

# Distribution patterns of disjunct and endemic vascular plants in the interior wetbelt of northwest North America<sup>1</sup>

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**Abstract:** A region of contrastively wetter and milder climate occurs in inland northwest North America, separated from similar climates of the Pacific coast by 200–400 km. Researchers have long noted that numerous vascular plants divide their ranges between the interior wetbelt and coastal regions, although many such disjunctions have hitherto gone undocumented. Here I summarize all vascular plants shared between coastal and interior wetbelt regions, disjunct by at least 200 km. These disjunct taxa are assigned to north-coast and south-coast lists according to whether the coastal portions of the ranges occur primarily north or south of the southern limits of maximum continental glaciation. A list of interior wetbelt endemic taxa is also presented, focusing on those that occur at forested elevations. Presence/absence for coastal disjunct and endemic taxa were assigned to grid of 1° × 1° latitude–longitude cells. Using this grid, concentrations of disjunct and endemic taxa were detected, and total values per cell were tested in linear regression for a relationship to mean annual precipitation. In total, 116 coastal disjunct taxa were detected, 31 of them north-coastal and 85 south-coastal. Interior wetbelt endemic and subendemic taxa total 95, and of these, 46 were found primarily at forested elevations. North-coast taxa were found over a wide latitudinal range both north and south of the glacial limits, and their distribution had a weak positive relationship with annual precipitation. South-coast and endemic taxa were found mostly south of the glacial limits, and their distribution did not correlate to annual precipitation. The greatest concentrations of south coastal disjunct and endemic taxa occurred in the Clearwater region of north-central Idaho; a region noted by previous researchers to be a likely ice-age refugium for wet-climate dependent plants and animals. Inferences are made from these patterns, both for biogeographical understanding of the roles played by the interior wetbelt and some regions connecting to the coast, as well as for preservation of biodiversity and ecosystem continuity.

*Key words:* biogeography, Clearwater refugia, disjunct distributions, endemics, inland rainforest, vascular plants.

**Résumé :** On retrouve une région contrastée humide à climat plus doux à l'intérieur des terres dans le nord-ouest de l'Amérique du Nord, laquelle est éloignée de climats similaires sur la côte du Pacifique de 200 à 400 km. Les chercheurs ont noté depuis longtemps que de nombreuses plantes vasculaires divisent leurs aires entre la ceinture humide dans les terres et les régions côtières, bien que de telles disjonctions soient restées non documentées jusqu'ici. L'auteur résume l'ensemble des plantes vasculaires partagées entre les régions côtières et la ceinture humide dans les terres, séparées par au moins 200 km. Il attribue ces taxons disjoints aux listes côte nord et côte sud, selon que les portions côtières des aires se retrouvent prioritairement au nord ou au sud des limites sud de la glaciation continentale maximale. Il présente également une liste d'espèces endémiques de la ceinture humide de l'intérieur, avec accent sur celles qui se retrouvent dans les forêts de haute élévation. Il a attribué à des grilles cellulaires de 1° × 1° degré de latitude–longitude, la présence/absence des taxons disjoints et endémiques. À l'aide de cette grille, l'on a pu détecter les concentrations de taxons disjoints et endémiques, et tester les valeurs totales par régression linéaire afin d'établir une relation avec la précipitation annuelle moyenne. Au total, on a décelé 116 taxons disjoints, 31 d'entre eux nord côtiers et 85 sud côtiers. Les endémiques de la ceinture à l'intérieur des terres regroupent 95 taxons, 46 d'entre eux retrouvés prioritairement dans les forêts en altitude. On retrouve les taxons endémiques nord côtiers sur une grande aire latitudinale, surtout à la limite glaciaire sud, et leur distribution ne montre pas de corrélation avec la précipitation annuelle. Les plus grandes concentrations de taxons endémiques disjoints sud côtiers se retrouvent dans la région de Clearwater au centre nord de l'Idaho, une région désignée par des chercheurs antécédents comme refuge probable de l'âge glaciaire pour les plantes et les animaux dépendants d'un climat humide. À partir de ces patrons, l'auteur déduit des conséquences à la fois pour la compréhension biogéographique des rôles joués par la ceinture humide de l'intérieur des terres et certaines régions reliées à la côte, ainsi que pour la préservation de la biodiversité et la continuité des écosystèmes.

*Mots-clés :* biogéographie, refuge de Clearwater, distributions disjointes, endémiques, forêt ombrophile de l'intérieur, plantes vasculaires.

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## Introduction

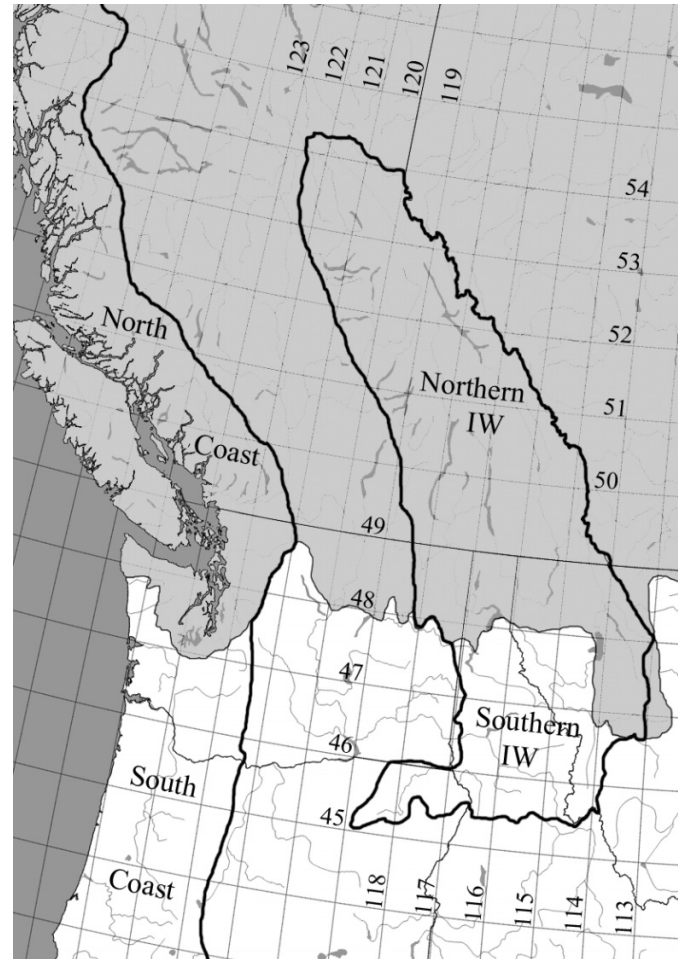
The disjunct distributions of a large array of organisms in the widely separated coastal and inland wetbelt regions of northwestern North America (Fig. 1) have been studied by researchers in both the United States and Canada. This distribution has been highlighted among plants (Leiberg 1900; Schofield 1969; Johnson and Steele 1978; Lorain 1988; Schofield 2004), lichens (Goward and Spribille 2005), and animals (Wilke and Duncan 2004; Carstens et al. 2005a; Carstens et al. 2005b). Until recently, most researchers assumed these disjunctions are such that coastal regions were the geographical source and inland regions the sink. Some researchers, however, have hypothesized that some organisms secondarily colonized coastal regions from inland wet-forest regions (Daubenmire 1975; Brunsfeld et al. 2007). Additional studies focusing on disjunct or endemic organisms suggest that the wet forests of the Interior Wetbelt (IW) have persisted over very long periods within some landscapes in inland regions (Brunsfeld and Sullivan 2006; Brunsfeld et al. 2007). Other studies, especially those sampling pollen deposits (Mack et al. 1976; Thompson et al. 1993; Gavin et al. 2009) suggest that the IW wet-forest ecosystems are of a young age, having replaced tundra, cold-grassland, or dry forest vegetation of the Wisconsin Glaciation up to 12 000–10 000 years before present (ybp).

Attempts have been made previously to reconstruct historic ranges of coast–IW disjunct organisms, and to hypothesize their pathways of migration (Daubenmire 1975; Lorain 1988). Such reconstructions for individual species are not possible based on current-time distributions alone without the certainty provided by ample fossil data. However, it may be of use to begin such assessments by surveying a wide range of current distributions to detect patterns of frequently overlapping distributional phenomena. If this is followed by investigation using available fossil, pollen, or molecular data among numerous species, then migration pathways and historic ranges may be interpreted with greater confidence. This may be particularly valuable in the coming decades and centuries of expected rapid climate change. The migration of many plant species may not be able to outpace the rate of climate change, but preserving the connecting corridors of wild, non-degraded plant habitat may improve their chances.

In the case of vascular plants, the subjects of previous biogeography research have been either subjectively chosen, or preceded a sufficient understanding of the full array of coast–IW disjunctions. Since the extensive overview made by Lorain (1988) of the distributions of coast–inland disjunct vascular plants, numerous additional disjunctive distributions have come to light, and others previously thought to be disjunct are now known to occupy the dry regions that separate the coast and IW. Additionally, information on the distributions of vascular plants on both sides of the Canada–US border has been difficult to gather, but abundant recent additions to the print and on-line literature now make the task of studying plant biogeographical patterns easier and more accurate.

Regional endemic vascular plants of the IW were treated alongside the disjunct plants in Lorain (1988). Surveying the biogeography of endemics is important in complement to

**Fig. 1.** Overview of the Interior Wetbelt (IW) and adjacent portions of the Pacific coast of northwest North America. The IW study area is shown bound by the heavy black line in the interior, while the heavy black line to the west outlines the coastal regions. These lines outline regions having wet forest, but do not outline the wet forests themselves. The shaded area represents areas under continental glaciation at its maximum (after Alt and Hyndman 1986 and Lorain 1988), not shown are hypothesized nunataks or areas of alpine glaciation, including the proposed ice-free corridor in Alberta.



disjuncts in biogeography studies, since the geographic limitations of both groups may either mutually amplify patterns among their distributions, or suggest different geographical histories. Similarly to the coast–IW disjunct plants, distributions of IW endemic plants are better understood today, necessitating a further consideration of the biogeography of these endemics. Thus it is the aim of this study to derive a complete, non-subjective survey of both disjunct and endemic vascular plants of the IW.

## Study area

The IW spans a latitudinal range between 45° and 55°N, occupying most of the ranges of the Columbia Mountains, eastward to small portions of the Rocky Mountain Trench and windward slopes of the Rocky Mountains, and westward through wetter portions of the Blue Mountains of northeast Oregon. While the IW is very diverse in its forest and non-forest vegetation, it is vegetated over most of its area with

wet coniferous forests distinguished by a canopy of *Thuja plicata* and *Tsuga heterophylla* at lower elevations, and at higher elevations sub-alpine forests of *Abies lasiocarpa*, *Picea engelmannii*, and *Tsuga mertensiana*. The former two tree species are also the dominants throughout large portions of the lowland coastal regions to the west (Daubenmire and Daubenmire 1968; Meidinger and Pojar 1991), and *A. lasiocarpa* and *T. mertensiana* are the two most dominant sub-alpine trees there. The wet forests in the IW are additionally populated with a variety of tree species, including *Abies grandis*, *Acer glabrum*, *Betula papyrifera*, *Larix laricina*, *Larix lyallii*, *Larix occidentalis*, *Picea engelmannii* × *glauca*, *Picea glauca*, *Picea mariana*, *Pinus albicaulis*, *Pinus contorta*, *Pinus monticola*, *Populus tremuloides*, *Populus trichocarpa*, *Pseudotsuga menziesii*, and *Taxus brevifolia*. Some dry valleys within the IW are vegetated by grassland and savanna or woodlands of *Pinus contorta*, *Pinus ponderosa*, and *Pseudotsuga menziesii* (i.e., the Snake River Canyons and tributaries in Idaho, Oregon, and Washington, and the dry intermontane valleys of western Montana and southeastern British Columbia). Some of the wetter portions of the IW in Idaho and, especially, British Columbia support temperate old-growth rainforest, a globally rare and threatened forest type (Alaback 1991; Goward and Spribille 2005). Non-coastal temperate conifer rainforest is not known to occur in any other region in the world.

The IW encompasses a broad range of climate types, varying in temperature and amount and seasonality of rain, snow, humidity, and fog frequency, but it is unified throughout by much greater amounts of precipitation and milder temperatures than surrounding regions. The IW is bordered to the west throughout its latitudinal span by the arid to semiarid rain-shadow of the Coast/Cascade Ranges. Northern portions of this rain-shadow in British Columbia are grassland alternating with *Pinus contorta* and *Picea glauca* – *Betula papyrifera* – *Populus tremuloides* sub-boreal forest. This northern rain-shadow region is colder and less severely dry than southern rain-shadow regions where treeless (semi)arid steppe and desert dominates the Columbia Basin of central Washington and Oregon. To the south of the IW is extensive high-elevation terrain dissected by deep canyons, where climates are either too cold or too warm and dry to support extensive wet forest habitats. East of the IW is the strongly continental climate of the Canadian Prairies and Great Plains, where annual precipitation amounts and timing of precipitation are relatively unpredictable, and the winters bring lower humidity and strongly fluctuating temperatures. North of the IW is a drier and much colder boreal forest ecosystem.

Mean annual precipitation in forested elevations of the IW, as reported from official weather stations, is as high as 1725 mm at Glacier Avalanche Ranger Station in the Canadian portion of the IW, and as high as 1046 mm at Pierce, Idaho, in the US portion. IW regions between 45° and 48°N and west of the Idaho–Montana border have a winter peak in precipitation, and a large portion of this area experiences a Mediterranean-like climate with mild winter temperatures and a pronounced summer drought. The remainder of the IW is either somewhat monsoonal, with a distinct summer peak in precipitation, or lacks any dry period through all

seasons. In some portions of the IW, the complicated topography of alternating windward and leeward faces of mountain ranges results in orographic precipitation patterns interspersed with dry rain-shadows, especially in the canyons of the Imnaha River – Snake River – Salmon River regions in the southwest, the intermontane valleys of Montana in the southeast, and the Rocky Mountain Trench in British Columbia. The relatively mild, wet winters and wetter spring months south of 47°N and west of 115°W allow for earlier plant growth and reproduction than in northern portions of the IW, resulting in a comparable growing period despite the drier summers there. Owing to the consistently cold winter temperatures in the northern IW and the concomitant plant dormancy, the relatively low winter precipitation and humidity fails to amount to an annual moisture deficit relevant to plants occupying the northern IW. This IW climatic gradient echoes that of coastal regions, where similar interactions of rain, humidity, and temperature are arrayed along similar latitudes.

The mountains that form the complex terrain of the IW mostly originated 180 million years ago (mya) with the uplift of sedimentary rocks forming the Rocky Mountains (Eyles and Miall 2007). At roughly the same time, the accretion of numerous island arcs onto the continental margin formed the Columbia Mountains (Mathews and Monger 2005) and the core of the Blue Mountain system in Oregon stretching into Idaho (Alt and Hyndman 1978). The Coast Ranges in British Columbia originated about 95 mya, and have continued to uplift to the present time as the offshore land masses of Haida Gwaii and Vancouver Island dock onto the continental margin (Mathews and Monger 2005). Volcanic activity began to raise the Cascade Range 35 mya, but these volcanoes did not form a high mountain chain until about 5 mya (Alt and Hyndman 1978, 1994). During this period the climate of the region was gradually cooling and drying from its former subtropical type to its present-day temperate to boreal types (Bishop 2003). The development of xeric to subxeric conditions in the intervening low elevations between the coast region and the IW slowly developed through this period, and began to fully express the current dry climate around 2 mya (Brunsfield et al. 2001). Thus, the region of wet climates in the IW has been fully disjunct from the coast wet climates for approximately 2 million years.

During glacial periods, most of the IW was under the Cordilleran ice sheet. In coastal regions, the southern extent of this continental glaciation was around 47°N. In the IW, the southern glacial limits extended to around 48°N, except in easternmost portions, where the ice sheet pushed south beyond 47°N (Fig. 1). South of the glacial limits, ice fields formed over some of the mountain ranges, with tongues of the glaciers extending down the valleys, but for the most part, alpine glaciation was not extensive in the southern IW.

## Methods

A list was generated of all vascular plants occurring natively both east and west of the divide formed by the crest of the Cascade Mountains and British Columbia Coast Ranges. Out of this list of slightly more than 1000 taxa, all were rejected from the analyses that have geographical

ranges lacking discontinuities of at least 200 km between their coast and IW ranges. Those rejected taxa that connect between the Coastal regions and the IW via narrow isthmus connections of slightly wetter mountain ranges were accumulated in lists to assess possible migration corridors. Taxa were rejected from the analyses and lists that are distributed widely throughout wet regions of North America. This reduced the list down to include only taxa having >200 km disjunct distributions, split between coastal regions and the IW, occurring in forested elevations, and that are not widespread across North America.

A list of regional endemics and sub-endemics of the IW was also compiled, limited to taxa having all or the majority of their global ranges limited to the IW. Most of these endemics are found in the drier portions of the IW, especially in low-elevation grassland and savanna/woodland habitats of the canyons in southwestern portions of the IW in Idaho, Oregon, and Washington, and in the intermontane valleys of Montana. These were rejected from the statistical analyses, since they do not occupy forested elevations, although they are given mention as IW endemics. Likewise, disjuncts and endemics of alpine tundra were rejected from the statistical analyses, since they occur only above forested elevations and likely had a different mode of expansion into their current ranges compared with plants of forested elevations. These also, though excluded from the statistical analyses, are given mention in the text. Taxonomically questionable plants were omitted entirely from the study, as were taxa that await publication new to science.

Geographical ranges were assessed using published records and range maps, and supplemented with specimens housed at the herbaria at the University of Idaho (ID), The University of Montana (MONTU), The University of British Columbia (UBC), and Washington State University (WS). Many of the range maps had to be corrected or rejected, since the ranges of wet-climate taxa are often erroneously shown as occurring across the dry regions. Several plants have been erroneously reported over large geographical areas of the IW or coast (i.e., *Ligusticum canbyi* given a broad range through the western US owing to the inclusion of the more widespread species *L. grayi* Coulter & Rose, and *Ligusticum verticillatum* misreported from British Columbia). Unlikely records were rejected, such as *Elliottia pyroliflora* from the dry Okanagan Valley of British Columbia. Additional data were gathered from online resources: Idaho Conservation Data Center (2008), the Montana Natural Heritage Program (2009), Oregon Plant Atlas (Oregon Flora Project, 2009), and the Washington Natural Heritage Program (2009). The habitats of each species were assessed according to ecological descriptions in published floras.

Coastal disjunct taxa were divided between two floras: north coastal, more frequent and widespread north of the southernmost coastal limits of the Wisconsin glaciation; and south coastal, more frequent and widespread south of the glacial limits (Fig. 1). Distributions of known populations of disjunct taxa in the IW were recorded for 1° × 1° latitude–longitude cells in a grid across the entire IW and adjacent dry regions. Very broad habitat classes were assigned for all species, these are: forest (including woodland, riparian forest, sub-alpine forest, and forested creek-side habitats), wetland (including ephemeral pools and sub-

merged aquatic habitats as well as marshes and bogs), and open, dry upland habitats (all upland non-forested habitats, including seeps that are dry through most of the year). In the case of taxa occupying more than one habitat, their most frequent habitat preference was assigned.

To test for correlations between distributions of coastal disjunct and endemic taxa to regional climate, the mean annual precipitation for the wettest reporting station was gathered for each of the 1° × 1° cells (Table 1). Data were obtained from Climate-Charts.com (2009) for the US, and from Reynolds (1980) for British Columbia. No data are available for some cells, especially in the far northern IW. Since many climate stations are positioned in towns, which tend to be located in the driest portions of each cell, the reported precipitation for many cells may be lower than is actually experienced for forested elevations. Accordingly, a separate analysis was run based on the highest precipitation for forested elevations estimated by the Prism model (Prism Group, Oregon State University 2008). This value was obtained by entering the median between the low and high of the range of precipitation amounts in the highest-value isobar at forested elevations. Linear correlations were tested for these precipitation amounts and numbers of disjunct and endemic plants using SPSS 16.0 (SPSS Inc., Chicago, Illinois). In all statistical tests,  $\alpha = 0.05$ .

A few of the species included in the analyses require mention as to their inclusion in the data. *Howellia aquatilis* is here treated as an IW endemic, although rare populations have been reported also in northern California (Mendocino County), northwest Oregon (extirpated), and western Washington (Clark and Pierce Counties). Many populations fall just outside the IW in savannas in eastern Washington (Spokane County), but in total, the bulk of existing populations occur within the IW, especially in the Swan Valley of Montana (Center for Plant Conservation 2008). Most of the remaining sub-endemic taxa extend only short distances beyond the IW, but *Ionactis stenomeris* and *Trifolium douglasii* extend south to near 43°N. The bulk of known populations of these two taxa occur within the IW, so they were included. *Ligusticum canbyi* is here treated in the strict sense, exclusive of *L. grayi*. *Allium dictuon*, *Castilleja cervina*, *Collomia debilis* var. *camporum*, *Delphinium sutherlandii*, *Erigeron davisii*, *Eriogonum scopulorum*, *Grindelia howellii*, *Ionactis stenomeris*, *Lewisia columbiana* var. *wallowensis*, and *Lomatium serpentinum* occur in relatively dry forest, or dry, well-insolated rock outcrops, but are retained in the analyses since they do not occur at grassland/savanna elevations. *Amelastorbus jackii* is a poorly known fertile bigeneric hybrid recorded from only two localities. Its occurrence in forest habitats is presumed based on the localities and elevations reported for the populations and on the habitat preference of one of the parent species (*Sorbus scopulina*). *Calochortus apiculatus*, *Castilleja chrysantha*, *Lomatium sandbergii*, and *Senecio megacephalus* sometimes grow in upper sub-alpine elevations but are added in the analyses, since they do not extend higher in elevation into truly non-forested, alpine elevations.

## Results

Out of a total of 116 coastal disjunct taxa in the IW, 31

**Table 1.** Mean annual precipitation in mm for 1° × 1° cells in the IW.

Cell			Precip.			Cell			Precip.			Cell			Precip.					
No.	Loc. (°)		RP	MR		No.	Loc. (°)		RP	MR		No.	Loc. (°)		RP	MR				
55	54×123		n.d.	875	44	52×120	964	1200	33	50×118	1171	1600	22	48×117	704	1270	11	46×118	483	1270
54	54×122		897	1125	43	52×119	1200	1600	32	50×117	n.d.	1600	21	48×116	819	1600	10	46×117	599	1270
53	54×121		963	1375	42	52×118	1419	1600	31	50×116	725	1600	20	48×115	904	1140	9	46×116	948	1400
52	54×120		n.d.	1375	41	52×117	n.d.	1200	30	50×115	369	1200	19	48×114	569	890	8	46×115	1046	1650
51	53×123		464	875	40	51×120	762	900	29	50×114	n.d.	900	18	48×113	750	1200	7	46×114	990	1140
50	53×122		648	875	39	51×119	812	1600	28	49×118	656	900	17	47×118	470	380	6	46×113	474	635
49	53×121		n.d.	1125	38	51×118	1064	1600	27	49×117	914	1600	16	47×117	569	890	5	45×118	823	1270
48	53×120		840	1375	37	51×117	1725	2000	26	49×116	940	1600	15	47×116	775	1140	4	45×117	690	1270
47	53×119		630	1375	36	51×116	477	1200	25	49×115	1127	1200	14	47×115	956	1400	3	45×116	597	1140
46	53×118		n.d.	1125	35	51×115	n.d.	1200	24	49×114	637	1200	13	47×114	579	635	2	45×115	763	1140
45	52×121		739	1200	34	50×119	640	900	23	48×118	507	890	12	47×113	729	890	1	45×114	415	1140

**Note:** No., cell number corresponding to those in Appendices A–C; Loc., location in latitude and longitude; RP, reported precipitation means from official weather stations; MR, median between ends of the range for wettest isobars modeled for wet-forest elevations in each cell, data from the Prism model. The abbreviation n.d. stands for no data.

have predominately northern coastal ranges, while 85 are predominately southern coastal. Four of the coastal disjunct taxa have not previously been reported from interior regions (*Carex stylosa*, *Carex echinata* var. *phyllomanica*, *Lathyrus polyphyllus*, and *Piperia candida*). IW endemic species totaled 95. After removing taxa occurring mostly below or above wet-forest elevations, 46 IW endemics remain. Among these are two genera fully endemic to the IW, *Ame-lasorbus* and *Dasynotus*, and a third having most of its populations in the IW (*Howellia*).

The coastal disjunct taxa differ somewhat in habitat, with north-coast disjuncts more frequent in forest habitats (21) than in wetland (7) or dry/open habitats (3), while a smaller portion of south-coast disjuncts are of forest habitats (35), as opposed to wetland (20) and dry/open habitats (30). Considering the full suite of IW endemics, these are largely of dry/open/alpine habitats (66) as opposed to forest (25) or wetland (3) habitats, although if the endemics of alpine and low-elevation grassland ecosystems are excluded, then the remainder occurs mostly in forest habitats (24) as opposed to wetland (3) or dry/open habitats (19).

Among the north-coast disjuncts, 22 are endemic to wet regions of western North America, 1 is interruptedly circum-boreal (*Blechnum spicant*), and 7 are also disjunct in wet regions of northeast Asia (*Carex stylosa*, *Claytonia sibirica* var. *sibirica*, *Galium kamtschaticum*, *Gymnocarpium dis-junctum*, *Huperzia chinensis*, *Maianthemum dilatatum*, *Myr-iophyllum ussuriense*, and *Polypodium glycyrrhiza*). All of the south-coast disjunct taxa are endemic to wet regions of western North America except three species disjunct southward in the southern Rocky Mountains or Great Basin (*Claytonia cordifolia*, *Cypripedium fasciculatum*, and *Juncus occidentalis*), one species that extends into the drier Medi-terranean-climate regions of California and Baja (*Penta-gramma triangularis*), and one species that is scattered through small areas of the southern Rocky Mountains, eastern deciduous forests, and temperate east Asia (*Trautvetteria carolinensis*).

North-coast disjuncts are distributed rather evenly through the latitudinal range of the IW, with numbers of disjuncts peaking north of the glacial limits in the 48° and 50° latitudinal belts (Table 2). Meanwhile, the south-coast disjuncts and endemic plants occur mostly in the 45° through 47° latitudinal belts, dropping off precipitously northward across the glacial limits. Seventeen north coast disjuncts are found exclusively north of the glacial limits (Appendix A), while only one, *Polypodium glycyrrhiza*, is found exclusively south. Among the south-coast disjuncts, 53 are found exclusively south of the glacial limits (Appendix B), while 6 are found exclusively north. Thirty-one forested-elevation IW endemics occur only south of the glacial limits, and of the total list of IW endemics, including the grassland, savanna, and alpine species, 73 occur only south of the glacial limits. North of the glacial limits, only three IW endemics are known; all of them grow in alpine habitats (Appendix C).

In testing linear regression for endemic, north-coast dis-junct and south-coast disjunct taxa to precipitation as measured by reporting weather stations in the 1° × 1° cells for which climate data are available, no significant relationship is found ( $R^2 = 0.001$ ,  $p = 0.861$ ;  $R^2 = 0.001$ ,  $p = 0.852$ ;  $R^2 = 0.063$ ,  $p = 0.117$ , respectively,  $n = 44$ ). When the highest

**Table 2.** Numbers of Pacific coast disjuncts and IW endemics in latitudinal belts.

	Total	Tot.		Glaciated									
		UnGI	GI	45	46	47	48	49	50	51	52	53	54
Endemic	46	46	14	29	42	27	14	10	4	1	0	0	0
NC disj	31	13	30	8	11	11	15	12	17	12	10	7	6
SC disj	85	79	33	48	61	50	26	17	14	9	2	2	0
AllC disj	116	92	63	56	72	61	41	29	31	21	12	9	6

**Note:** The latitudinal belts are represented by numbers in bold in the top row. NC disj, north coast disjuncts; SC disj, south coast disjuncts; AllC disj, all coastal disjuncts; UnGI, unglaciated wetbelt latitudes; GI, glaciated wetbelt latitudes.

forest-elevation precipitation predicted by the Prism model is used in place of weather station data, endemic and south-coast disjunct taxa have no significant relationship to predicted precipitation ( $R^2 = 0.015$ ,  $p = 0.381$ ;  $R^2 = 0.019$ ,  $p = 0.310$ , respectively,  $n = 55$ ). North-coast disjuncts, however, are found to have a significant positive relationship with predicted precipitation ( $R^2 = 0.183$ ,  $p = 0.001$ ,  $n = 55$ , with the equation of line of best fit: north coast =  $-2.185 + 0.006$  (predicted precipitation)).

## Discussion

The list of coastal disjunct plants in the IW presented here expands by 80 taxa the list published by Lorain (1988), which is the only other comprehensive assessment of the coast-IW disjunct vascular plant taxa. Certain taxa treated by Lorain were found to have non-disjunct distributions between the IW and the coast (ie., *Alnus rhombifolia* and *Tiarrella trifoliata*). Others reported by Lorain were based on misidentified specimens (ie., *Acer circinatum* and *Carex tumulicola*, and inland British Columbia populations of *Ribes sanguineum*) or are questionably native in the IW (*Dicentra formosa* and *Juncus effusus* var. *pacificus*). The number of IW endemic plants is also greatly expanded here over those noted by Lorain, especially if the full suite, including alpine and grassland taxa, of IW endemics and sub-endemics is considered.

The much larger number of south-coastal than north-coastal taxa disjunct in the IW may be reflective of the larger species pool south of the glacial limits. The vascular plant flora of north coastal regions (northwest Washington to Pacific coastal Alaska) is far smaller than that of southwest Washington to northern California. For its vascular plant species richness and endemism, the south coastal Klamath-Siskiyou region has been noted to be a conservation priority at the global scale (Olson and Dinerstein 2002). Similarly, on average, interior regions south of the southern limits of continental glaciation appear to harbour a much richer flora, and far more regionally endemic plants than interior regions north of the glacial limits.

Most of the IW endemics are of small geographical range within the IW, concentrated largely in the region where the borders of Idaho, Oregon, and Washington converge, and in the Clearwater and Salmon Regions of Idaho. The occurrence of a small number of endemics in the southern IW has been noted before (Schofield 1969; Daubenmire 1975; Lorain 1988; Brunsfeld et al. 2007). However, the southern IW has not been noted to be a major hotspot of endemism previously. Indeed, portions of the southern IW may host concentrations of regional endemics equal to or exceeding those of previously noted endemism hotspots in northwest North America (i.e., the Columbia River Gorge, the Olympic Mountains, the Wenatchee Mountains, and Beringian Alaska).

When examining the ranges of taxa shared between coastal and IW regions and considering those that are almost disjunct but with populations in the intervening dry regions, patterns emerge that suggest isthmus or stepping-stone connections. The southern isthmus is through the Ochoco and Blue Mountains in Oregon, which approach the Cascade Mountains at around 44°N. The middle isthmus occurs in

the Okanagan Mountains, which straddle the British Columbia – Washington border at 49°N. Between the Ochoco and Okanagan connections lies the arid to semi-arid Columbia Basin, which is covered in desert, shrub-steppe, and grassland vegetation. The northern isthmus is through the Babine and Omineca Mountains around 54°–56°N. Between the middle and northern connections lie the Cariboo–Chilcotin, Thompson, and Fraser grasslands, shrub-steppe, and dry, sparse forests. Each of these isthmus regions is drier than the mountains of the coast and IW, but wet enough to support some taxa of wet forest habitats, at least in some cool/humid microhabitats.

Lorain (1988) highlighted a number of species she hypothesized arrived into interior regions via a route through the Ochoco and Blue Mountains, including some that are not treated here since they occur in dry regions shortly to the west or south of the IW. Among these rejected disjunct taxa are *Aconogonon davisiae* (W.H. Brewer ex A. Gray) Soják (reported in Lorain (1988) as *Polygonum newberryi* Small), *Ceanothus prostratus* Benthams, and *Pellaea bridgesii* Hooker. A number of additional taxa can be added to this south coast – dry interior range disjunction (primarily California to eastern Washington or central Idaho): *Alopecurus saccatus* Vasey, *Anelsonia eurycarpa* (A. Gray) J.F. Macbride & Payson, *Antennaria geyeri* A. Gray, *Arnica nevadensis* A. Gray, *Boechea acutina* (E. Greene) Windham & Al-Shehbaz, *Boechea pratincola* (E. Greene) Windham & Al-Shehbaz, *Callitriche marginata* Torrey, *Carex luzulifolia* W. Boott, *Centaureum muhlenbergii* (Grisebach) Piper, *Crepis pleurocarpa* A. Gray, *Downingia yina* Applegate, *Hordeum brachyantherum* Nevski subsp. *californicum* (Covas & Stebbins) van Bothmer, *Hulsea nana* A. Gray, *Juncus uncialis* E. Greene, *Melica californica* Scribner, *Mimulus pulsiferae* A. Gray, *Phacelia procera* A. Gray, *Phacelia rattanii* A. Gray, *Psilocarphus tenellus* Nuttall var. *tenellus*, and *Sclerolinon digynum* (A. Gray) C. Rogers.

The broad habitat classes among disjunct and endemic taxa reveal patterns that require comment. North-coast disjunct taxa are mostly of forest habitats, with few occurring in wetlands or in open/dry habitats. The flora of the north coast occupies a landscape that was almost entirely under ice through the last glacial maximum, and the recovery of vegetation quickly led to the dominance of rain-forest ecosystems (Hebda 1995). Thus, the migration of plants from ice-age refugia to the north coast, then into their current inland landscapes may have filtered out taxa such that the north coast, as a potential source flora, would be depauperate in plants of wetlands and open/dry habitats. This may be a reasonable hypothesis for dry/open habitat plants, given that in coastal regions, dry rock outcrops and similar habitats are now islands within a “sea” of forests, so dispersal from and to these habitat islands would be inhibited merely for reasons of their being small in area and widely separated. Dispersal inhibition of wetland taxa, however, is not expected given the frequent observation that wetland plants tend to have broad geographical ranges (Ridley 1930; Santamaría 2002), being readily dispersed by water birds that carry dispersal units directly from wetland to wetland (Figueroa and Green 2002), and where the establishment of wetland-adapted plants may be eased by the buffering effects in wetlands against heat and drought. This general

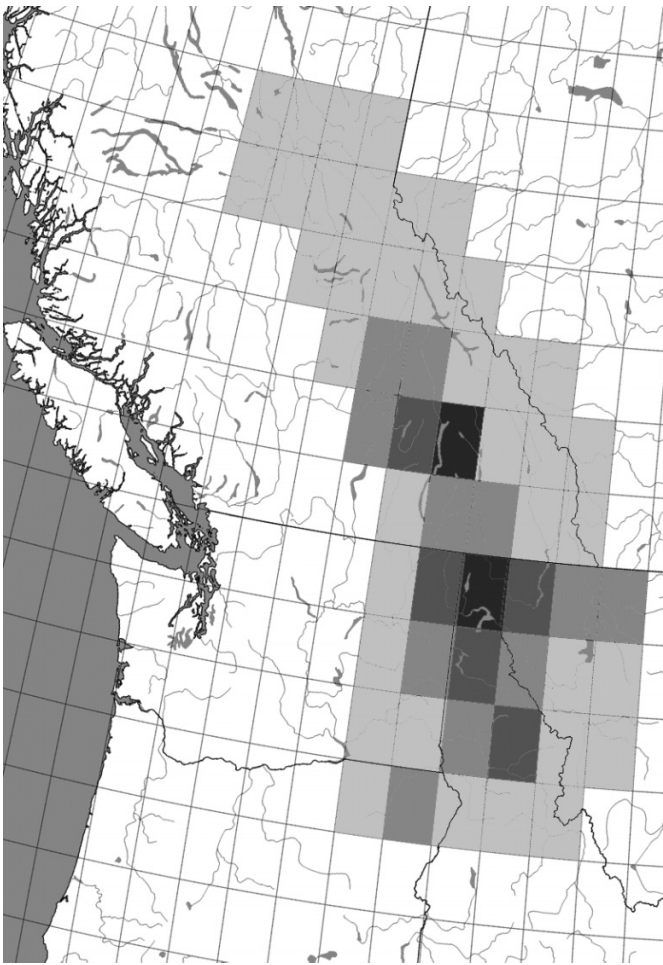
ease of dispersal for wetland plants may explain the lack of IW endemics occupying wetland habitats. Even if wetland plants evolved in the IW, they may more readily invade other regions than plants of forest or dry/open habitats. Indeed, one of the three IW wetland (sub)endemics, *Howellia aquatilis* is found well outside the IW in few, widely separated localities, and is the only IW sub-endemic with such a broad geographical range. Conversely, any local evolution of wetland taxa may be swamped by competition from quickly immigrating wetland plants.

The degree to which the wet climate of the IW has remained uninterrupted by dry periods is a matter for debate, but long-term continuity is suggested by phylogeographic studies of wet-forest dependent giant salamanders (Steele et al. 2005), plethodontid salamanders (Carstens et al. 2004), and tailed frogs (Nielson et al. 2001). These organisms in the IW are found to have been distinct from their coastal relatives for 1.2–4.1 million years (Carstens et al. 2005a). However, the major vegetation of the southern, unglaciated IW has been interpreted, based mostly on fossil pollen data, as having been too dry or cold to support wet forest ecosystems (Mack et al. 1976; Gavin et al. 2009). As Pielou (1991) points out, inferences of vegetation south of the glacial limits are unreliable, owing to a lack of pollen data there. Packrat midden data that have helped generate a picture of climatic and vegetation history (i.e., in the Great Basin) are lacking in the southern IW, as are the fen habitats that yield pollen cores. Added to this is the difficulty of reconstructing vegetation and climate conditions using pollen or fragments from plants of unknown ecological amplitude. For example, pollen of *Artemisia* does not necessarily indicate a dry climate, because it cannot be identified to species, and several *Artemisia* species such as *A. campestris*, *A. douglasiana*, *A. ludoviciana*, *A. michauxiana*, *A. norvegica*, *A. suksdorfii*, and *A. tilesii* are currently known from wet climate regions and can be locally common.

If coastal disjunct taxa are of recent (post-pleistocene) appearance in the interior, they might be expected to be most concentrated in the wettest regions of the IW in the Columbia Mountains between 50° and 53°N, where the most extensive, coast-like inland rainforest occurs (Arsenault and Goward 2000; Goward and Spribille 2005). While it is true that the number of north-coast disjunct plants increases with predicted precipitation, this relationship is weak, and the second highest peak in concentration of these taxa occurs in 48° × 116° (Fig. 2), where the climate is considerably drier and warmer than in the wettest regions of the British Columbia IW, but which lies only shortly north of the glacial limits. This suggests that among these are some number of taxa that have colonized the glaciated IW from refugia to the south and been unable to colonize wetter regions further north.

This is not to argue that all of the taxa treated here will have entered the IW via the same mode or age of arrival. Some are likely recent arrivals, as suggested by molecular studies in *Alnus rubra* (Streng 1994), *Tellima grandiflora*, and *Tiarella trifoliata* (Soltis et al. 1997). It should be noted that the last of these is not dependent on particularly wet climates, and it has a scarcely interrupted distribution across central British Columbia. The finding that a large number of taxa bridge the coast and IW regions via three identified

**Fig. 2.** Concentrations of disjunct taxa in the Northern and Southern IW. Ranges of values are indicated as follows: pale gray = 0–5 taxa, light gray = 6–10, medium gray = 11–15, dark gray = 15+.



isthmus connections (Appendix D), while not identifying active migration, points to there being possible migration corridors that may facilitate coast–IW migration. Some plants will have originated in the IW and secondarily colonized the coast. This scenario was inferred from phylogeographic studies on *Salix melanopsis* Nuttall “mesic race” (Brunsfeld et al. 2007), *Pinus albicaulis* Engelm., and the rodent *Microtus richardsoni* (Carstens et al. 2005a). Other organisms might have colonized the IW and (or) the coast from a third region no longer supporting the taxa (a southern Rocky Mountain refugium, as posited by Brunsfeld et al. 2007).

If these and other possible scenarios of mode of arrival are considered, it becomes clear that the two hypotheses usually posited of disjunctions, “recent dispersal” versus “ancient vicariance”, are only two of several possibilities. The components of these hypotheses are best broken down into separate questions, the answers to which, it should be remembered, may be scale-dependent: (i) How old is the disjunction? (ii) Are current-time populations within the disjunct range of young or old age? (iii) What is the mode of arrival, i.e., long distance dispersal, vicariance, hop-dispersal (Raven 1972; Schofield 1974), or a travelling wave of populations? (iv) What is the original source region of the migration? These questions may give a clearer answer as to the

IW’s contribution to the evolution and biogeography of biomes of wet regions of northwestern North America.

The tight clustering of south coast and IW endemic plants in northern Idaho south of the glacial limits shown in Figs. 3 and 4 adds emphasis to the hypothesis that this region has acted as a refugium for disjunct and endemic species through major climate change episodes (Brunsfeld et al. 2007). *Cardamine constancei* (Brunsfeld and Sullivan 2006), *Salix melanopsis* “mesic race” (Brunsfeld et al. 2007), Idaho giant salamander (Carstens et al. 2005a), and the tailed frog (Nielson et al. 2001) have geographical distributions of genotypes that suggest they remained in place through the glacial maxima, in some cases even in the Coeur d’Alene basin, which was separated from the cordilleran ice sheet by a minor range of mountains only about 2000 m in elevation. That some of these organisms occupied refugia even in the northernmost ice-free valleys brings into question the ideas that periglacial regions were tundra, dry grassland or dry forest; today, these species do not occupy such habitats.

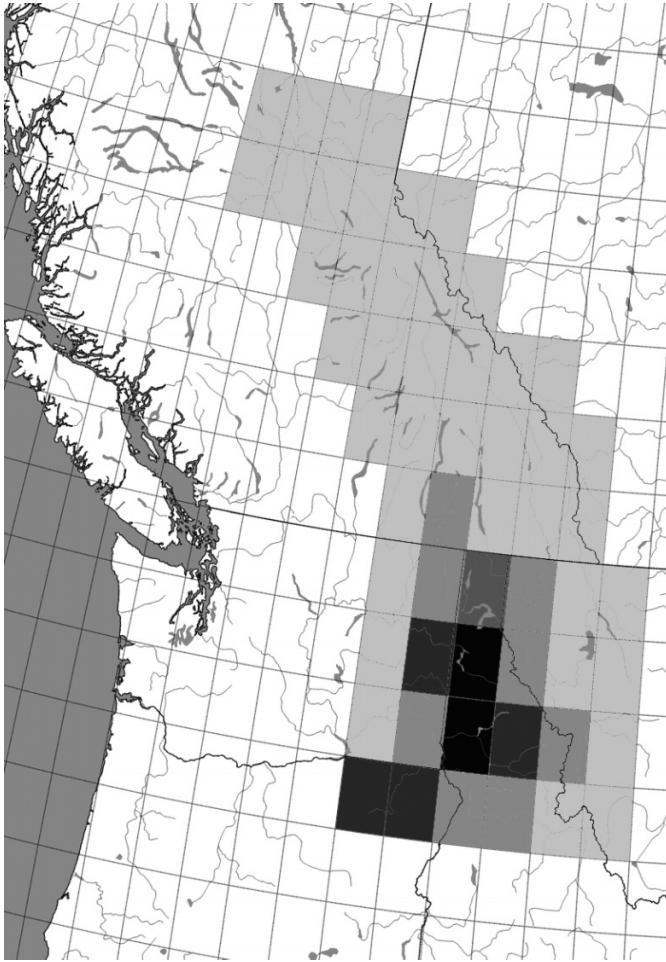
The low elevations in the canyons and valleys of the southern IW, some of which are occupied by dry savanna or sparse woodland or even grassland today, might in the past have been host to wet forest habitats during periods when the proximity of the Cordilleran ice sheet might have made conditions too harsh at the higher elevations currently occupied by wet forests. Although some elevational migration is not unlikely during glacial periods, it does seem unlikely that wet-forest biomes would have extended downward to the lowest elevations of the valleys and canyons that are currently occupied by dry climate habitats, given that these dry canyons and valleys are today home to the largest number of IW endemics; these are not only rock outcrop species that might have persisted during periods of dense forest vegetation on the island-like open habitats of their outcrops, but also zonal grassland and savanna species that probably could not have competed with tall, shading forest vegetation of wet forests that under this scenario would have occupied zonal sites.

Although coastal-disjunct and IW-endemic taxa are largely absent in the far northern IW, especially north of 52°, wet forests cover a large area there in the Fraser River Valley in the Rocky Mountain Trench, the valley of the North Thompson River, in the eastern Quesnel Lake area, and northern Wells Gray Provincial Park (Arsenault and Goward 2000; Goward and Spribille 2005). Precipitation is not particularly high in this region, but the lower precipitation there is compensated by low evapotranspiration, owing to cool growing-season temperatures and perhaps also to the lower intensity of the low-angle sunlight at such northern latitudes (Daubenmire 1974). The result of this is rain-forest conditions allowing the widespread growth of large diameter *Thuja* and *Tsuga*, this in combination with an understory of boreal vascular plants.

Goward and Spribille (2005) found that certain coastal macrolichen species make their most conspicuous appearance in these far northern IW forests, as well as some further south in forests between 50° and 52°N. These species were mostly not known to the authors to occur in the IW south of 50°. Most of the coast–IW disjunct vascular plants treated in the present study are not generally found in rain-



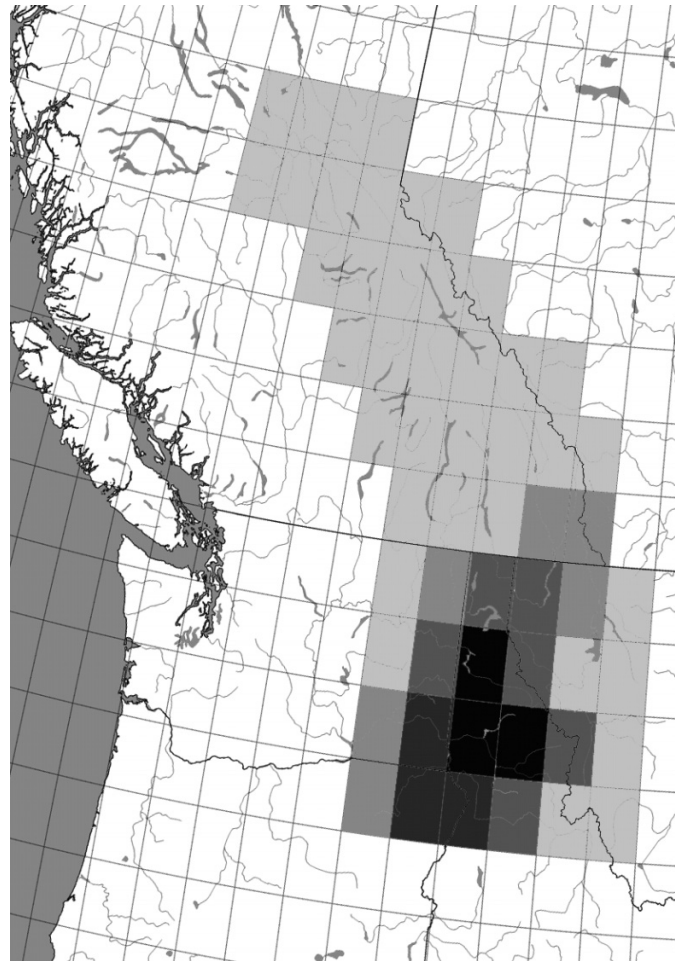
**Fig. 3.** Concentrations of south coast disjunct taxa in the IW. Ranges of values are indicated as follows: pale gray = 0–10 taxa, light gray = 11–20, medium gray = 21–30, dark gray = 31–40, black = 40+.



forest, where the understory is very poor in vascular plant diversity. The lichens studied by Goward and Spribille (2005) are all canopy epiphytes and have ecological amplitudes that may cause them to preferentially colonize colder rain-forest types. This may partly explain the contrastive distribution patterns of coast–IW disjunct lichen and vascular plant taxa, as may the greater dispersal capability of lichens, which have lighter propagules, and so may have benefitted from a more rapid colonization than vascular plants into these once glaciated northern IW landscapes.

Some of the coastal disjunct taxa have a history of human use, and so may have been introduced into inland regions intentionally. These include, for example, *Alnus rubra*, *Asarum caudatum*, *Frangula purshiana*, *Gaultheria shallon*, *Polystichum munitum*, *Rubus spectabilis*, and *Rubus ursinus* (Turner 1998). It is difficult to imagine that most of the remaining taxa would have been introduced, these being of no known use for food, clothing, shelter, ornament, or otherwise. However, the question of possible coastal provenance of some of the coastal disjunct taxa could be resolved with detailed archaeological, ethnobotanical and phylogeographic studies. Until such time, all the species reported here are best treated as native in the IW.

**Fig. 4.** Concentrations of IW endemics and sub-endemics of forested elevations, excluding those that grow in dry savanna. Ranges of values are indicated as follows: pale gray = 0–5 taxa, light gray = 6–10, medium gray = 11–15, dark gray = 15–20, black = 20+.



Six rare, regionally endemic taxa of the non-coastal, leeward side of the Cascade Mountains are also found disjunctively in the IW: *Campanula parryi* A. Gray var. *idahoensis* McVaugh, *Eriogonum compositum* Douglas ex Bentham var. *leianthum* Hooker, *Eriogonum umbellatum* Torrey var. *ellipticum* (Nuttall) Reveal, *Ivesia tweedyi* Rydberg, *Micranthes idahoensis* (Piper) Brouillet & Gornall, and *Sedum rupicolum* G.N. Jones. These are concentrated in the Wenatchee Range, another area noteworthy for its concentration of endemic plants, and in the IW are limited to non-glaciated regions. The IW sub-endemics *Sedum leibergii* and *Trillium petiolatum* have few disjunct populations also in the central Washington Cascades. Similarly to the southern IW – Wenatchee Range disjunction, rare coast–IW disjunct plants and species pairs provide evidence of a biogeographical history shared between the southern IW and with the Siskiyou–Klamath Mountains of southwestern Oregon and northwestern California. With this region is shared a bicentric distribution of *Symphyotrichum hendersonii* (Fernald) Nesom (which may be another IW sub-endemic, but owing to recently fluctuating taxonomic concepts, range data were too sparse to include in the analyses). A southern IW–Siskiyou connection is also suggested by the taxon pairs *Frasera*

*fastigiata* (Pursh) A.A. Heller and *Frasera umpquaensis* (M.E. Peck) Applegate, and *Calochortus elegans* Pursh (expressed in the Siskiyou as var. *nanus* Alph. Wood, and in the IW by *C. elegans* var. *elegans* and *C. elegans* var. *selwayensis*). A southern IW – Siskiyou Mountain disjunction was also found for the slug *Prophysaon coeruleum* (Wilke and Duncan 2004).

Other than the coast–IW disjunctions, no suite of native disjunct vascular plant distributions involves the IW, except among alpine taxa and some species disjunct from forested regions of eastern North America. Among the latter is a small number of greatly disjunct species otherwise known no closer than the Great Lakes region (*Carex aquatilis* Wahlenberg var. *substricta* Kukenthal, *Carex canescens* Linnaeus var. *disjuncta* (Fernald) Toivonen, *Carex pallescens* Linnaeus var. *neogaea* Fernald, *Dicentra cucullaria* (Linnaeus) Bernhardt, *Iris versicolor* Linnaeus, *Ludwigia polycarpa* Short & Peter, and *Polystichum braunii* (Spenner) Fee). These mirror a suite of northwestern North American vascular plants having disjunct populations in the Great Lakes region, such as *Adenocaulon bicolor*, *Botrychium ascendens* W.H. Wagner, *Botrychium spathulatum* W.H. Wagner, *Oplopanax horridus*, *Rubus parviflorus* Nuttall, and *Woodsia oregana* D.C. Eaton (Schofield 1969; Marquis and Voss 1981). Other plants are disjunct in the IW from shorter distances east or northeast: *Bidens beckii* Torrey ex Sprengel, *Carex comosa* Boott, *Carex lacustris* Willdenow, *Dryopteris cristata* (Linnaeus) A. Gray, *Eutrochium maculatum* (Linnaeus) E.E. Lamont var. *bruneri* (A. Gray) E.E. Lamont, *Galium palustre* Linnaeus, *Juncus vaseyi* Engelman, *Primula mistassinica* Michaux, *Sagittaria latifolia* Willdenow, *Sagittaria rigida* Pursh, *Sparganium fluctuans* (Engelmann ex Morong) B.L. Robinson, *Vallisneria americana* Michaux, and *Viola septentrionalis* E. Greene. This concentration of eastern North American disjuncts has been given mention previously, listing fewer taxa than detected in the present study (Fernald 1942; Spribille et al. 2002). Interestingly, all of the eastern North American taxa disjunct in the IW except *Dicentra cucullaria* and *Polystichum braunii* are found primarily in wetland habitats.

Most of the IW endemic plants, being of small global range, are of high conservation priority, since their few populations make the species more vulnerable to localized destructive events and stochastic outcomes. *Cardamine constancei*, *Corydalis caseana* var. *hastata*, and *Dasynotus daubenmirei*, for example, are species tracked by the state of Idaho and US Forest Service (Idaho Conservation Data Center 2008). Some of the coastal disjunct taxa are also a high priority for conservation in their interior ranges. Some are known from fewer than five IW populations (such as *Oxalis trilliifolia*, *Polypodium glycyrrhiza*, *Ribes sanguineum*, *Spiranthes porrifolia*, and *Thelypteris nevadensis*). *Dryopteris arguta* was reported based on only a single individual in the IW (Johnson and Steele 1978); its current status in the IW is unknown. Others appear to have become regionally extinct and now occur only in coastal regions (*Eryngium articulatum*, *Juncus bolanderi*, *Lewisia columbiana* var. *columbiana*, *Lotus pinnatus*, and *Navarretia squarrosa*).

These cases of rarity and extirpation may be the result of poor adaptation of the taxa to relatively dry climatic conditions in the portions of the IW in their current or former ranges. Alternately, their near or complete loss may be due

to the major disturbances to ecosystem integrity suffered by the region throughout most of its area. This is the result of logging, mining, artificially intense fires, non-indigenous plants brought by Eurasian settlers, and land development for urban and agricultural use. Losses of wild, high-quality ecosystems continue to the present day in large swathes of the IW, particularly in British Columbia, where insufficiently controlled logging is resulting in isolation of old-growth lowland forest and other original habitats in small island-like pockets surrounded by young, commercially managed forest. A glimpse of the region as seen at 50 km scale in Google Earth (Google, Inc., Mountain View, California 2008) reveals that the forest-elevation landscapes of the IW are a patchwork of recent and revegetating clear-cuts with few, ever smaller forest preserves. In the southern IW, logging, invasive plants and other human-caused disturbances, though at a slower rate in recent decades than in British Columbia, are disrupting forest-ecosystem continuity that stretches back in time within that region possibly more than 2 million years. The 120 year history of logging and mining in large areas of the southern IW resulted in losses echoed by those seen in British Columbia today.

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## **Appendices A–D**

Appendices A–D appear on the following pages.

Appendix A. Table A1. North coast disjunct taxa in the IW.

Habitat	Loc.	Taxon	GCO
F		<i>Alnus rubra</i> Bongard	8, 9, 14–16, 20–22
F		<i>Blechnum spicant</i> (Linnaeus) Roth	8, 9, 15, 32, 33, 38
W	+	<i>Carex stylosa</i> C.A. Meyer	39
W		<i>Cirsium brevistylum</i> Cronquist	14–16, 19–22, 24, 27, 32–34
W		<i>Claytonia sibirica</i> Linnaeus var. <i>sibirica</i>	2–5, 8–11, 14–23, 25, 27
F	+	<i>Elliottia pyroliflorus</i> (Bongard) Brim & P.F. Stevens	55
W	+	<i>Epilobium luteum</i> Pursh	31–33, 45, 50
F	+	<i>Galium kamtschaticum</i> Steller	49
F		<i>Gaultheria ovatifolia</i> A. Gray	2, 5, 8, 9, 14, 15, 18–22, 26, 27, 32–34, 38, 39
F	+	<i>Gaultheria shallon</i> Pursh	26
F		<i>Gymnocarpium disjunctum</i> (Ruprecht) Ching	5, 7–9, 13–16, 18–23, 26–28, 31–34, 39, 40
F	+	<i>Heuchera glabra</i> Willdenow ex Roemer & Schultes	32, 33, 39, 40, 43, 44, 53
F	+	<i>Huperzia chinensis</i> (Christ) Ching	32
F		<i>Huperzia occidentalis</i> (Clute) Kartesz & Gandhi	4, 8, 9, 15, 18–21, 32, 34, 39, 40, 43
W	+	<i>Isoëtes maritima</i> L. Underwood	28, 34, 45, 54
F	+	<i>Maianthemum dilatatum</i> (Alph. Wood) A. Nelson & J.F. Macbride	21, 27
W	+	<i>Myriophyllum ussuriense</i> (Regel) Maxim.	26, 27, 33, 34
F	*	<i>Polypodium glycyrrhiza</i> D.C. Eaton	8
F		<i>Polystichum andersonii</i> M. Hopkins	1, 4, 5, 8, 9, 14–16, 18–22, 32, 34
F	+	<i>Prenanthes alata</i> (Hooker) D. Dietrich	32, 44, 46, 48, 50
O	+	<i>Ranunculus cooleyae</i> Vasey & Rose	45, 48, 54
O	+	<i>Ribes laxiflorum</i> Pursh	20, 21, 36, 38, 42, 45, 52–54
F	+	<i>Rubus spectabilis</i> Pursh	21
F		<i>Sambucus racemosa</i> Linnaeus var. <i>arborescens</i> (Torrey & A. Gray) A. Gray	4, 9, 15, 16, 22
O	+	<i>Sedum divergens</i> S. Watson	32, 39, 46, 47
F	+	<i>Streptopus streptopoides</i> (Ledebour) Frye & Rigg subsp. <i>brevipes</i> Baker	21, 22, 24, 27, 37, 38
F	+	<i>Tellima grandiflora</i> (Pursh) Douglas ex Lindley	18–22, 25–27, 32–34, 36, 38–40, 47
W		<i>Triantha occidentalis</i> (S. Watson) R.R. Gates subsp. <i>brevistyla</i> (C.L. Hitchcock) Packer	4, 21
F		<i>Tsuga heterophylla</i> (Rafinesque) Sargent	4, 5, 7, 8, 12–15, 20, 21, 32, 33, 37, 39, 43, 44
F		<i>Tsuga mertensiana</i> (Bongard) Carrier	7, 8, 14, 15, 20, 21, 37–39, 43
F	+	<i>Vaccinium parvifolium</i> Smith in A. Rees	26, 32–34, 44

**Note:** F, forest; O, open sites (ie., meadows and rock outcrops); W, wetlands; Loc., location; +, taxa found in the IW exclusively north of the glacial limits; \*, taxa found in the IW exclusively south of the glacial limits; GCO, grid cells occupied (see Table 1 for the latitude–longitude zone corresponding to these numbers).

Appendix B. Table B1. South coast disjunct taxa in the IW.

Habitat	Loc.	Taxon	GCO
O		<i>Aconogonon phytolaccifolium</i> (Meisner ex Small) Rydberg	1–4, 7–10, 14–16, 21
F	*	<i>Allotropa virgata</i> Torrey & A. Gray ex A. Gray	1, 2, 7, 8
F		<i>Asarum caudatum</i> Lindley	4, 5, 8–11, 14–16, 19–23, 27, 32–34, 39, 40, 49
F		<i>Berberis nervosa</i> Pursh	4, 5, 9, 15, 16, 21, 22, 27, 32, 33, 40
O	*	<i>Boechera cascadenis</i> Windham & Al-Shehbaz	4
O	*	<i>Boechera paddoensis</i> (Rollins) Windham & Al-Shehbaz	4
W	*	<i>Boykinia major</i> A. Gray	8–10
O	*	<i>Bromus laevipes</i> Shear	4
O	*	<i>Bromus subvelutinus</i> Shear	9
O	*	<i>Bromus suksdorfii</i> Vasey	4, 5, 16
F	*	<i>Calamagrostis tweedyi</i> (Scribner) Scribner,	9, 14
W	*	<i>Carex angustata</i> Boott in W.J. Hooker	8, 9, 14, 15
W	*	<i>Carex californica</i> L.H. Bailey	8
W	*	<i>Carex echinata</i> Murray subsp. <i>phyllomanica</i> (W. Boott) Reznicek	9, 15
F	*	<i>Carex hendersonii</i> L.H. Bailey	8–10, 15
F	*	<i>Cephalanthera austiniae</i> (A. Gray) A.A. Heller	4, 5, 8–11, 14, 15
W		<i>Claytonia cordifolia</i> S. Watson	1–10, 14–16, 19, 26–28
O	*	<i>Claytonia exigua</i> Douglas ex Torrey & A. Gray subsp. <i>exigua</i>	15, 16
F		<i>Clinopodium douglasii</i> (Bentham) Kuntze	1–5, 7–11, 13–16, 20–22, 29, 33, 34
O	*	<i>Collomia heterophylla</i> Hooker	8, 15
F	*	<i>Cornus nuttallii</i> Audubon	8
O		<i>Cryptogramma cascadenis</i> E. Alverson	3, 4, 7, 8, 14, 15, 20–22
F		<i>Cypripedium fasciculatum</i> Kellogg ex S. Watson	4, 7–10, 12–15, 20
O	+	<i>Delphinium menziesii</i> de Candolle ssp. <i>menziesii</i>	34
F	*	<i>Dodecatheon dentatum</i> Hooker	4, 8, 15
O	*	<i>Dodecatheon hendersonii</i> A. Gray	3, 5, 8, 9
F	*	<i>Dryopteris arguta</i> (Kaulfuss) Maxon	8
O		<i>Equisetum telmateia</i> Ehrhart ssp. <i>braunii</i> (C. Milde) Hauke	2, 3, 5, 7–9
W	*	<i>Eryngium articulatum</i> Hooker	15
F	*	<i>Festuca subuliflora</i> Scribn.	8, 9
F		<i>Frangula purshiana</i> (de Candolle) J.G. Cooper subsp. <i>purshiana</i>	1–11, 13–17, 20–23, 26–28, 32–34, 38
O		<i>Githopsis specularioides</i> Nuttall	4, 20
W		<i>Glyceria occidentalis</i> (Piper) J.C. Nelson	9, 15, 16, 21, 22
F	+	<i>Hemitomes congestum</i> A. Gray	26, 27
O	*	<i>Heuchera micrantha</i> Lindley var. <i>micrantha</i>	3–5, 8, 9
F	*	<i>Hydrophyllum fendleri</i> (A. Gray) A.A. Heller var. <i>albifrons</i> (A.A. Heller) J.F. Macbride	3–6, 8–10
W		<i>Juncus bolanderi</i> Engelmann	15, 37
W		<i>Juncus covillei</i> Piper var. <i>covillei</i>	5, 8, 9, 14, 15, 21
W	*	<i>Juncus covillei</i> Piper var. <i>obtusatus</i> C.L. Hitchcock	1, 2, 5, 7, 8, 15
W	*	<i>Juncus howellii</i> F.J. Hermann	4, 5, 9
W	*	<i>Juncus occidentalis</i> (Coville) Wiegand	4, 15, 16
F	*	<i>Lathyrus polyphyllus</i> Nuttall	15, 16
O	+	<i>Lewisia columbiana</i> (Howell ex A.Gray) B.L. Robinson in A. Gray et al. var. <i>columbiana</i>	21

Appendix B. Table B1 (concluded).

Habitat	Loc.	Taxon	GCO
O	*	<i>Lomatium dissectum</i> (Nuttall) Mathias & Constance var. <i>dissectum</i>	3, 9
W	*	<i>Lonicera cauriana</i> Fernald	4, 8, 15, 16
W	*	<i>Lotus pinnatus</i> Hooker	9, 10, 15, 16
O	*	<i>Lupinus bicolor</i> Lindley	4, 5, 10
O	*	<i>Lupinus lepidus</i> Douglas var. <i>lepidus</i>	8, 9, 15, 16
F		<i>Luzula fastigiata</i> E. Meyer	8, 9, 14–16, 20–22
O	*	<i>Melica californica</i> Scribner	4, 5
O	*	<i>Melica harfordii</i> Bolander	4
W	*	<i>Mertensia bella</i> Piper	4, 7–9
O	*	<i>Mimulus alsinoides</i> Benthams	14, 15
F		<i>Mitella caulescens</i> Nuttall	5, 8–10, 14–16, 20–22
O	*	<i>Navarretia squarrosa</i> (Eschscholtz) Hooker & Arnott	15, 16
O	*	<i>Orobanche pinorum</i> Hooker	9, 15, 16
F	+	<i>Oxalis trilliifolia</i> Hooker	21
O	*	<i>Pentagramma triangularis</i> (Kaulfuss) Yatskievych, Windham & Wollenweber	3, 9, 10
F		<i>Physocarpus capitatus</i> (Pursh) Kuntze	4, 5, 8, 9, 14, 15, 28, 33, 34
F		<i>Piperia candida</i> Rand. Morgan & Ackerman	8
F		<i>Piperia elegans</i> (Lindley) Rydberg ssp. <i>elegans</i>	4, 5, 15, 16, 20–22, 26, 32, 34
O	+	<i>Piperia elongata</i> Rydberg	19, 20, 23, 25, 32, 40
F		<i>Polemonium californicum</i> Eastwood	2–5, 8–11, 14–16, 21, 22
F		<i>Polystichum munitum</i> (Kaulfuss) C. Presl	4, 5, 7–10, 13–16, 18–23, 27, 33, 34
W	*	<i>Ranunculus alismifolius</i> Geyer ex Benthams var. <i>alismifolius</i>	5, 9, 10, 15, 16
W	*	<i>Ranunculus orthorhynchus</i> Hooker var. <i>orthorhynchus</i>	9, 15, 16
W	*	<i>Ranunculus populago</i> E. Greene	4, 5, 7
W	+	<i>Ribes acerifolium</i> T.J. Howell	21, 22, 24, 44
O	*	<i>Ribes sanguineum</i> Pursh var. <i>sanguineum</i>	15
F	*	<i>Rubus nivalis</i> Douglas ex Hooker	8, 9, 27, 31, 32, 38
F	*	<i>Rubus ursinus</i> Chamisso & Schlechtendal	3–5, 8, 9, 14–16, 21, 31
F	*	<i>Rupertia physodes</i> (Douglas ex Hooker) J. Grimes	5, 9
F	*	<i>Senecio integerrimus</i> Nuttall var. <i>ochroleucus</i> (A. Gray) Cronquist	9, 10, 15, 16
O	*	<i>Spiranthes porrifolia</i> Lindley	9, 16
F	*	<i>Symphoricarpos hesperius</i> G.N. Jones	2–4, 8–10, 15, 16
F		<i>Taxus brevifolia</i> Nuttall	1–5, 7–11, 13–16, 18–28, 31–34, 36–40, 42, 44, 48–50
F	*	<i>Thelypteris nevadensis</i> (Baker) Clute ex C.V. Morton	8
F		<i>Trautvetteria caroliensis</i> (Walter) Vail	1–5, 7–11, 14–16, 21–23, 27, 28
O		<i>Trichostemma oblongum</i> Benthams	5, 9, 15, 16, 27
F		<i>Trientalis borealis</i> Rafinesque subsp. <i>latifolia</i> (Hooker) Hultén	3–5, 8, 9, 11, 15, 21
F		<i>Trillium ovatum</i> Pursh var. <i>ovatum</i>	2–4, 7–10, 13–16, 18–28, 34
O	*	<i>Triteleia howellii</i> S. Watson	3, 8, 9
O		<i>Valeriana scouleri</i> Rydberg	4, 5, 27, 38
W	*	<i>Veratrum californicum</i> Durand var. <i>caudatum</i> (A.A. Heller) C.L. Hitchcock	9, 15
F		<i>Viola sempervirens</i> E. Greene	8, 15, 16, 21, 27

**Note:** F, forest; O, open sites (ie., meadows and rock outcrops); W, wetlands. Loc., location; +, taxa found in the IW exclusively north of the glacial limits; \*, taxa found exclusively south of the glacial limits; GCO, grid cells occupied (see Table 1 for the latitude-longitude zone corresponding to these numbers).

**Appendix C. Table C1.** IW endemic and subendemic (100% or >50% of the taxon's global range, respectively; the former are in bold).

Habitat	Loc.	Taxon	GCO
O	*	<b><i>Achnatherum wallowaense</i> J.K. Maze &amp; K.A. Robson</b>	
O	#*	<b><i>Allium dictuon</i> H. St. John</b>	4, 5, 10
O	*	<i>Allium fibrillum</i> M.E. Jones ex Abrams	
F?	#*	<b><i>Amelastorbus jackii</i> Rehder</b>	4, 8
F	#	<b><i>Anemone piperi</i> Britton ex Rydberg</b>	3–5, 8–11, 13–16, 19–22, 27
F	#	<i>Angelica dawsonii</i> S. Watson	2, 7, 8, 14, 18–20, 24
O	*	<i>Arabis crucisetosa</i> Constance & Rollins	
O	*	<b><i>Astragalus arthuri</i> M.E. Jones</b>	
O	*	<b><i>Astragalus asotinensis</i> Björk &amp; Fishbein</b>	
O	#*	<b><i>Astragalus reventus</i> A. Gray</b>	3–5, 9–11
O	#*	<b><i>Astragalus sheldonii</i> (Rydberg) Barneby</b>	3–5, 9–11
F	#	<b><i>Calochortus apiculatus</i> Baker</b>	8–9, 14–16, 18–22, 24, 25, 30
O	*	<i>Calochortus elegans</i> Pursh var. <i>elegans</i>	
F	#*	<b><i>Calochortus elegans</i> Pursh var. <i>selwayensis</i> (H. St. John) Ownbey</b>	1, 7, 8, 14, 15
O	*	<b><i>Calochortus macrocarpus</i> Douglas var. <i>maculosus</i> (A. Nelson &amp; J.F. Macbride) A. Nelson</b>	
O	#*	<i>Calochortus nitidus</i> Douglas	3, 4, 8–10, 13
F	#*	<b><i>Cardamine constancei</i> Detling</b>	8, 9, 15
O	*	<b><i>Cardamine rupicola</i> (Ryddberg) C.L. Hitchcock</b>	
O	#	<i>Castilleja cervina</i> Greenman	12, 19, 21, 24, 25, 27, 28, 30, 34
O	#*	<b><i>Castilleja chrysantha</i> Greenman</b>	3–5
O	*	<b><i>Castilleja covilleana</i> L.F. Henderson</b>	
O	*	<b><i>Castilleja fraterna</i> Greenman</b>	
O	*	<b><i>Castilleja glandulifera</i> Pennell</b>	
O	*	<b><i>Castilleja rubida</i> Piper</b>	
O	*	<i>Claytonia arenicola</i> L.F. Henderson	
O	#*	<b><i>Collomia debilis</i> (S. Watson) E. Greene var. <i>camporum</i> Payson</b>	6
F	#	<b><i>Coptis occidentalis</i> (Nuttall) Torrey &amp; A. Gray</b>	2–4, 7–10, 14–16, 20, 21
F	#*	<b><i>Corydalis caseana</i> A. Gray var. <i>hastata</i> (Rydberg) Ownbey</b>	8, 9, 15
O	*	<i>Crepis bakeri</i> E. Greene var. <i>idahoensis</i> Babcock & Stebbins	
F	#*	<b><i>Dasynotus daubenmirei</i> I.M. Johnston</b>	8
F	#	<i>Delphinium sutherlandii</i> M.J. Warnock	9, 10, 14–16, 20–22, 30, 32
O	*	<i>Erigeron aureus</i> E. Greene	
O	#*	<b><i>Erigeron davisii</i> (Cronquist) G.L. Nesom</b>	3, 4, 9
O	#*	<b><i>Eriogonum scopulorum</i> Reveal</b>	3, 4
O	*	<i>Eriogonum strictum</i> Bentham var. <i>strictum</i>	
F	#*	<b><i>Erythronium grandiflorum</i> Pursh var. <i>candidum</i> Piper</b>	8–10, 15, 16, 19–21
F	#*	<b><i>Frasera fastigiata</i> (Pursh) A.A. Heller</b>	8–10, 14–16
O	#	<b><i>Grindelia howellii</i> Steyermark</b>	6, 12, 15
O	*	<i>Hackelia hispida</i> (A. Gray) I.M. Johnston	
W	#	<i>Howellia aquatilis</i> A. Gray	9, 12, 16
O	#	<i>Ionactis stenomeris</i> (A. Gray) E. Greene	1, 2, 7–9, 14–16, 20–22, 25–27
F	#	<i>Lathyrus bijugatus</i> White	8–10, 15, 16, 19–21, 25
F	#*	<b><i>Lathyrus nevadensis</i> S. Wats. subsp. <i>cusickii</i> (S. Watson) Broich</b>	3–5, 9, 10



Appendix C. Table C1 (continued).

Habitat	Loc.	Taxon	GCO
F	##	<b><i>Lathyrus nevadensis</i> S. Wats. subsp. <i>parkeri</i> (H. St. John) C.L. Hitchcock</b>	3, 8, 9
O	##	<i>Lewisia columbiana</i> (Howell ex A. Gray) Robinson var. <i>wallowensis</i> C.L. Hitchcock	1–4, 7–8
F	#	<b><i>Ligusticum canbyi</i> Coulter &amp; Rose</b>	1–5, 8–11, 13–16, 19–22, 25–27, 30–33, 38, 39
F	##	<b><i>Ligusticum verticillatum</i> (Geyer) Coulter &amp; Rose</b>	7–9, 14, 15
O	*	<b><i>Lomatium greenmanii</i> Mathias</b>	
O	*	<b><i>Lomatium oreganum</i> Coulter &amp; Rose</b>	
O	*	<i>Lomatium rollinsii</i> Mathias & Constance	
O	##	<b><i>Lomatium sandbergii</i> Coulter &amp; Rose</b>	13–15, 18–22, 24–26
O	#	<i>Lomatium serpentinum</i> (M.E. Jones) Mathias	2–4, 9–11
F	*	<b><i>Lupinus sabinianus</i> Douglas</b>	
O	*	<i>Lupinus sericeus</i> Pursh var. <i>asotinensis</i> (L.L. Phillips) C.L. Hitchcock	
O	*	<b><i>Mimulus ampliatus</i> A.L. Grant</b>	
O	##	<b><i>Mimulus clivicola</i> Greenman</b>	2–4, 9, 15, 16
O	*	<b><i>Mimulus hymenophyllus</i> Meinke</b>	
O	*	<i>Mimulus patulus</i> Pennell	
O	*	<i>Mirabilis macfarlanei</i> Constance & Rollins	
O	*	<i>Nemophila kirtleyi</i> L.F. Henderson	
O		<i>Oxytropis campestris</i> (Linnaeus) de Candolle var. <i>columbiana</i> (H. St. John) Barneby	
O	+	<b><i>Papaver pygmaeum</i> Rydberg</b>	
O		<i>Penstemon ellipticus</i> J. Coulter & Fisher	
O		<i>Penstemon lyallii</i> A. Gray	
O	*	<b><i>Penstemon pennellianus</i> Keck</b>	
O	*	<b><i>Penstemon spatulatus</i> Pennell</b>	
O	*	<i>Phlox colubrina</i> Wherry & Constance	
W	##	<b><i>Phlox idahonis</i> Wherry &amp; Constance</b>	8
O	*	<b><i>Phlox mollis</i> Wherry</b>	
O	*	<i>Physaria geyeri</i> (Hooker) A. Gray var. <i>geyeri</i>	
O	*	<b><i>Physaria humilis</i> (Rollins) O’Kane &amp; Al-Shehbaz</b>	
O	*	<b><i>Physaria kingii</i> (S. Watson) O’Kane &amp; Al-Shehbaz ssp. <i>diversifolia</i> (E. Greene) O’Kane &amp; Al-Shehbaz</b>	
O	*	<i>Physaria oregana</i> S. Watson	
F	#	<i>Prenanthes sagittata</i> (A. Gray) A. Nelson	2, 7, 8, 12, 14, 15, 18–20, 24
F	##	<b><i>Pseudostellaria oxyphylla</i> (Torrey) W.A. Weber &amp; Hartman</b>	15
O	*	<i>Pyrocoma scaberula</i> E. Greene	
O	*	<i>Ribes cereum</i> Douglas var. <i>colubrinum</i> C.L. Hitchcock	
O	*	<i>Sedum leibergii</i> Britton	
F	##	<i>Selaginella douglasii</i> (Hooker & Greville) Spring	2, 3, 7–9
O	#	<b><i>Senecio megacephalus</i> Nuttall</b>	1, 7, 8, 14, 15, 18–22, 24, 28
O	+	<b><i>Senecio spribillei</i> W.A. Weber</b>	
O	*	<i>Silene spaldingii</i> S. Watson	
O	*	<i>Symphotrichum jessicae</i> (Piper) G.L. Nesom	
O	+	<b><i>Synthyris canbyi</i> Pennell</b>	
F	##	<b><i>Synthyris missourica</i> (Rafinesque) Pennell var. <i>major</i> (Hooker) Pennell</b>	8, 9

Appendix C. Table C1 (concluded).

Habitat	Loc.	Taxon	GCO
F	#*	<i>Synthyris platycarpa</i> Gail & Pennell	2, 7, 8
W	#*	<i>Tauschia tenuissima</i> (Geyer ex Hooker) Mathias & Constance	8, 9, 15, 16
O	#*	<i>Trifolium douglasii</i> House	3–5, 8–10, 15, 16
O	#*	<i>Trifolium eriocephalum</i> Nuttall var. <i>arcuatum</i> (Piper) M.E. Peck	2–5, 9–11
O	#	<i>Trifolium latifolium</i> (Hooker) E. Greene	2–4, 7–10, 14–15, 21
O	*	<i>Trifolium plumosum</i> Douglas var. <i>amplifolium</i> J.S. M artin	
O	*	<i>Trifolium plumosum</i> Douglas var. <i>plumosum</i>	
F	#*	<i>Trillium petiolatum</i> Pursh	3–5, 8–10, 15, 16
F	#*	<i>Waldsteinia idahoensis</i> Piper	2, 7, 8, 14

**Note:** F, forest; O, open sites (ie., meadows and rock outcrops); W, wetlands. Loc., location, i.e., #, taxa found primarily within forested elevations (not including dry *Pinus ponderosa* or *Juniperus* forest and also excluding grassland and alpine taxa); +, taxa found in the IW exclusively north of the glacial limits; \*, taxa found exclusively south of the glacial limits; GCO, grid cells occupied (see Table 1 for the latitude-longitude zone corresponding to these numbers).

**Appendix D. Table D1.** Coast–IW taxa having isthmus connections through the Babine–Omineca Mountains (column 1), Okanagan Mountains (column 2) and Ochoco–Blue Mountains (column 3).

North	Middle	South	Taxon
		x	<i>Abies grandis</i> (Douglas ex D. Don) Lindley
	x	x	<i>Adenocaulon bicolor</i> Hooker
	x	x	<i>Adiantum aleuticum</i> (Ruprecht) Paris
	x		<i>Agoseris grandiflora</i> (Nuttall) E. Greene var. <i>leptophylla</i> G.I. Baird
		x	<i>Agrostis pallens</i> Trinart
		x	<i>Alnus rhombifolia</i> Nuttall
x	x		<i>Anemone occidentalis</i> S. Watson
x	x		<i>Angelica genuflexa</i> Nuttall ex Torrey & A. Gray
x			<i>Angelica lucida</i> Linnaeus
x			<i>Arabidopsis lyrata</i> (Linnaeus) O’Kane & Al-Shehbaz subsp. <i>kamchatica</i> (Fischer ex de Candolle) O’Kane & Al-Shehbaz
	x	x	<i>Arnica amplexicaulis</i> Nuttall
x			<i>Artemisia tilesii</i> (Ledebour) subsp. <i>unalaschcensis</i> (Bessey) Hultén
x	x		<i>Aruncus dioicus</i> (Walter) Fernald var. <i>acuminatus</i> (Rydberg) Hara
	x	x	<i>Aspidotis densa</i> (Brackenridge) Lellinger
		x	<i>Athysanus pusillus</i> (Hooker) E. Greene
		x	<i>Bromus orcuttianus</i> Vasey
x	x	x	<i>Bromus vulgaris</i> (Hooker) Shear
	x	x	<i>Callitropsis nootkaensis</i> (D. Don) Florin
	x		<i>Calypso bulbosa</i> (Linnaeus) Oakes var. <i>occidentalis</i> (Holzinger) B. Boivin
	x	x	<i>Carex amplifolia</i> Boott
	x		<i>Carex aperta</i> Boott
		x	<i>Carex fracta</i> MacKenzie
		x	<i>Carex lenticularis</i> Michaux var. <i>impressa</i> (L.H. Bailey) L.A. Standley
	x	x	<i>Carex leptopoda</i> MacKenzie
	x	x	<i>Carex mertensii</i> J.D. Prescott ex Bongard
	x		<i>Carex preslii</i> Steudel
	x		<i>Carex scirpoidea</i> Michaux subsp. <i>stenochlaena</i> (T. Holm) Á. Löve & D. Löve
	x		<i>Carex sitchensis</i> Prescott ex Bongard
	x		<i>Carex scopulorum</i> (T. Holm) var. <i>prionophylla</i> (T. Holm) L.A. Standley
x	x		<i>Carex spectabilis</i> Dewey
x			<i>Castilleja parviflora</i> Bongard
		x	<i>Centaurium muhlenbergii</i> (Grisebach) Piper
		x	<i>Chimaphila menziesii</i> (D. Don) Sprengel
x	x		<i>Cirsium edule</i> Nuttall var. <i>macounii</i> (E. Greene) D.J. Keil
		x	<i>Claytonia parviflora</i> Douglas ex Hooker subsp. <i>parviflora</i>
		x	<i>Cryptantha intermedia</i> (A. Gray) E. Greene
x			<i>Cryptogramma sitchensis</i> (Ruprecht) T. Moore
x			<i>Elymus hirsutus</i> Presl
	x		<i>Erigeron aureus</i> E. Greene var. <i>aureus</i>
x			<i>Erigeron inornatus</i> A. Gray var. <i>inornatus</i>
		x	<i>Eriogonum elatum</i> Douglas ex Bentham var. <i>elatum</i>
	x	x	<i>Erythronium grandiflorum</i> Pursh var. <i>grandiflorum</i>
	x		<i>Eucephalus engelmannii</i> (D.C. Eaton) E. Greene
	x		<i>Festuca viridula</i> Vasey
	x		<i>Fritillaria affinis</i> (Schultes & Schultes f.) Sealy
x			<i>Fritillaria camschatcensis</i> (Linnaeus) Ker Gawler
		x	<i>Gilia capitata</i> Sims var. <i>capitata</i>
	x		<i>Hemieva ranunculifolia</i> (Hooker) Rafinesque
	x		<i>Hippuris montana</i> Ledebour
		x	<i>Kelloggia galioides</i> Torrey
	x		<i>Larix lyallii</i> Parlatores
	x	x	<i>Larix occidentalis</i> A. Gray
x	x		<i>Leptarrhena pyrolifolia</i> (D. Don) R. Brown
	x		<i>Lilium columbianum</i> Baker
		x	<i>Lomatium nudicaule</i> (Pursh) Coulter & Rose
	x		<i>Lotus nevadensis</i> (S. Watson) E. Greene var. <i>douglasii</i> (E. Greene) Ottley

Appendix D. Table D1 (concluded).

North	Middle	South	Taxon
	x		<i>Luetkea pectinata</i> (Pursh) Kuntze
x	x		<i>Lupinus arcticus</i> S. Watson var. <i>subalpinus</i> (Piper & B.L. Robinson) Dunn
	x		<i>Luzula hitchcockii</i> Hämet-Ahti
x	x		<i>Luzula piperi</i> (Coville) M.E. Jones
	x		<i>Lysichiton americanus</i> Hultén & St. John
		x	<i>Madia citriodora</i> E. Greene
x	x		<i>Melica smithii</i> (Porter) Vasey
x	x		<i>Micranthes lyallii</i> (Engler) Small var. <i>hultenii</i> (Calder & Saville) comb. ined.
	x	x	<i>Mimulus breweri</i> (E. Greene) Coville
	x		<i>Mimulus lewisii</i> Pursh
	x		<i>Mitella breweri</i> A. Gray
x	x		<i>Monotropa hypopitys</i> Linnaeus
		x	<i>Navarretia divaricata</i> (A. Gray) E. Greene var. <i>divaricata</i>
x	x		<i>Oplopanax horridus</i> (Small) Miquel
	x	x	<i>Osmorhiza purpurea</i> (Coulter & Rose) Suksdorf
x	x		<i>Pedicularis bracteosa</i> Bentham var. <i>bracteosa</i>
		x	<i>Phacelia procera</i> A. Gray
	x	x	<i>Pinus monticola</i> Douglas ex D. Don
		x	<i>Poa bolanderi</i> Vasey
	x		<i>Prosartes hookeri</i> Torrey
		x	<i>Pseudotsuga menziesii</i> (Mirbel) Franco var. <i>menziesii</i>
		x	<i>Ranunculus alismifolius</i> Geyer ex Bentham var. <i>alismellus</i> A. Gray
x	x		<i>Rhododendron albiflorum</i> Hooker
	x	x	<i>Rosa gymnocarpa</i> Nuttall
x	x		<i>Rubus pedatus</i> J.E. Smith
x	x		<i>Sanguisorba stipulata</i> Rafinesque
	x		<i>Saxifraga mertensiana</i> Bongard
x	x		<i>Sorbus sitchensis</i> Roemer var. <i>sitchensis</i>
	x		<i>Stellaria borealis</i> Bigelow var. <i>sitchana</i> (Steudel) Piper & Beattie
	x	x	<i>Stellaria crispa</i> Chamisso & Schlechtendal
	x		<i>Stenanthium occidentale</i> A. Gray
			<i>Streptanthus cordatus</i> Nuttall var. <i>cordatus</i>
	x		<i>Suksdorfia violacea</i> A. Gray
x			<i>Symphyotrichum foliaceum</i> (Lindley) Nesom var. <i>foliaceum</i>
	x		<i>Thuja plicata</i> Donn ex D. Don
x	x	x	<i>Tiarella trifoliata</i> Linnaeus var. <i>unifoliata</i> (Hooker) Kurtz
	x	x	<i>Trisetum canescens</i> Buckley
		x	<i>Trisetum cernuum</i> Trinart
		x	<i>Triteleia hyacinthina</i> (Lindley) E. Greene
	x		<i>Trollius albiflorus</i> (A. Gray) Rydberg
		x	<i>Uropappus lindleyi</i> (de Candolle) Nuttall
x	x		<i>Vaccinium ovalifolium</i> Smith
x	x	x	<i>Valeriana sitchensis</i> Bongard
x	x	x	<i>Veratrum viride</i> Aiton var. <i>eschsoltzianum</i> (Roemer & Schultes) Breitung
		x	<i>Veronica cusickii</i> A. Gray
	x	x	<i>Viola glabella</i> Nuttall
x	x		<i>Viola orbiculata</i> Geyer ex Holtzinger
		x	<i>Viola praemorsa</i> Douglas subsp. <i>praemorsa</i>
	x		<i>Xerophyllum tenax</i> (Pursh) Nuttall
		x	<i>Yabea microcarpa</i> (Hooker & Arnott) Kozo-Polianski