurately measure. We also found that sufficient populations of trees large enough to provide core samples exist at various sites throughout the study area to potentially create a regional chronology.

Washington Park had the most numerous sampled trees and the most intact samples of any site we visited. However, the Washington Park chronology still only exhibits moderately strong interseries correlation, mean sensitivity, and climate correlations indicating that the growth of Seaside junipers in Washington Park is not strongly climate limited, which would result in poor crossdating across all sites regardless of sample size, and/or is sensitive to climate variables not explored by this study. The minimum age of trees at the Shaw, Orcas, and Hope Island sites are all more recent than 1850 (Fig. 12), corresponding to the approximate period of major European settlement and deforestation in the Pacific Northwest (Rienstra et al., 2001) suggesting intentional cutting in those locations. Shaw Island is specifically known to have been logged for conversion to pasture in 1880 (Mills, 2008) and at that site we found only one tree with an innermost ring year earlier than 1880, indicating that the vast majority of the stand regrew following deforestation. The lack of a strong climate response and apparently few sites with trees appreciably older than instrumental records suggests that Seaside juniper is likely a poor candidate for paleoclimatology; however, successful crossdating of the Washington Park site indicates the potential for use in dendroecology.

Many Washington State presence sites are located within public lands (Fig. 4; Appendix A) and are therefore protected from development and cutting. While there is no such protection for trees on private lands such as the Orcas Island site, human development represents an overall isolated and lower priority risk when compared to region-wide climatic stressors, which represent a threat to the entire species. Seaside juniper's high phenotypic plasticity allows for adaptations to minor climate changes, however severe changes to minimum temperatures, cloud cover, or precipitation dynamics threaten to reduce survivorship of a species already exhibiting low recruitment (NatureServe, 2017).

Due to the geographic isolation of island habitats, Seaside juniper on the San Juan Islands may not be able to respond to detrimental climatic changes through dispersal and migration, potentially resulting in extirpation. junipers of intermediate size and age between 50 and 200 years are the most vulnerable to changes in environmental conditions (Couralet et al., 2005) and are also the most reproductively active (Herman, 1958) suggesting climate changes may have severe repercussions to reproductivity. Specifically, summer high temperatures and multi-year drought are the most common climate anomalies linked to mortality in juniper species, both of which are expected to increase in the Salish Sea region over the next century (Allen et al., 2010; Mote and Salathe, 2010). Migration in response to climate change is unlikely to be a viable means of survival as climate change is predicted to outpace tree migration of species with small and isolated populations (Aitken et al., 2008) such as Seaside juniper (Fig 4). Many Seaside juniper populations exist on islands and low elevation sites (Fig. 4), creating geographic and topographic constraints that further prevent migration, presenting an extirpation risk to those populations if future climate is unfavorable to recruitment. Other juniper species typically increase their population density within their existing spatial range rather than expand territory through migration and limit what little expansion occurs to areas with very little topographic relief (Weisberg et al., 2007). If these population dynamics are also true of Seaside juniper, this represents an additional barrier to migration.

Future Research

Future research is needed to complete a comprehensive dendrochronological body of knowledge on the Seaside juniper. Canadian sites, many remaining San Juan Islands, the Gulf Islands, and the north face of the Olympic Mountains could also be sampled. Many mature trees remain unsampled at the Hope Island and Sucia Island sites, of which Sucia is the more viable dendrochronology site due to the relatively high population density and longevity of junipers on the island. If these trees are sampled and appended to the existing samples, then the sites may still prove to create viable chronologies, especially if the new samples are structurally sound enough to be accurately measured. Chronologies of these sites may be used to expand upon the climate-growth response observed in this study and potentially to elucidate establishment dynamics and controls on the species.

While genetic and morphological differences between Seaside juniper and Rocky Mountain juniper are known (Adams, 2014), it is not known if there are functional differences between the species. One non-climatic variable not reviewed by this study is salt spray, which is a potential growth stressor ubiquitous to the Seaside juniper as they are typically found in coastal environments (Adams, 2014; Fig. 2). Rocky Mountain juniper are known to be sensitive to salt spray (Miyamoto et al., 2004) but are typically located inland where salt spray is not present (Adams, 2014, Fig. 2). Since the relationship of salt spray to shore distance is known (Boyce, 1954; Barbour, 1978), the ring width measurements and locations of trees in this study combined with a survey of young trees to determine establishment dynamics may be used to determine if absolute growth and/or recruitment is a function of distance to shore as a proxy for sea spray salt concentrations. If salt spray affects the growth of Seaside juniper then coastal erosion represents an increasing risk to future habitat. However, if salt spray concentration does not affect the growth or establishment of Seaside juniper, then this may indicate an evolved trait with a functional difference from Rocky Mountain juniper.

The climate envelope model we produced (Fig. 7) is a useful tool for identifying climatic trends however there are more robust methods of habitat modeling which may be used to further elucidate the current habitat range of the Seaside juniper and to predict the effects of climate change on the species. For example, MAXENT is a presence-only modeling method which achieves a high predictive accuracy with minimal user calibration and permits a wide variety of predictor variables (Phillips and Dudik, 2008). The use of MAXENT or other habitat modeling methods was outside the scope of this study, however can be performed using the 145 known presence locations we compiled (Appendix A), which is likely to be sufficient data to produce reliable results from most habitat modeling methods (Hernandez et al., 2006).

Conclusion

Seaside juniper is a rare endemic tree species residing exclusively in a narrowly defined habitat that is not optimal to its growth as evidenced by a lack of complacent growth. Annual radial growth of Seaside junipers in Washington Park correlates to current and prior year growing season minimum temperatures and cloud cover, potentially indicating either heat limited or solar-stressed growth. Current presence locations are typically drier and warmer than the remainder of the Salish Sea region and are generally in exposed areas with southerly aspects. These findings suggest that the habitat preference of Seaside juniper is consistent with the relatively arid habitats of other juniper species; however, the endemic range of Seaside juniper is generally dissimilar in climate to those of other juniper species. This results in climate sensitive growth which while beneficial to dendrochronological research also indicates that there exists some ubiquitous environmental stressor which represents a potential threat to the long-term survival of the species if aggravated in the future. Climate change in the Salish Sea region is predicted to result in increased temperatures and increased seasonality of precipitation (Mote and Salathe, 2010). If predicted reduction of precipitation in summer is indicative of reduced cloud cover and the positive correlation between radial growth and minimum temperature is indicative of solar stress, then this may represent a threat to Seaside juniper growth. Conversely, if the relationship to minimum temperatures is direct, and the lack of correlation to precipitation indicates that water is already available in excess of what is necessary, then the predicted increase of temperatures in the Salish Sea may benefit Seaside juniper growth. However, any benefit received by Seaside juniper is likely to be outweighed by intrusion of competitive species diminishing the already limited habitat range. Seaside juniper may be able to adapt to minor increases in environmental stress caused by climate change, but the species has little means of migration in response to widespread loss of habitat due to its frequently segmented, small, and island-locked populations. Facilitated migration may be required to maintain the population.

We have successfully demonstrated that Seaside juniper is capable of crossdating and therefore is a candidate for dendrochronological research albeit a difficult study subject due to frequent missing rings, lobate growth, low population, and frequently inaccessible locations. However, we found these challenges to be surmountable if there is sufficient sample depth and time investment. Further dendrochronological and climate modeling research is necessary to elucidate the climate-growth response mechanism of Seaside juniper and the predicted effects of climate change on the narrowly defined habitat of this rare endemic.

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Tables and Figures

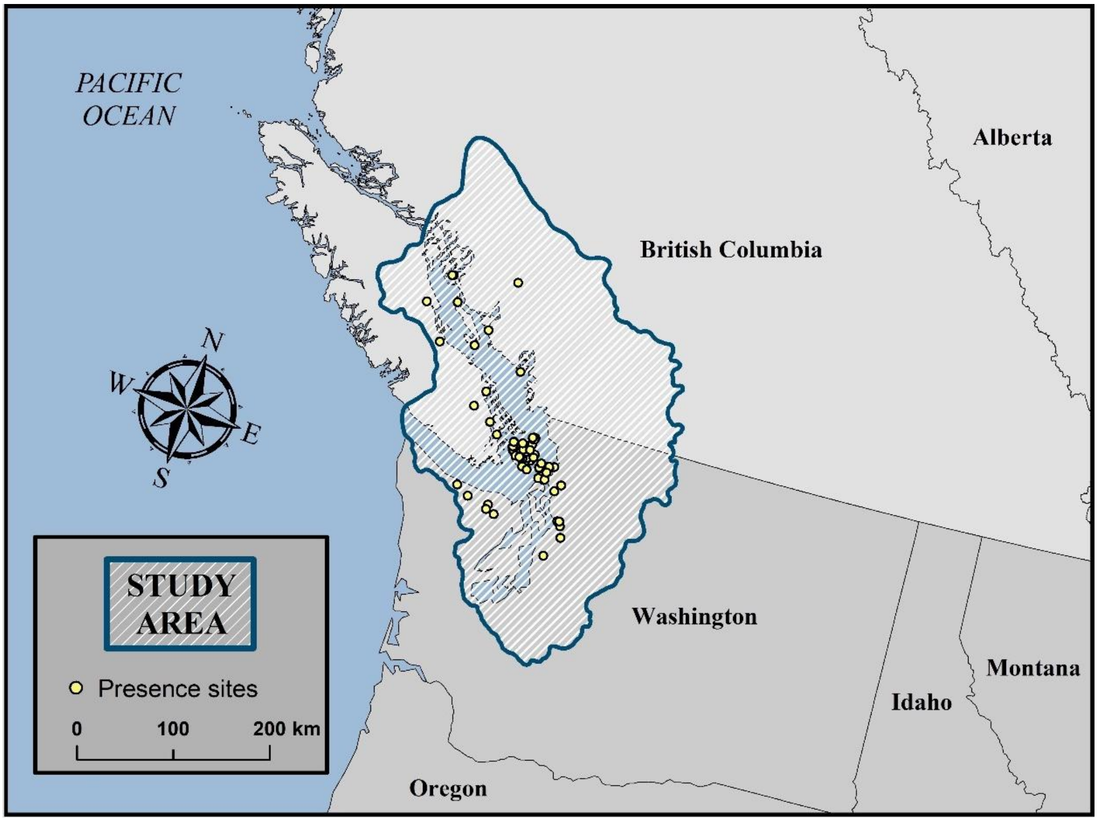

Figure 1. Endemic range of Seaside juniper. All known presence sites lie within the Salish Sea basin boundary. The Salish Sea basin is defined as the hydrological source of the Salish Sea inferred from topography (Freelan, 2009), and represents the topographic constraint of juniper migration in the near future. Lambert conformal conic projection.

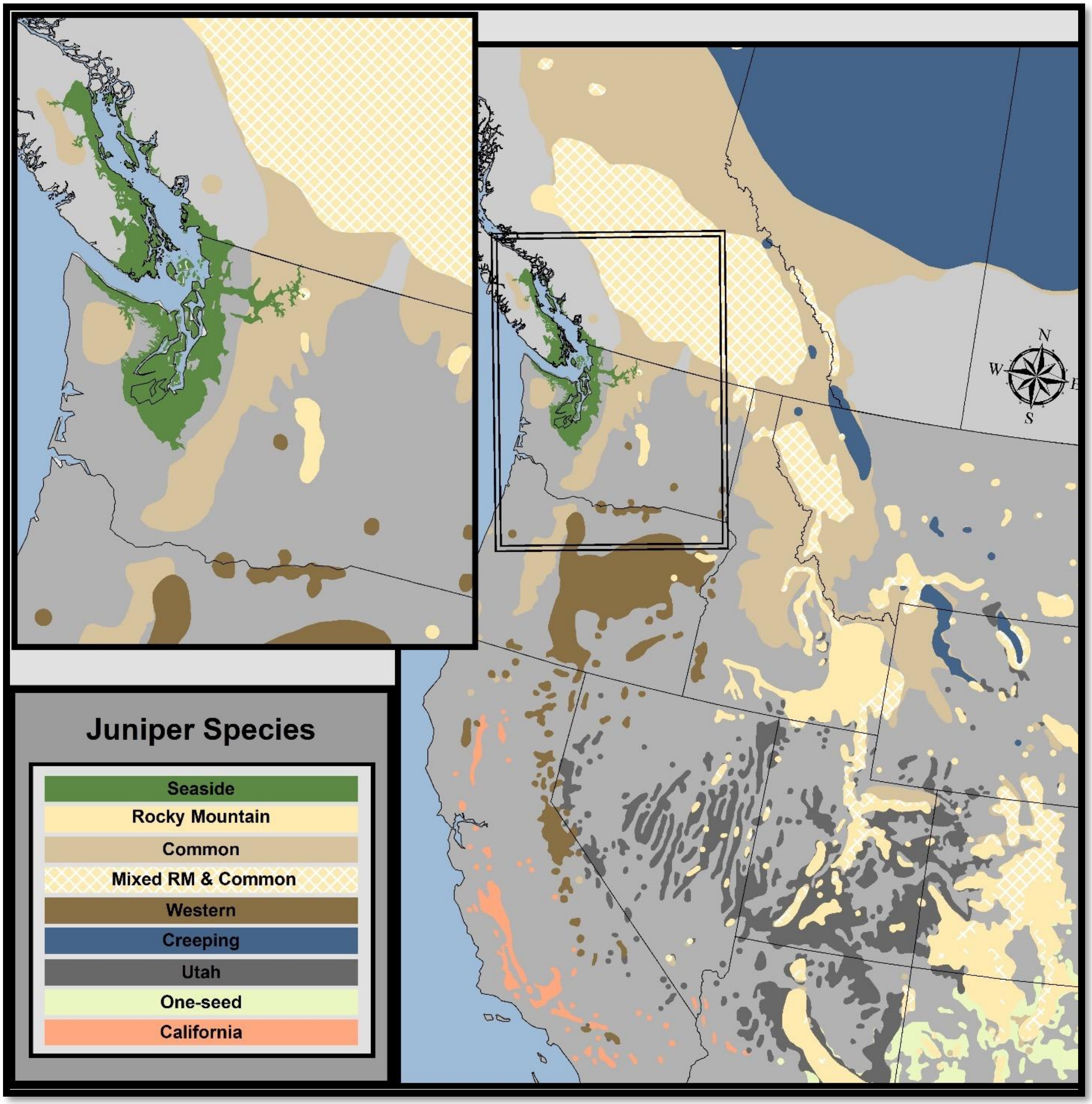

Figure 2. Map of species distributions of several juniper species common in western North America. Distribution of Seaside juniper was determined from our climate envelope model (Fig. 7). All other distributions adapted from (Little, 1971). Lambert conformal conic projection.

Figure 3. The extent of the Cordilleran Ice Sheet at last glacial maximum, approximately 20,000 years before present. Adams (2010) theorizes that Seaside juniper originates from a glacial refugium in the Olympic Mountains, caused by the Puget lobe separating two populations of ancestral Rocky Mountain juniper. Washington state plane north projection.

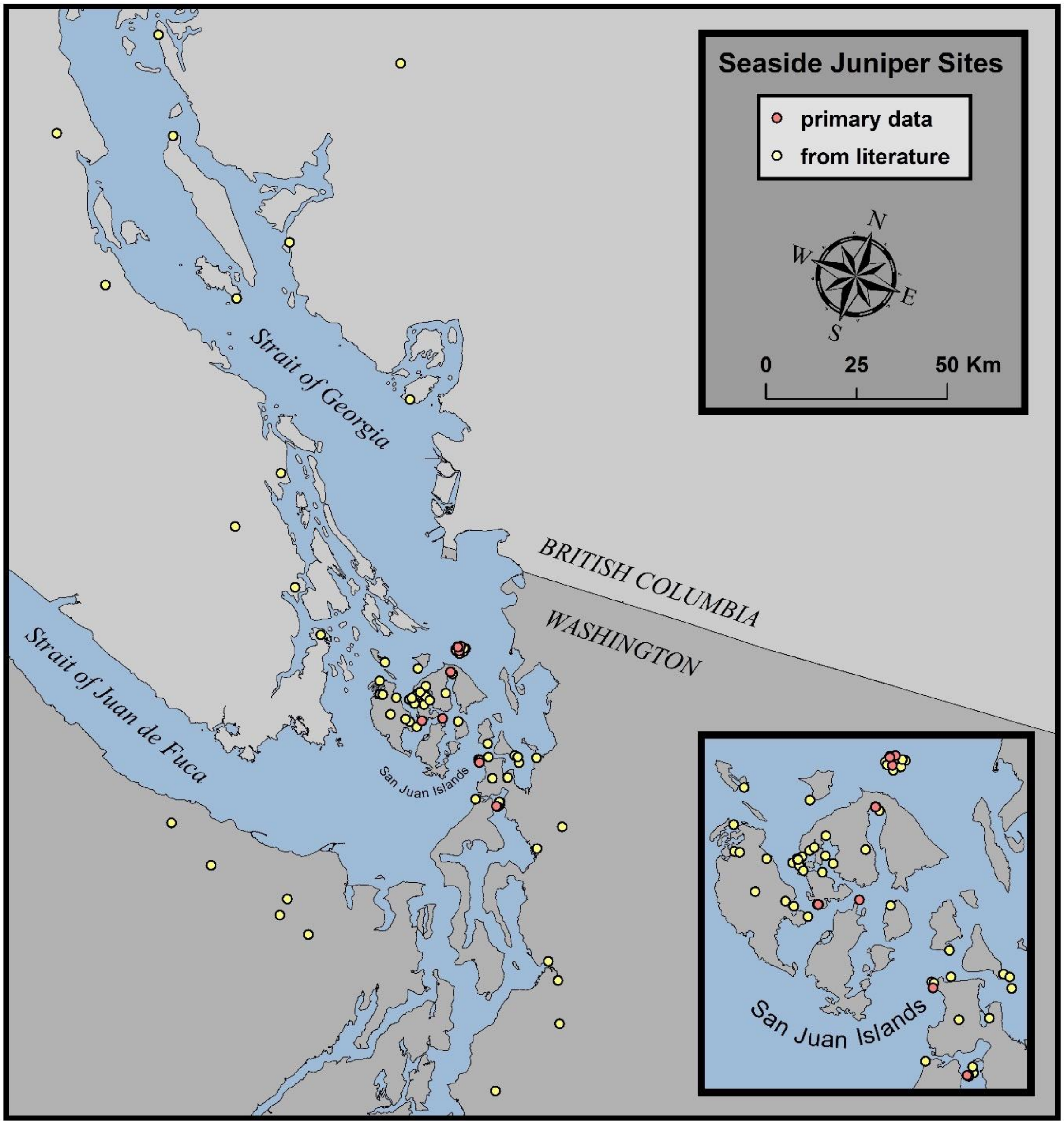

Figure 4. Known sites of Seaside juniper presence. Primary data sites were collected by Garmin GPSMAP 64 during tree core sampling. All "from literature" sites are interpreted from available literature (Sprenger and Dunwiddie, 2011; Adams, 2014; Burke Museum, 2017). Any trees identified in literature as Rocky Mountain juniper within the Salish Sea basin boundary were presumed to be misidentified Seaside juniper. Lambert conformal conic projection. See Appendix A for details of each location.

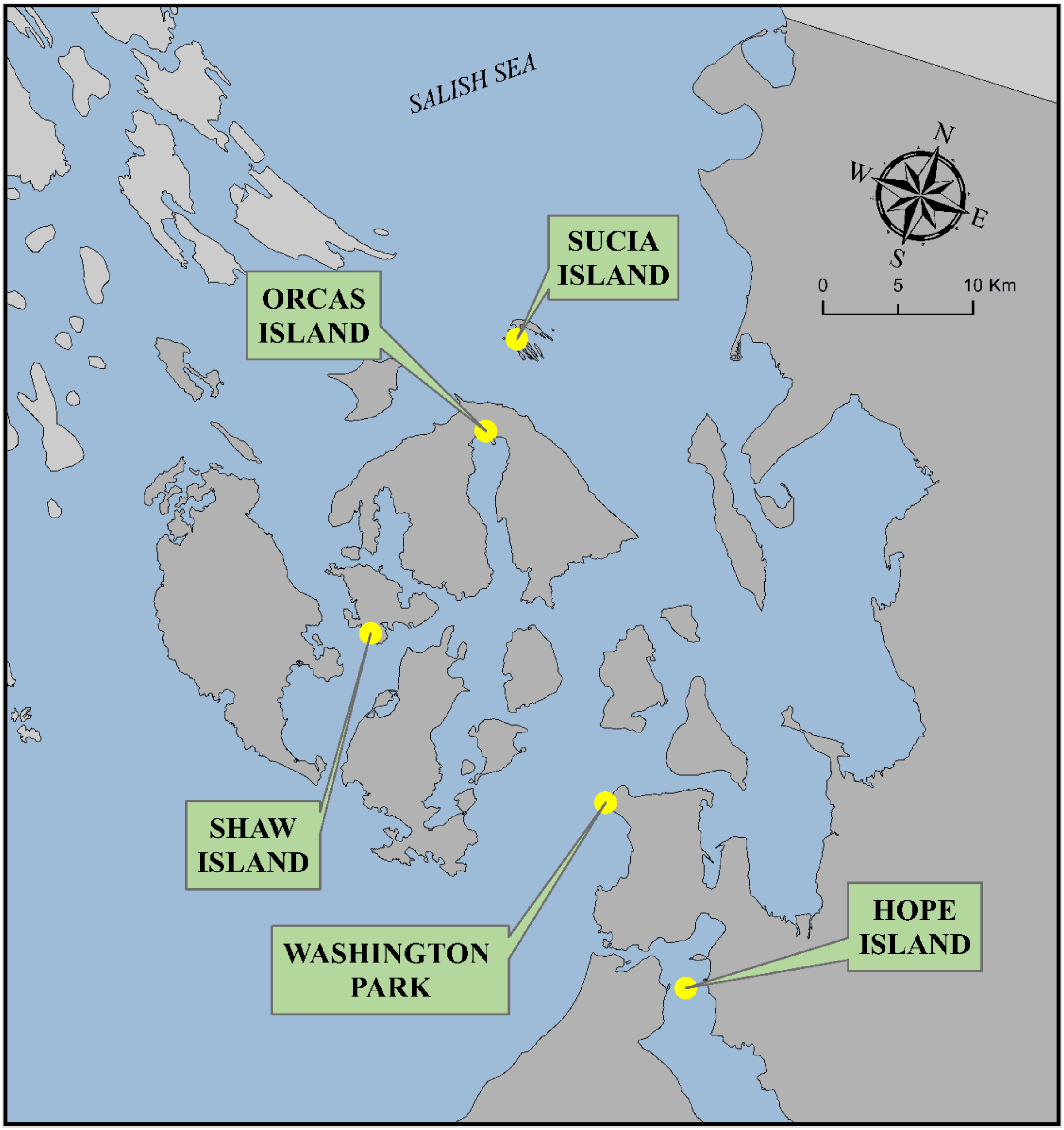

Figure 5. Locations of field sites. Lambert conformal conic projection.

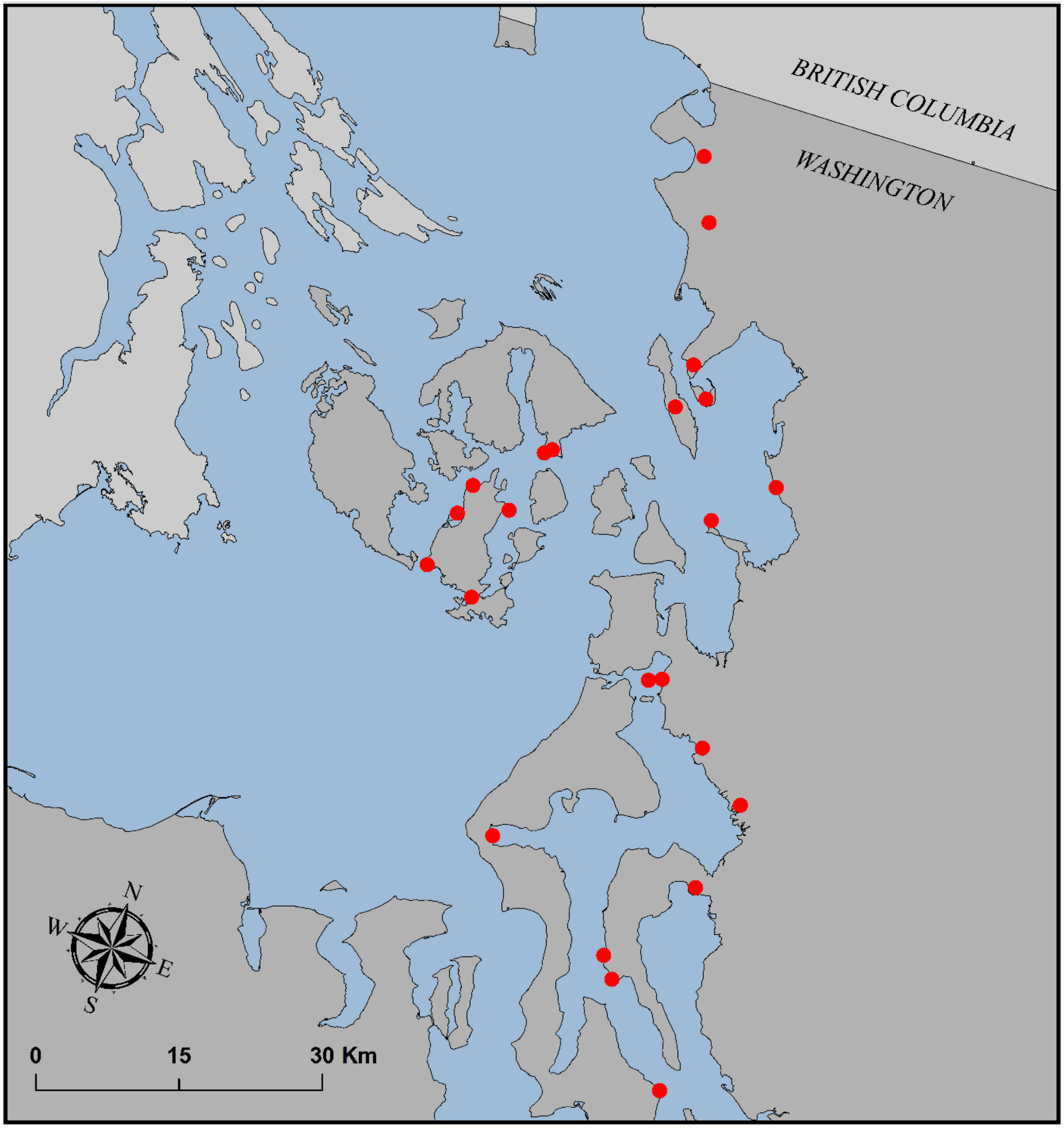

Figure 6. Observed Seaside juniper absence sites throughout the San Juan Islands and nearby mainland. Sites include (from south to north) Clinton ferry landing, Camano Island State Park, Cama Beach State Park, Juniper Beach, Coupeville, WDFW Skagit Wildlife Area, Fish Town, Flagstaff Point, Kukutali Preserve, all of Lopez Island other than upright head, Samish Island, Larrabee State Park, Obstruction Pass State Park, Lummi Island, Portage Island, Lummi peninsula, Lake Terrell, and Birch Bay. Lambert conformal conic projection.

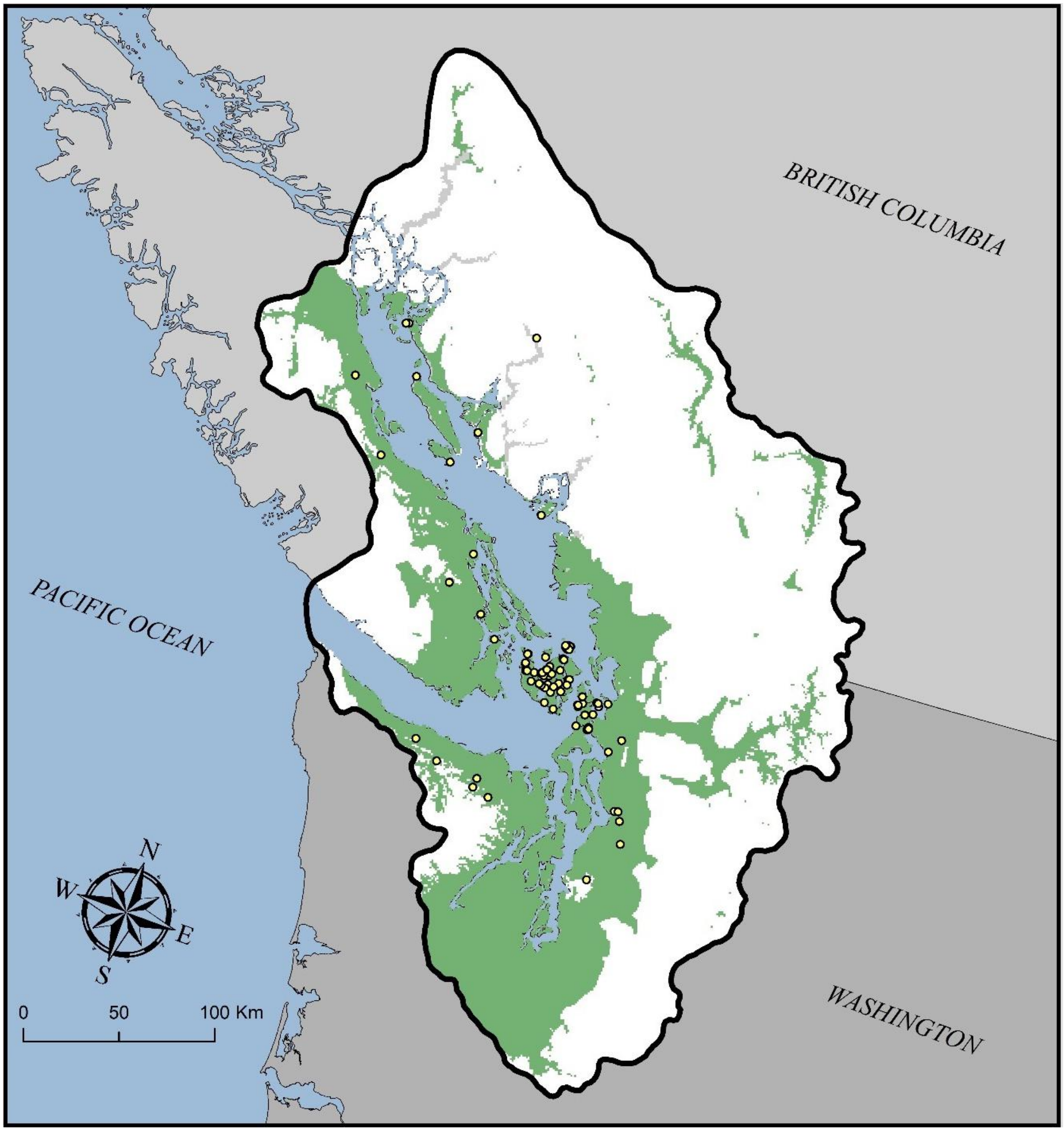

Figure 7. Climate Envelope Model of present day Seaside juniper habitat within the Salish Sea basin boundary. Green indicates suitable habitat, defined as climate parameters lying within the median 95 percentile of known sites mean growing season minimum temperatures and mean summer precipitation. Lambert Conformal Conic projection.

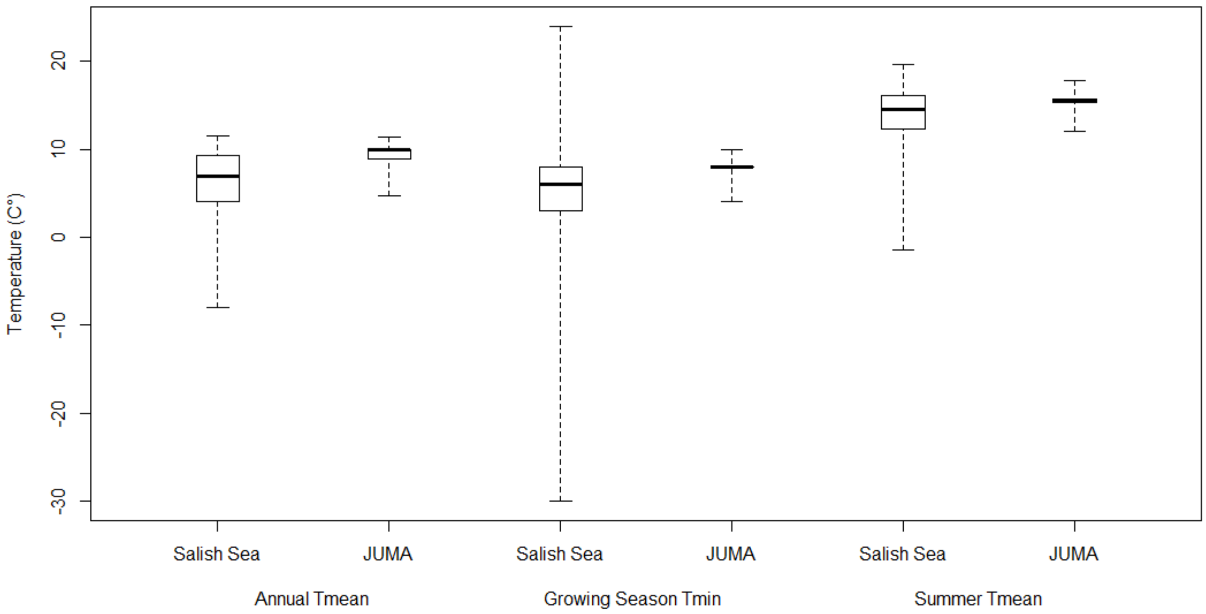

Figure 8. Box plot comparing ranges of temperature variables between the entire Salish Sea basin and Seaside juniper (“JUMA”) presence sites. Values shown are minimum, lower quartile, median, upper quartile, and maximum as calculated from 1 km rasters of 1961 to 1990 climate normal values for Annual mean temperature (Annual Tmean), April through September mean minimum temperature (Growing Season Tmin), and June through August mean temperature (Summer Tmean) (Hamann et al., 2013). “Salish Sea” indicates values for terrestrial cells within the Salish Sea basin. “JUMA” indicates values for cells containing Seaside juniper.

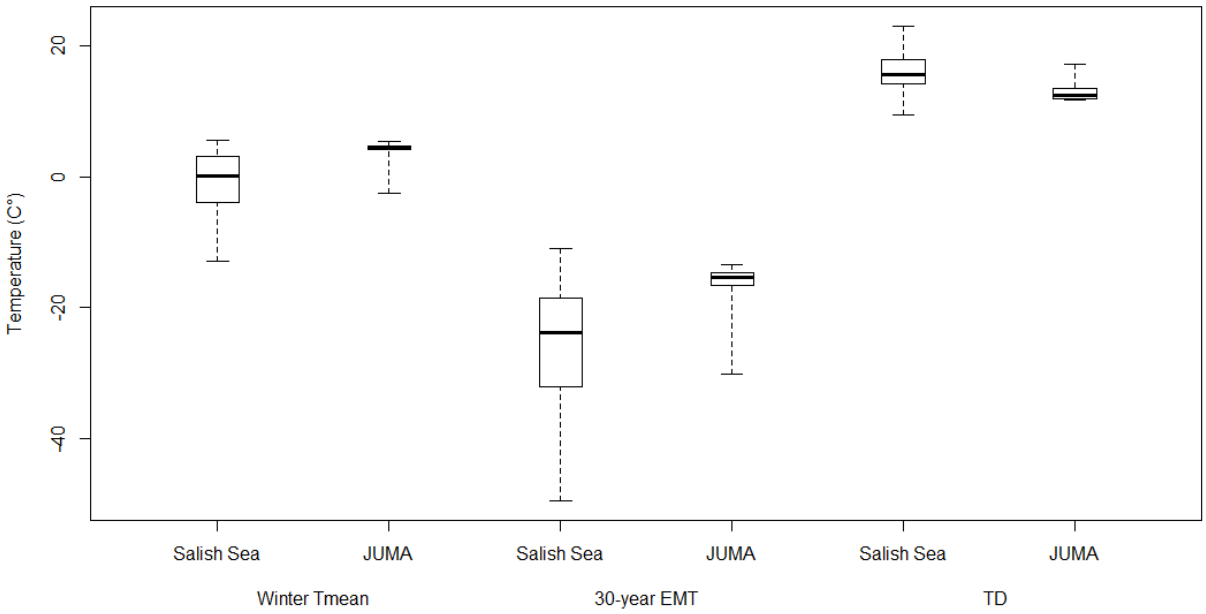

Figure 9. Box plot comparing ranges of temperature variables between the entire Salish Sea basin and Seaside juniper presence sites. Values indicated are minimum, lower quartile, median, upper quartile, and maximum as calculated from 1 km rasters of 1961 to 1990 climate normal values for December (previous year) through February mean temperature, 30 year extreme minimum temperature (30-year EMT), and Temperature difference (TD) defined as the difference between the mean temperature of the warmest and coldest months as a measure of continentality (Hamann et al., 2013). “Salish Sea” indicates values for terrestrial cells within the Salish Sea basin. “JUMA” indicates values for cells containing Seaside juniper.

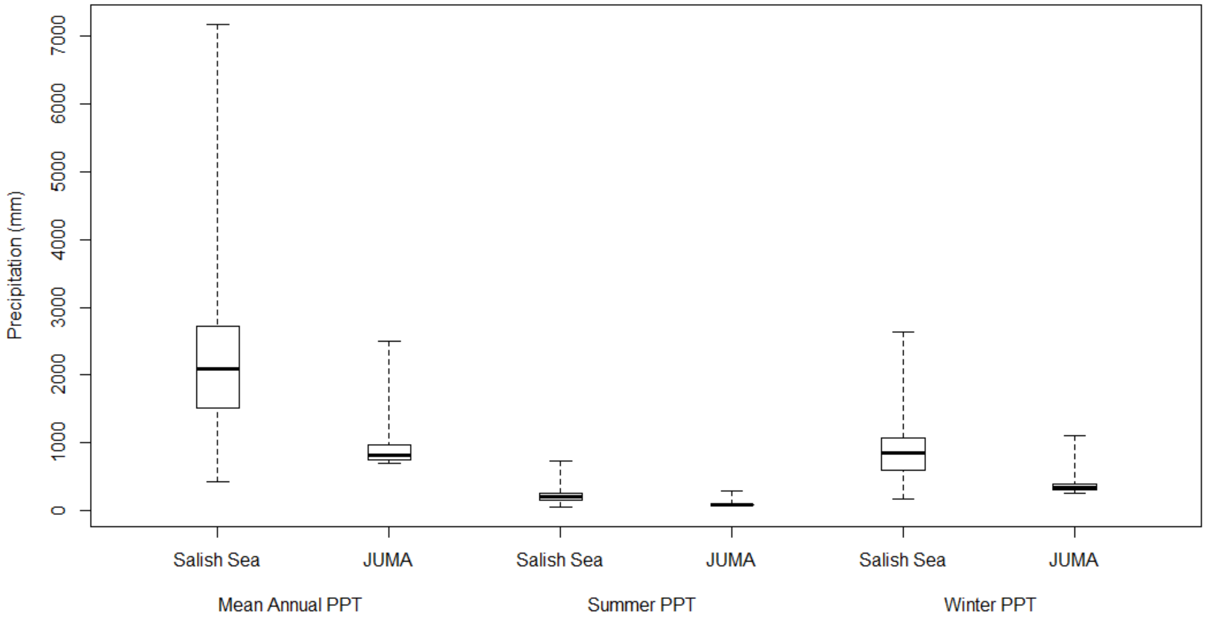

Figure 10. Box plot comparing ranges of precipitation variables between the entire Salish Sea basin and Seaside juniper presence sites. Values shown are minimum, lower quartile, median, upper quartile, and maximum as calculated from 1 km rasters of 1961 to 1990 climate normal values for Mean annual precipitation (Mean Annual PPT), June through August precipitation (Summer PPT), and December (previous year) through February precipitation (Winter PPT) (Hamann et al., 2013). “Salish Sea” indicates values for all terrestrial cells within the Salish Sea basin. “JUMA” indicates values for cells containing Seaside juniper.

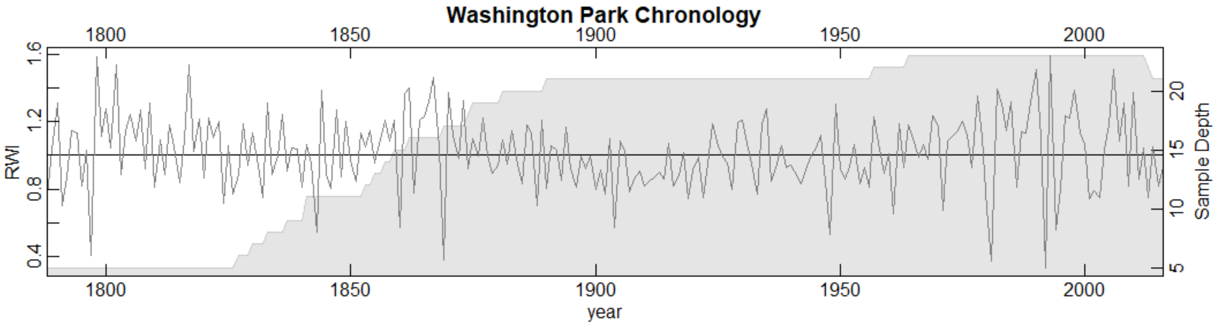

Figure 11. Chronology of Seaside juniper in Washington Park, Anacortes, WA. Mean interseries correlation r = 0.39, p <0.001. Mean sensitivity = 0.261

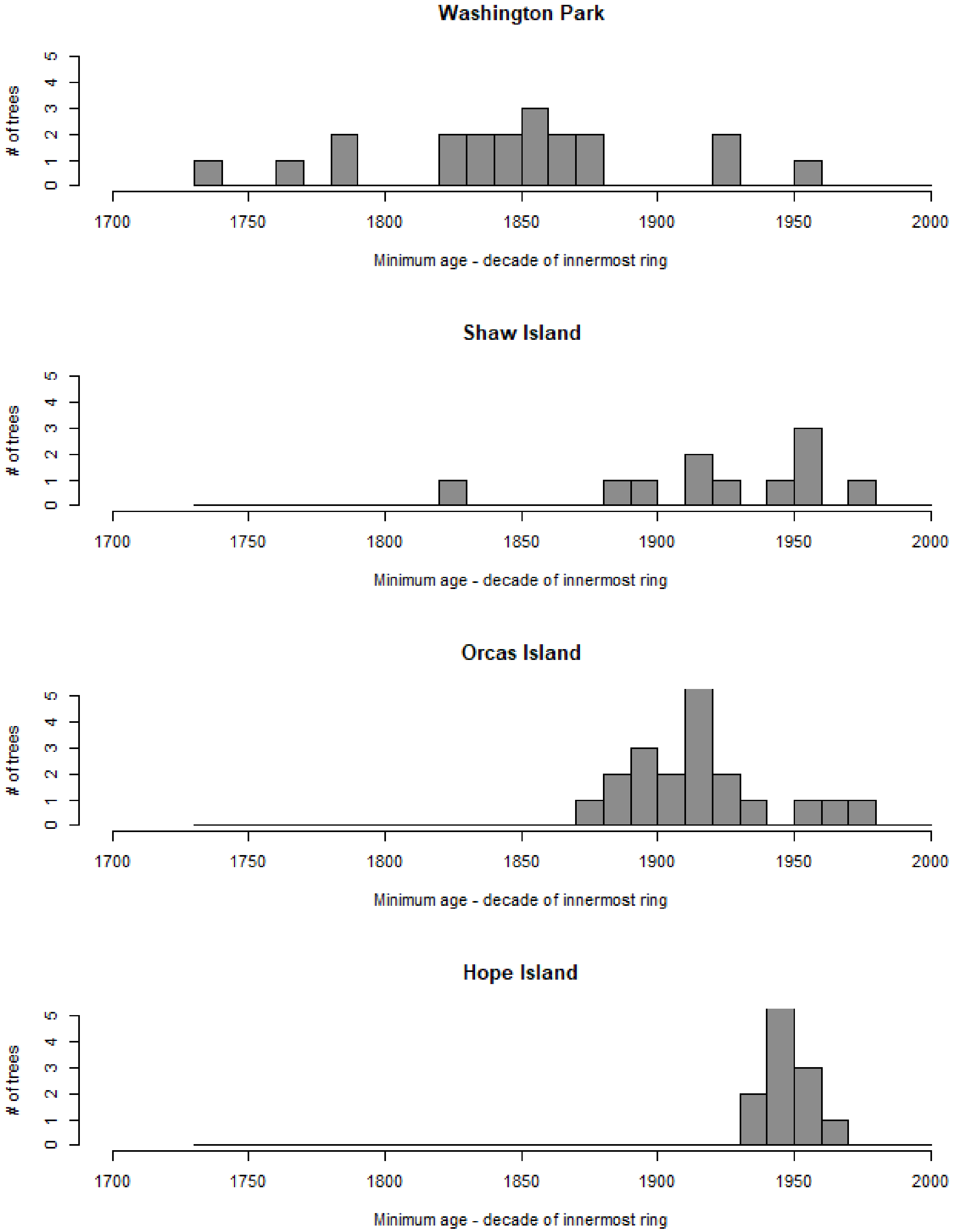

Figure 12: Minimum age of sampled trees in each of four sites categorized by decade. Sucia Island is omitted due to a lack of measureable cores.

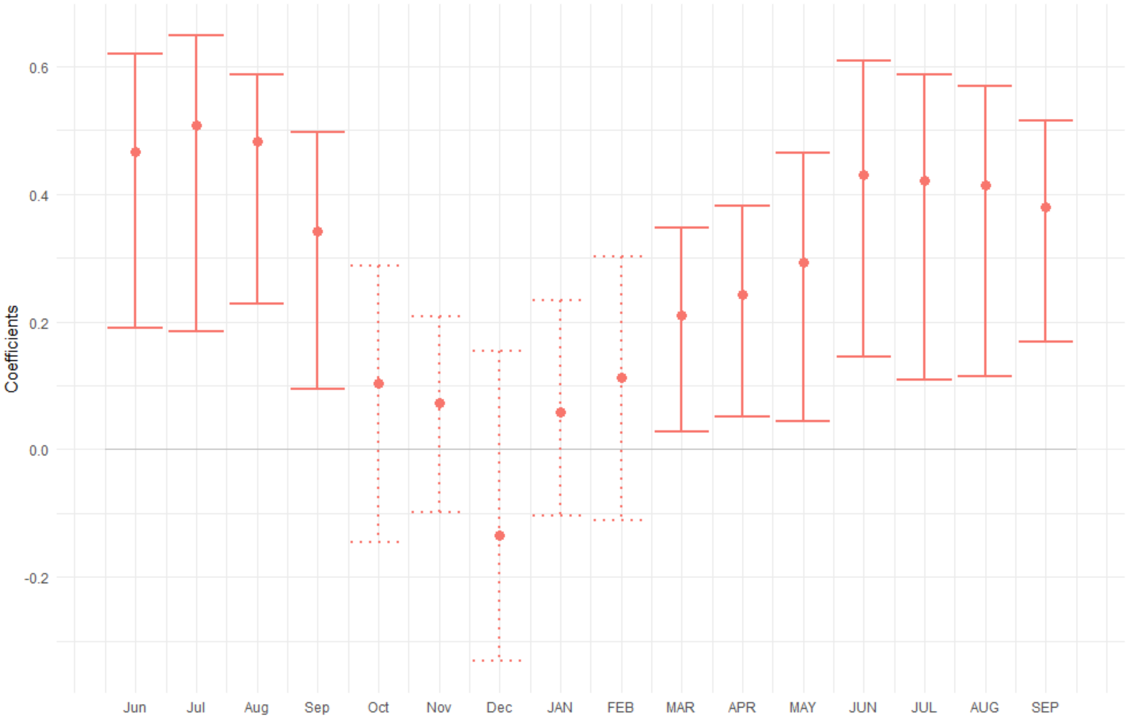

Figure 13. Bootstrapped correlation function analysis of Washington Park chronology to monthly mean minimum temperature from prior year June (Jun) through current year September (SEP). Solid line indicates significance at p<0.05. Bars indicate 95% confidence interval.

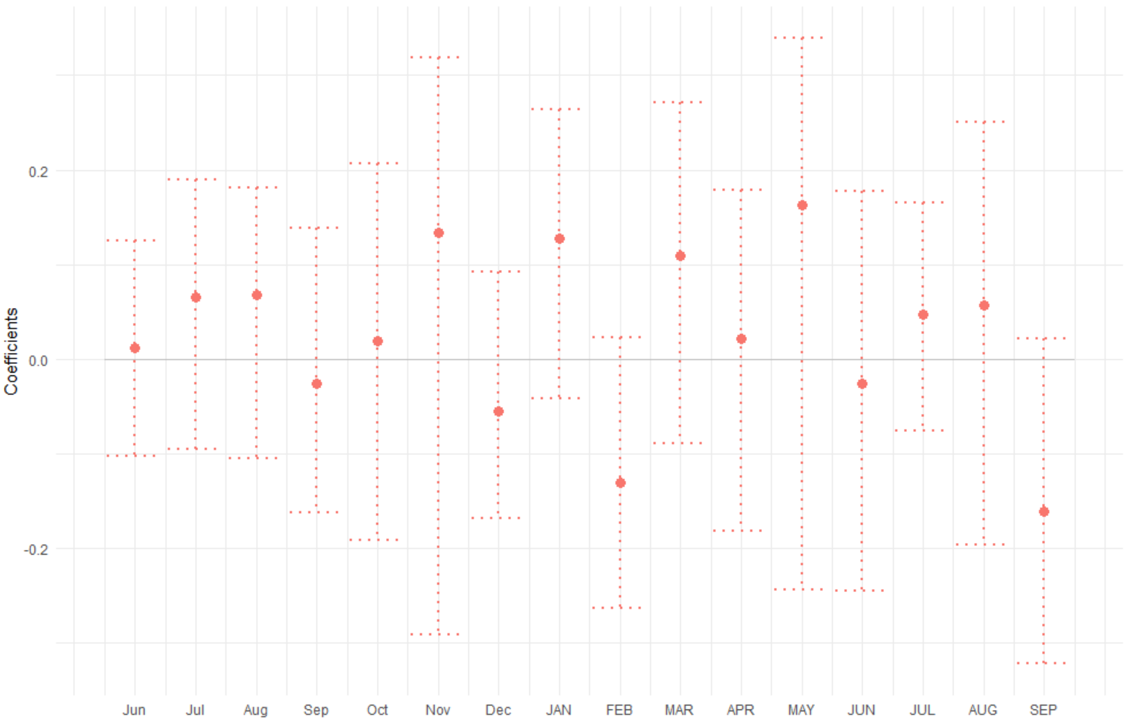

Figure 14. Bootstrapped correlation function analysis of Washington Park chronology to monthly precipitation from prior year June (Jun) through current year September (SEP). No correlation is significant at $p<0.05$. Bars indicate 95% confidence interval.

Table 1: Climate of Seaside juniper sites compared to entire Salish Sea basin. Data acquired from ClimateWNA v5.51 (Hamann et al., 2013).

	Juniper sites mean	**Juniper sites std. dev**	**Salish Sea mean**	**Salish Sea std. dev**
Mean Summer Temperature (C°)	15.50	0.95	13.99	2.63
Mean Apr-Sep Minimum Temperature (C°)	7.81	1.05	5.18	2.96
Mean Summer Precipitation (mm)	103.78	36.66	210.77	92.56
Mean Annual Precipitation (mm)	874.19	348.41	2197.89	900.04

Table 2: Field site locations and characteristics. Minimum age indicates the year of the earliest measured ring. DBH indicates Diameter at Breast Height (cm). Soil depth was assessed as a subjective categorical scale from 1 (shallow) to 5 (deep) of soils beneath each sampled tree's canopy.

	Hope Island	**Washington Park**	**Shaw Island**	**Orcas Island**	**Sucia Island**
Latitude (N)	48°23'48"	48°29'29"	48°33'1"	48°41'42"	48°45'18"
Longitude (W)	122°34'29"	122°41'34"	122°57'29"	122°54'31"	122°54'12"
Elevation (m)	0 - 67	0 - 68	0 - 16	0 - 15	0 – 45
Trees sampled (Qty)	12	21	11	21	7
Cores collected (Qty)	19	41	22	36	13
Oldest Minimum Age (earliest year)	1933	1739	1821	1875	1720
Median Minimum Age (earliest year)	1950	1853	1948	1933	1860
DBH mean (cm)	26.65	40.45	45.83	37.58	68.98
DBH Std. Dev.	7.36	8.90	15.82	12.01	14.91
DBH min (cm)	13.6	26.2	26.1	22	47.5
DBH max (cm)	40.2	65.5	79.0	68.6	97.7
Soil depth mean	2.08	2.19	2.3	2.84	2.57
Soil depth Std. Dev.	0.29	1.17	1.06	0.37	0.98

Table 3. Simple correlation of instrumental climate record and interpolated values (PRISM climate group, 2018) with Washington Park chronology, years 1895 through 2016. All correlations are significant at p<0.1 threshold. Boldface indicates significance at p<0.01 threshold.

Climate parameter	**Pearson's r coefficient**
Current year Apr-Sep mean daily minimum temperature	**.524**
Current year Apr-Sep mean daily temperature	**.341**
Current year Apr-Sep mean diurnal temperature range	**- .466**
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Current year Sep mean daily maximum temperature	**.210**
Current year Sep mean daily minimum temperature	**.377**
Current year Sep mean daily temperature	**.344**
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Prior year Apr-Sep mean daily minimum temperature	**.547**
Prior year Apr-Sep mean temperature	**.399**
Prior year Apr-Sep mean daily maximum temperature	.169
Prior year Apr-Sep total precipitation	.157
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Prior June mean daily minimum temperature	**.469**
Prior July mean daily minimum temperature	**.508**
Prior August mean daily minimum temperature	**.484**
Prior August mean daily mean temperature	**.409**
Prior year Apr-Sep mean diurnal temperature range	**-.392**

Table 4. Non-significant correlations of instrumental climate record and interpolated values (PRISM climate group, 2018) with Washington Park Seaside Juniper chronology of years 1895 through 2016.

Climate parameter	**Pearson's r coefficient**
Current year Apr-Sep mean maximum temperature	.085
Current year mean annual precipitation	.068
Current year Apr-Sep total precipitation	.068
Prior year mean annual precipitation	.157
Current year Apr-Sep mean PDSI	.017
Current year ENSO index	.130
Prior year Apr-Sep mean PDSI	.029

Appendix A. Known Presence Locations of Seaside Juniper

This appendix includes all Seaside juniper sites presently available in literature in addition to GPS coordinates of our study sites. It is provided to assist in the future research of the species. All primary data shows the location of individual trees sampled for this study. Sites from Burke Museum (2017) include all entries listed as either Seaside juniper or Rocky Mountain juniper on the presumption of misidentification. Sites from Adams (2014) are interpreted visually from maps and from image captions referencing locations, which may not represent exact locations. Some sites are redundant between sources and are provided here as confirmation.

ID	Latitude	Longitude	Source	Location	Notes
1	48.753333	-122.902496	Primary	Sucia Island	Located throughout entire island.
2	48.766667	-122.902496	Primary	Sucia Island	
3	48.763056	-122.91333	Primary	Sucia Island	
4	48.76222	-122.911942	Primary	Sucia Island	
5	48.75087	-122.909488	Primary	Sucia Island	Oldest individual on record, minimum age 298 years.
6	48.396045	-122.575936	Primary	Hope Island	
7	48.396026	-122.575815	Primary	Hope Island	
8	48.395664	-122.575024	Primary	Hope Island	
9	48.395685	-122.575033	Primary	Hope Island	
10	48.39569	-122.574993	Primary	Hope Island	
11	48.395671	-122.574931	Primary	Hope Island	
12	48.395724	-122.574946	Primary	Hope Island	
13	48.395719	-122.574699	Primary	Hope Island	
14	48.39573	-122.574455	Primary	Hope Island	
15	48.395599	-122.5739	Primary	Hope Island	

16	48.395601	-122.573918	Primary	Hope Island	
17	48.396142	-122.577677	Primary	Hope Island	
18	48.69516	-122.909272	Primary	Orcas Island	All Orcas Island samples found in Eastsound.
19	48.695114	-122.909826	Primary	Orcas Island	
20	48.695126	-122.909813	Primary	Orcas Island	
21	48.694766	-122.909629	Primary	Orcas Island	
22	48.694721	-122.909244	Primary	Orcas Island	
23	48.694765	-122.909283	Primary	Orcas Island	
24	48.694809	-122.90928	Primary	Orcas Island	
25	48.694739	-122.909257	Primary	Orcas Island	
26	48.694727	-122.90923	Primary	Orcas Island	
27	48.694664	-122.909205	Primary	Orcas Island	
28	48.69464	-122.909216	Primary	Orcas Island	
29	48.694501	-122.90947	Primary	Orcas Island	
30	48.694586	-122.909604	Primary	Orcas Island	
31	48.695109	-122.908799	Primary	Orcas Island	
32	48.695021	-122.908757	Primary	Orcas Island	
33	48.69499	-122.908792	Primary	Orcas Island	
34	48.69498	-122.908816	Primary	Orcas Island	
35	48.694927	-122.90887	Primary	Orcas Island	
36	48.694919	-122.908861	Primary	Orcas Island	

37	48.694696	-122.909433	Primary	Orcas Island	
38	48.550103	-122.960212	Primary	Shaw Island	All in Cedar Rock Nature Preserve.
39	48.550322	-122.960389	Primary	Shaw Island	
40	48.549736	-122.959151	Primary	Shaw Island	Oldest tree found at site. 165 years min.
41	48.549864	-122.959255	Primary	Shaw Island	
42	48.550193	-122.958153	Primary	Shaw Island	
43	48.550412	-122.958216	Primary	Shaw Island	
44	48.550413	-122.958279	Primary	Shaw Island	
45	48.550421	-122.958253	Primary	Shaw Island	
46	48.550447	-122.958315	Primary	Shaw Island	
47	48.550741	-122.958169	Primary	Shaw Island	
48	48.550442	-122.958962	Primary	Lopez Island	Along Upright Head Trail
49	48.572493	-122.883909	Primary	Lopez Island	Along Upright Head Trail
50	48.491904	-122.692825	Primary	Washington Park	Named “graduation tree” locally. Public parking available here.
51	48.49162484	-122.6918924	Primary	Washington Park	
52	48.49164169	-122.6918948	Primary	Washington Park	
53	48.4924736	-122.6915087	Primary	Washington Park	
54	48.49119251	-122.6919765	Primary	Washington Park	
55	48.49121799	-122.696338	Primary	Washington Park	
56	48.49091196	-122.6934842	Primary	Washington Park	

57	48.49115747	-122.6926713	Primary	Washington Park	
58	48.49162158	-122.6918942	Primary	Washington Park	
59	48.4916525	-122.6918884	Primary	Washington Park	
60	48.49201477	-122.6919131	Primary	Washington Park	
61	48.49202164	-122.6919896	Primary	Washington Park	
62	48.49199248	-122.6921993	Primary	Washington Park	
63	48.49156424	-122.6939876	Primary	Washington Park	
64	48.49163272	-122.6953275	Primary	Washington Park	
65	48.49162736	-122.6952932	Primary	Washington Park	
66	48.49139954	-122.6959264	Primary	Washington Park	
67	48.49147221	-122.696012	Primary	Washington Park	
68	48.49155318	-122.6963968	Primary	Washington Park	
69	48.49134489	-122.6961046	Primary	Washington Park	
70	48.49135964	-122.695967	Primary	Washington Park	
71	48.49224209	-122.6912994	Primary	Washington Park	
72	48.49205744	-122.691459	Primary	Washington Park	Oldest tree found at site. 285 years min.
73	48.753333	-122.902496	(Burke Museum, 2017)	Sucia Island	Confirmed
74	48.766667	-122.902496	(Burke Museum, 2017)	Sucia Island	Confirmed
75	48.586944	-123.083054	(Burke Museum, 2017)	San Juan Island	
76	48.583056	-123.148056	(Burke Museum, 2017)	San Juan Island	

77	48.58408	-123.137901	(Burke Museum, 2017)	San Juan Island	
78	48.592355	-123.031631	(Burke Museum, 2017)	Yellow Island	
79	48.498889	-122.699722	(Burke Museum, 2017)	Washington Park	Confirmed
80	48.397222	-122.663887	(Burke Museum, 2017)	Cranberry Lake	Growing in sand dunes, carpetlike.
81	49.630556	-124.050552	(Burke Museum, 2017)	Skardon Island	
82	50.164693	-123.851646	(Burke Museum, 2017)	Malibu Rapids	
83	47.998333	-123.248611	(Burke Museum, 2017)	Deer Park	Krummholz. Highest known elevation, 5600 ft.
84	47.951944	-123.256943	(Burke Museum, 2017)	Deer Park (deer ridge trail)	Krummholz. Mixed with common juniper.
85	48.02	-123.571671	(Burke Museum, 2017)	Griff Creek	
86	48.09348	-123.770561	(Burke Museum, 2017)	Lake Crescent	On Spruce Railroad Trail
87	47.926123	-123.127357	(Burke Museum, 2017)	3 o'clock ridge	
88	47.683333	-122.25	(Burke Museum, 2017)	Magnuson Dog Park – Seattle	Likely landscaped. Species not confirmed.
89	48.008554	-122.144081	(Burke Museum, 2017)	Spencer Island	
90	48.048611	-122.202499	(Burke Museum, 2017)	Ebey Slough	
91	47.901249	-122.088882	(Burke Museum, 2017)	Pilchuck River	
92	48.53666	-122.568893	(Burke Museum, 2017)	Huckleberry Island	
93	48.522222	-122.544998	(Burke Museum, 2017)	Hat Island	Not the larger "Hat Island" near Mukilteo
94	48.535556	-122.555557	(Burke Museum, 2017)	Saddlebag Island	
95	48.322222	-122.376114	(Burke Museum, 2017)	Milltown	Unconfirmed. Near DFW Skagit Natural Area

96	48.395833	-122.306389	(Burke Museum, 2017)	Little Mountain	
97	48.512767	-122.666008	(Burke Museum, 2017)	Anacortes Ferry Terminal	
98	48.49833	-122.694717	(Burke Museum, 2017)	Washington Park	Confirmed
99	48.545293	-122.684662	(Burke Museum, 2017)	Cypress Island	Large Stand, located throughout the island
100	48.401611	-122.567024	(Burke Museum, 2017)	Hope Island	Confirmed
101	48.47639	-122.569443	(Burke Museum, 2017)	Tommy Thompson Trail	
102	48.754541	-122.917709	(Burke Museum, 2017)	Little Sucia Island	Confirmed
103	48.76455	-122.880928	(Burke Museum, 2017)	Ewing Island	
104	48.754522	-122.885826	(Burke Museum, 2017)	N. Finger Island	Private Island, no access
105	48.76435	-122.887177	(Burke Museum, 2017)	Cluster Island	
106	48.603333	-123.017776	(Burke Museum, 2017)	Reef Island	
107	48.531111	-122.970833	(Burke Museum, 2017)	Turn Island State Park	
108	48.595	-123.020554	(Burke Museum, 2017)	Coon Island	
109	48.590278	-123.013885	(Burke Museum, 2017)	Cliff Island	
110	48.620278	-123.167503	(Burke Museum, 2017)	Pearl Island	
111	48.664444	-123.172775	(Burke Museum, 2017)	Stuart Island	
113	48.591111	-123.018059	(Burke Museum, 2017)	Nob Island	
114	48.598889	-123.025833	(Burke Museum, 2017)	McConnel Island	
115	48.592222	-122.970276	(Burke Museum, 2017)	Bell Island	
116	48.586667	-123.007225	(Burke Museum, 2017)	Shaw Island	

117	48.639167	-122.985832	(Burke Museum, 2017)	Skull Island	
118	48.613889	-122.974442	(Burke Museum, 2017)	Victim Island	
119	48.607222	-122.955002	(Burke Museum, 2017)	Oak Island	
120	48.614167	-123.006943	(Burke Museum, 2017)	Fawn Island	
121	48.598333	-123.023888	(Burke Museum, 2017)	McConnel Island	
122	48.691667	-122.900002	(Burke Museum, 2017)	Orcas Island	
123	48.619995	-123.000061	(Burke Museum, 2017)	Orcas Island	
124	48.6375	-122.902222	(Burke Museum, 2017)	Orcas Island	
125	48.538333	-123.003609	(Burke Museum, 2017)	Brown Island	
126	48.54111	-123.084717	(Burke Museum, 2017)	San Juan Island	
127	48.541389	-123.022499	(Burke Museum, 2017)	San Juan Island	
128	48.763056	-122.91333	(Burke Museum, 2017)	Sucia Island	
129	48.76222	-122.911942	(Burke Museum, 2017)	Sucia Island	
130	48.677833	-123.038045	(Sprenger and Dunwiddie, 2011)	Waldron Island	
131	50.024409	-124.840725	(Adams, 2014)	Townley Island	
132	49.681816	-124.978437	(Adams, 2014)	Courtenay, B.C.	
133	49.398286	-124.608808	(Adams, 2014)	Qualicum Bay	
134	49.062879	-123.770298	(Adams, 2014)	Roberts Memorial Provincial Park	
135	48.843892	-123.82499	(Adams, 2014)	Chemainus River	
136	48.823088	-123.590538	(Adams, 2014)	Maple Bay	

137	48.580024	-123.468992	(Adams, 2014)	Victoria, B.C.	Brentwood Bay
138	48.747231	-122.898375	(Adams, 2014)	Sucia Island	
139	48.532336	-122.807377	(Adams, 2014)	Blakely Island	
140	48.453477	-122.625555	(Adams, 2014)	Mt. Erie	may require rock climbing to access
141	49.442676	-124.177883	(Adams, 2014)	Lasqueti Island	Squitty Bay
142	49.795499	-124.631672	(Adams, 2014)	Texada Island	
143	48.536556	-122.486928	(Adams, 2014)	Padilla Bay	
144	49.335888	-123.402908	(Adams, 2014)	Bowen Island	
145	48.412008	-122.579704	(Adams, 2014)	Skagit Island	Home to largest JUMA on record (DBH 118cm)