Chapter 2
Geology and Historical Biogeography of the Olympic Peninsula

Abstract A brief introduction to the geologic and climatic history of the Olympic Peninsula is presented, focusing on the Middle Miocene to present (the past 20 million years). The period is marked by a general cooling and drying trend, with a corresponding loss of the mesic broadleaf forest and the rise of conifer-dominated forests. The causes of the regional climate changes are discussed with an eye on the relative roles of topographic uplift versus larger global-scale changes in atmospheric circulation and sea surface temperature. The patterns of endemism and disjunction on the peninsula are presented to emphasize insular aspects of its biogeography. A list of 29 endemic taxa is compiled from literature searches, though it is acknowledged the list will continue to grow. Mapped distributions of the endemic taxa suggest long-term persistence of certain habitat types, including dry meadows and wet riparian forests, through periods of glacial cycles.

> The gap that separates the Olympic Mountains from the Cascade Range…is only about a hundred miles wide and is filled by the dense forest already mentioned, affording continuity of range…but the higher parts of the Olympics…have been disconnected from corresponding zones to the north and east for at least several million years, a period long enough to admit a considerable amount of differentiation in the species stranded here…
> C. Hart Merriam, undated manuscript, quoted in Schultz (1994)

2.1 Late Cenozoic Geologic and Climatic History

During the Eocene, about 50 million years ago, a deep marine rift formed parallel to the continent as the oceanic (Kula) plate moved obliquely to the continental (North American) plate (Fig. 2.1). This rift caused immense amounts of lava to accumulate, forming a large region of basalts under the ocean (Babcock et al. 1992). Sediments accumulated on both the continental and oceanic side of the basalts. As the oceanic plate pushed against the continental plate, both the oceanic sediments and the basalt were compressed and turned upward. This process of subduction under the continental plate resulted in the accretion of a large wedge of sediments against the continent, which were pushed vertically and forced into an eastward-plunging arch (Tabor 1975). Younger sedimentary rocks were the last to be pushed against

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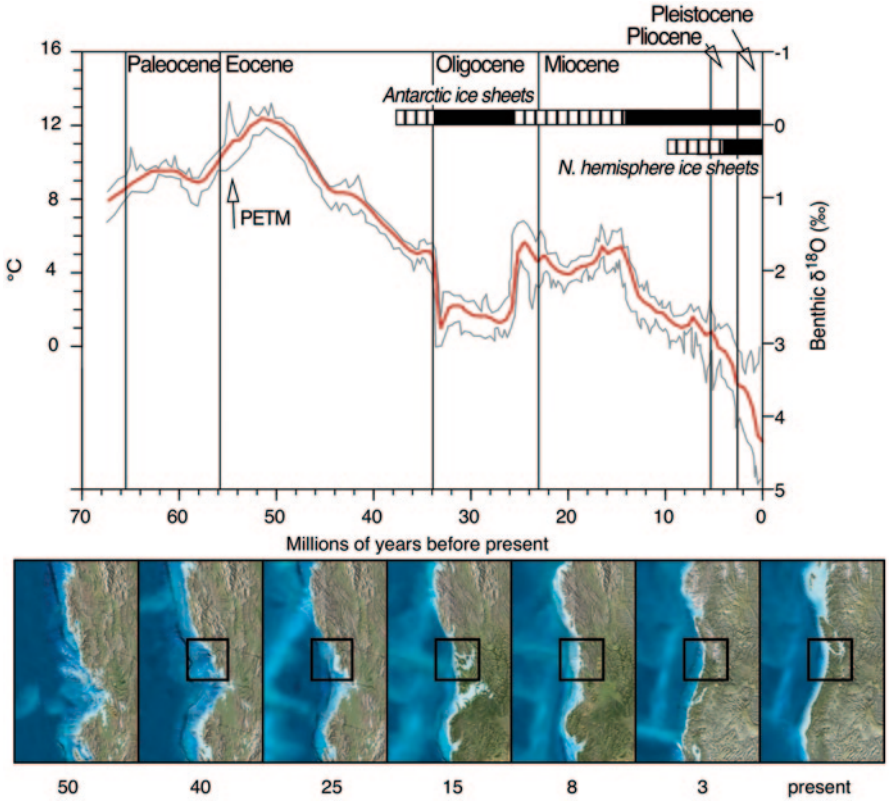

Fig. 2.1 *Top:* Global climate trajectory during the Cenozoic inferred from oxygen isotope ratios of benthic ocean sediment (modified from Zachos et al. 2001). *Bottom:* Paleogeography of western North America. Colors correspond to vegetation cover. (Maps from Ron Blakey, Colorado Plateau Geosystems, Inc, http://www.cpgeosystems.com/paleomaps.html)

the continent. Because the basalt mass, and the continent behind it, were much more rigid than the oceanic sediments, the marine sandstones, siltstones, and conglomerates making up the core of the Olympic Mountains were disrupted and folded. The horseshoe shape of the basalt Crescent Formation (Fig. 2.2) may have resulted from the ocean plate forcing the basalt mass into the "inside corner" between Vancouver Island and the continent. Beginning around 20 million years ago, the lighter sedimentary rocks rose relative to the dense oceanic crust leading to the uplift of the Olympic Mountains. Ages on the central core rocks of the peninsula, dated by the zircon fission track method, suggest the uplift of the mountains has been occurring for 17 million years and that the erosion of the terrain is in rough equilibrium with the uplift (Pazzaglia and Brandon 2001; Wegmann and Pazzaglia 2002). However, there remains much uncertainty about the age of the marine sedimentary rocks, which are often mapped within broad time periods (e.g., Miocene to Eocene).

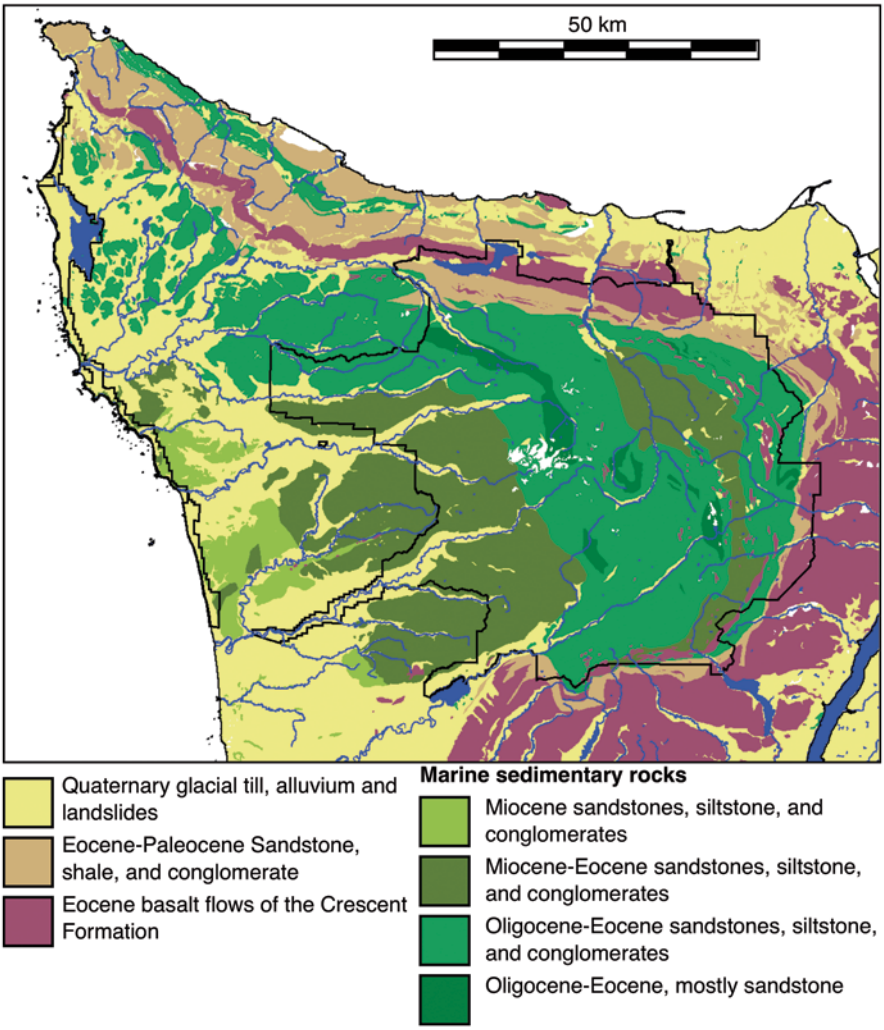

Fig. 2.2 Geological map of the Olympic Peninsula showing major units differentiated by age class. (Data from Washington Division of Geology and Earth Resources 2008)

During the uplift of the Olympic Mountains, from the Middle Miocene to present, the Olympic Mountains experienced large climatic changes. A warming in the Middle Miocene from 18 to 16 Ma, the Miocene Climatic Optimum, interrupted a general global cooling trend during the Cenozoic. Vegetation at this time in the Pacific Northwest indicates summer moisture and humidity sufficient to maintain a diversity of broadleaf deciduous trees. The warm sea surface temperatures of the Miocene fed summer moisture into western North America in what was likely a "Rocky Mountain Monsoon" with probably more than 400 mm of precipitation in the summer months alone (Lyle et al. 2003) and thus much stronger than the modest

modern monsoon in Arizona (note increased vegetation cover at 15 Ma as shown in Fig. 2.1). It is difficult to simulate the warm and wet climate of the Middle Miocene under the CO_2 levels estimated for that time, which were similar to modern levels (< 400 ppm; Goldner et al. 2013). During the late Miocene, the western USA began shifting from a summer-wet/winter-dry climate to a summer-dry/winter-wet climate. This gradual change, from 15 to 5 Ma, was likely linked to changes in sea surface temperature which would reduce summer rainfall (Lyle et al. 2008). The ultimate causes of sea surface temperatures, via atmospheric and oceanic circulation and the global energy balance, are poorly understood.

The uplift of the Cascade/Sierra ranges created a rain shadow to the east, but this uplift was probably not primarily responsible for the Miocene drying in the region. The mountain uplift occurred generally earlier than the gradual drying trend. More importantly, the drying trend occurred on the coast as well as in the modern rain shadow environment, suggesting a more fundamental change in atmospheric circulation (Lyle et al. 2008). The drying was likely accompanied by an increase in the strength of the Pacific subtropical high system and coastal upwelling, which are responsible for the summer aridity in western North America (Wolfe 1985). This climate change resulted in great losses of the deciduous element that required warm and moist summers, while promoting expansion of conifer forests. In addition, as uplift of the Cascade and Sierra Nevada Ranges proceeded, the interior rain shadow climate developed and resulted in the development of xeric steppe vegetation. The expansion of conifers and woodland vegetation continued into the Pliocene. Despite this major change in the vegetation formation, 90 genera of the Pacific Northwest Miocene flora occur today on the Olympic Peninsula (Buckingham et al. 1995).

Beginning 2.6 million years ago (the Pleistocene), global climate completed its transition from a “greenhouse” world that lacks ice sheets to an “ice-house” world marked by cyclic glaciations in the northern hemisphere. Glacial periods lasting ca. 90,000 years were marked by rapid climate changes and ice sheets extending over most of Canada. In contrast, interglacial periods lasting ca. 10,000 years resulted in species expanding their ranges into higher latitudes. The climate history of the late Pleistocene is the focus of Chaps. 3 and 4.

2.2 Endemism, Disjunction, and the Insular Nature of the Olympic Biota

The insular (island-like) nature of the plant and animal life of the Olympic Peninsula has been widely noted (Houston et al. 1994; McNulty 2009). Three main features of the biodiversity on the peninsula are consistent with long-term isolation and the effects of the mountains functioning as an ice-age refugium during the Pleistocene. First, 29 plant and animal taxa are known to be endemic to the Olympic Peninsula (Table 2.1, Fig. 2.3). Second, at least 13 species common in the Cascade Range were historically absent from the peninsula, suggesting the operation of a long-term

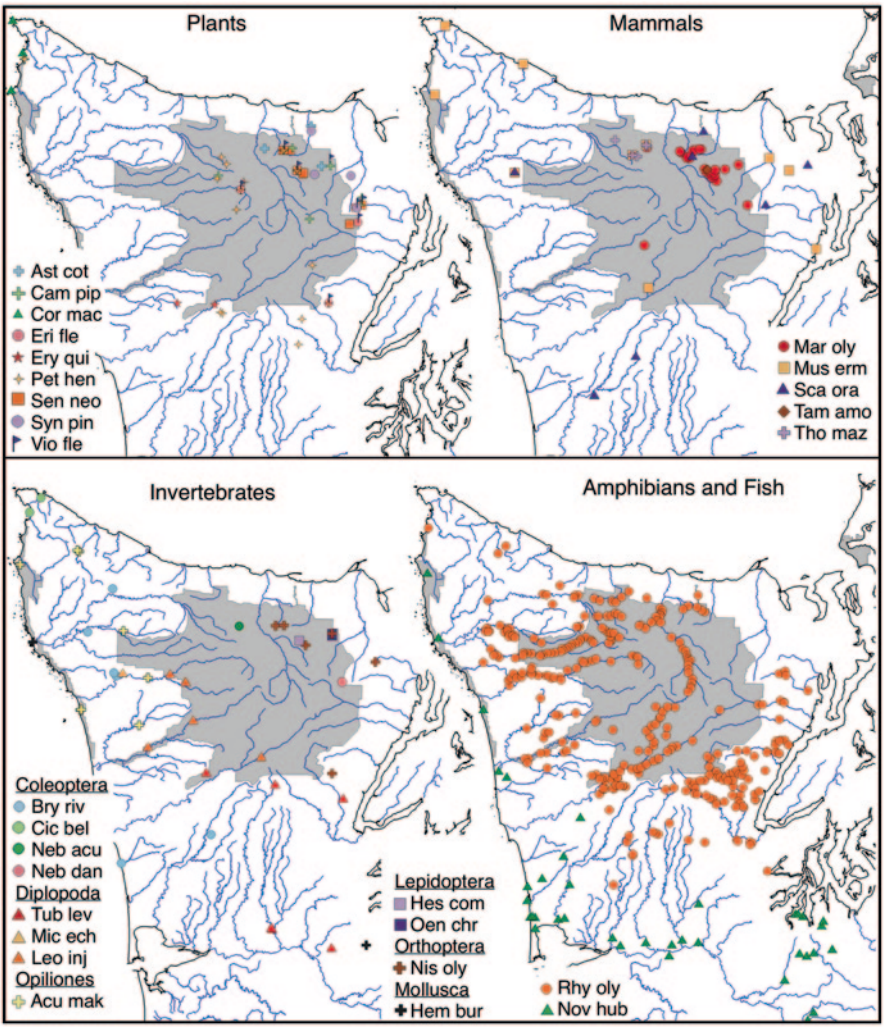

Fig. 2.3 Distribution of endemic (or near-endemic) taxa of the Olympic Peninsula. *Six-character species codes* are first characters of genus and species names listed in Table 2.1.

barrier to dispersal. Third, a large number of species on the peninsula are disjunct from their closest conspecifics or sister taxa by hundreds of kilometers.

The endemic taxa of the Olympic Peninsula are found in a small set of habitats, suggesting that these habitats are a long-term feature of the peninsula though not necessarily in their current extent and spatial distribution (Fig. 2.4). Of the 29 endemic taxa, 13 have ranges restricted to subalpine or higher elevations in the north or northeast. In particular, five species are associated with scree or rocky slopes. These dry meadow and woodland habitats are more extensive in the modern Rocky Mountains and may have been more common in the past on the Olympic Peninsula,

Table 2.1 Endemic taxa of the Olympic Peninsula. (This list was developed from Park Service web pages http://www.nps.gov/olym/naturescience/endemic-animals.htm, Houston et al. 1994, Buckingham et al. 1995, McNulty 2009, and several more recent studies. Plant taxonomy was checked against the flora of North America. Note that some taxa have ranges extending partly outside the peninsula)

Scientific name	Common name	Habitat association (and quadrant on Peninsula)	Source (for habitat association)
Vascular plants			
Astralagaus cottonii	Olympic Mountain milkvetch	Subalpine, open sites (northeastern mountains)	Buckingham et al. 1995
Campanula piperi	Piper's bellflower	Montane to alpine, rocky sites (Northeast to central)	Buckingham et al. 1995
Corallorhiza maculata var. *ozettensis*	Spotted coral root	Lowland, partial shade (Northwest)	Tisch 2001
Erigeron flettii	Flett's fleabane	Subalpine to alpine, open sites (Northeast to south)	Buckingham et al. 1995
Erigeron peregrinus ssp. *peregrinus* var. *thompsonii*	Thompson's wandering fleabane	Lowland, bog sites (Southwest)	Buckingham et al. 1995
Erythronium quinaultense	Quinault fawn lily	Lowland, open or partially open (Southwest)	Allen 2001
Petrophytum hendersonii	Olympic rock mat	Montane to alpine, rocky sites (South, north, and east)	Buckingham et al. 1995
Senecio neowebsteri	Olympic Mountain groundsel	Subalpine to alpine, scree sites (North, northeast, and central)	Buckingham et al. 1995
Synthyris pinnatifida var. *lanuginosa*	Olympic Mountain synthyris	Subalpine to alpine, scree sites (North, northeast, and central)	Buckingham et al. 1995
Viola flettii	Flett's violet	Subalpine to alpine, rocky sites (North, northeast, and central)	Buckingham et al. 1995
Amphibians			
Rhyacotriton olympicus	Olympic torrent salamander	Lowlands to montane, steep gradient streams (Southwest)	Adams and Bury 2002
Mammals			
Marmota olympus	Olympic marmot	Subalpine, open meadows (Throughout)	Edelman 2003
Tamias amoenus caurinus	Olympic yellow-pine chipmunk	Subalpine, forest, and parkland (North and northeast)	Sutton 1992; Demboski and Sullivan 2003
Scapanus orarius (Olympic clade)	coast mole	Subalpine (Northeast and southwest)	Welch 2008[a]
Thomomys mazama melanops	Olympic Mazama pocket gopher	Meadows, young forest (North and northeast)	Verts and Carraway 2000

Table 2.1 (continued)

Scientific name	Common name	Habitat association (and quadrant on Peninsula)	Source (for habitat association)
Mustela erminea olympica	Olympic ermine	Throughout (North, central, and southeast)	Hall 1945
Fish			
Novumbra hubbsi	Olympic mudminnow	Low gradient rivers, muddy sediment (South)	McPhail 1967
Opiliones (harvestmen)			
Acuclavella makah		Perennial headwater stream banks, woody debris	Richart and Hedin 2013
Orthoptera (grasshoppers)			
Nisquallia olympica	Olympic grasshopper	Subalpine to alpine, scree sites	Rehn 1952
Lepidoptera (butterflies and moths)			
Hesperia comma hulbirti	Hulbirt's skipper	Subalpine to alpine	Lindsey 1939
Oeneis chryxus valerata	Olympic arctic	Subalpine to alpine (Northeast)	Yake 2005
Coleoptera (beetles)			
Bryelmis rivularis	Riffle beetle	Streams 3–6 m wide, woody debris (West and NW Oregon)	Barr 2011
Cicindela bellissima frechini	Pacific coast tiger beetle	Sand dunes and deflation plains (West)	Leffler 1979
Nebria acuta quileute	Quileute gazelle beetle	River banks at mid-elevation (North)	Kavanaugh 1979
Nebria danmanni	Mann's gazzelle beetle	Montane to subalpine (Northeast)	Kavanaugh 1981
Diplopoda (millipedes)			
Leonardesmus injucundus	–	Litter and soil, dense forest (South)	Shelley and Shear 2006
Microlympia echina	–	Riparian forest, alder litter (West)	Shear and Leonard 2003
Tubaphe levii	Olympic peninsula millipede	Lowlands (West)	Causey 1954
Mollusks			
Hemphillia burringtoni	Arionid jumping slug	Dense riparian forest, possibly also in the Cascade Range	Burke 2005

[a] Welch (2008) found no phylogenetic support for a separate clade for *Scapanus townsendii olympicus*

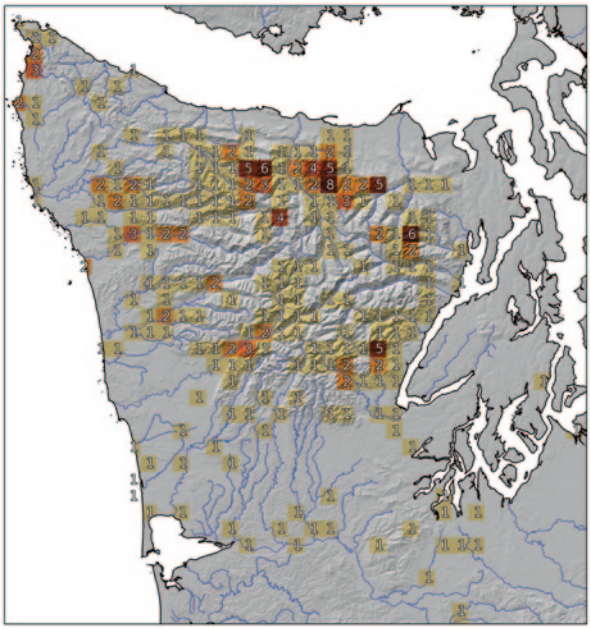

Fig. 2.4 Endemic species richness in 4-km grid cells. This map was developed from Fig. 2.3

such as on unglaciated mountainsides above the Cordilleran ice sheet (Buckingham et al. 1995).

Although not strictly endemic to the peninsula, seaside juniper (*Juniperus maritima*) exemplifies the association of endemics with northeastern subalpine ecosystems. This species was recently distinguished from *Juniperus scopulorum*, and it has a distribution pattern and genetics that are strongly suggestive of a glacial refugium in northeastern Olympic meadows (Adams et al. 2010). This species is normally associated with rocky outcrops at sea level in northern Puget Sound and Strait of Georgia, but was found to extend to 1700 m above sea level in meadows in the northeastern Olympic Peninsula. Genetic markers show that mid-elevation *Juniperus* on the peninsula are ancestral to more recently dispersed populations in Puget Sound (Adams et al. 2010). Thus, while this species is not strictly endemic to the peninsula, much of its genetic diversity is endemic and suggests unglaciated areas in the eastern peninsula served as glacial refugia.

Several other species are restricted to dry sites on the Olympic Peninsula with the nearest conspecific common in the eastern Cascades and/or Rocky Mountains (e.g., Englemann spruce, whitebark pine, and quaking aspen). Kuramoto and Bliss (1970) suggest that the phlox-bunchgrass community of the northeastern subalpine meadows is a remnant of the early Holocene warm period. However, the high number of endemic taxa of this vegetation type suggests that there was a longer history of persistence underlying these distribution patterns. Consistent with this longer history of dry conditions is the finding of Cactaceae pollen dating to 13,000 years

ago near Sequim, indicating that the local prickly pear cactus has existed on the northeastern peninsula since shortly after deglaciation (Petersen et al. 1983).

Nine endemic taxa are associated with stream and shaded sites on the southwestern Olympics. The Olympic mudminnow occurs on the southern peninsula, possibly colonized from a Chehalis River refugium after deglaciation (McPhail 1967), in combination with refugia along the western coast (DeHaan et al. 2013). In contrast, genetics of disjunct populations of mudminnows in eastern Puget Sound (not mapped in Fig. 2.3) suggests these are recent introductions from the southern Olympic Peninsula rather than the result of vicariance by the Puget Lobe of the Cordilleran Ice Sheet (DeHaan et al. 2013). Other shade and stream-associated taxa include little-studied arthropods with strong associations with perennial streams, such as riffle beetles (Barr 2011), harvestmen (Richart and Hedin 2013), and millipedes (Shear and Leonard 2003).

Given the rate of discovery, there are likely many more endemic lineages that suggest persistence through glacial cycles. Arthropod diversity, for example, is little described (e.g., Winchester and Ring 1999). Two frog species also show endemic clades. The Cascade frog (*Rana cascadae*) of the Olympic Peninsula, though not an endemic species to the peninsula, contains a distinct mtDNA lineage that suggests isolation through glacial periods (Monsen and Blouin 2003). The tailed frog (*Ascaphus truei*) also contains a distinct Olympic clade (Nielson et al. 2001), and is associated with similar habitats as the endemic Olympic torrent salamander (*Rhyacotriton olympicus*; Adams and Bury 2002). Similarly, Van Dyke's salamander (*Plethodon vandykei*) and Cope's giant salamander (*Dicamptodon copei*) feature co-distributed disjunctions in western Washington with unique Olympic clades, though details of the phylogeographic patterns suggest different dispersal histories of each taxon (Steele and Storfer 2007). Though discoveries continue, the current list of endemic taxa that both have a low capacity for dispersal (vagility) and that are associated with the moist lowland habitat suggests that this habitat type, namely the perennial streams and forest understory habitat, has existed through at least one glacial cycle on the peninsula, or at least nearby in southwest Washington.

Another set of peninsula taxa are disjunct by long distances (hundreds of kilometers) from the remainder of their population, or for endemics, to their sister taxon, thus also supporting the existence of a Pleistocene refugium. This list of species is long and difficult to compile, but generally falls into two groups. One group is a pattern of distribution on the peninsula and in the boreal and tundra biomes of the Yukon and Alaska. The ranges of these species likely split during the Pleistocene glaciations, with the Olympic Peninsula constituting an important southern refugium. An example of this pattern is the long-stalked whitlow grass. The second pattern is a distribution on the peninsula that is disjunct from an interior Rocky Mountain distribution and absent from the Cascade Range. Examples of this pattern are the least-bladdery milkvetch (*Astragalus microcystis*) and western sweetvetch (*Hedysarum occidentale*; Houston et al. 1994). Taxa that have low vagility and strong habitat associations with wet forest habitat often have a sister species occurring in similar wet forests of northern Idaho. This disjunct pattern is common between the Olympic

Peninsula and North Idaho, being found for riffle beetles, salamanders, harvestmen, and several other taxa (Table 2.1 and reviewed in Gavin 2009).

The isolation of the Olympic Peninsula has resulted in several species that have not naturally colonized the peninsula from the Cascade Range. Notable mammals and birds in this group include grizzly bear, wolverine, red fox (introduced in the twentieth century), coyote (now present), lynx, water vole, golden-mantled ground squirrel, northern bog lemming, porcupine (now entering the peninsula), pika, mountain sheep, mountain goat (introduced in the twentieth century), and the white-tailed ptarmigan. Absent trees include noble fir, ponderosa pine, subalpine larch, western larch, and western juniper (Houston et al. 1994). Other species may have become extinct in the Pleistocene, such as a trechine beetle discovered in the beach cliff at Kalaloch (Cong 1997).

In contrast to the insularity of the Olympic Peninsula, some biogeographic patterns reflect its limited connection to the archipelago of land bridge islands to the north (connected during lower sea levels). Buckingham et al. (1995) highlight several plant species that are endemic to the land bridge islands with their southern limit on the Olympic Peninsula, and thus suggest a northward expansion from an Olympic refugium. Six plant species are endemic to only the Olympic Peninsula and Vancouver Island, and dozens more spread further north along the coast. For well-dispersed species, north–south migration along the archipelago may have tracked climate change fairly closely. Marine taxa may have changed their distributions most readily. For example, a female walrus skeleton dating to ca. 70,000 years ago was found at Qualicum Beach on Vancouver Island, suggesting that during cold stadial periods of the late Pleistocene, the region was similar to the modern Bering Sea (Harington 2008).

A biogeographic pattern dubbed the "peninsula effect" is that species diversity is expected to decline from the base to the tip of a peninsula. For example, George Gaylord Simpson (1964) mapped North American mammal richness and found that major peninsulas contained markedly few species than areas of equal size in the interior. Though Simpson's coarse-resolution data could not resolve the Olympic Peninsula, this pattern would certainly be upheld on the peninsula at a finer resolution. A similar mapping of bird species richness by Cook (1969) invoked the peninsula effect that results from immigration and extinction dynamics (but like Simpson, Cook did not resolve patterns on the Olympic Peninsula). More recent work has shown that the peninsula effect rarely exists as a result of land geometry, especially for vagile species such as birds and winged insects, and richness gradients are mostly explained by habitat as controlled by physiographic factors (Wiggins 1999). This same explanation appears to largely hold for the set of Olympic endemic taxa (Fig. 2.4). The history of glaciation and continuation with coastal mountains to the north results in continuity of many species distributions off the tip of the Olympic Peninsula to the north.

In summary, the biogeographic distributions of several plant species and communities suggest the existence of glacial refugia in the north and northeastern Olympic Mountains (Houston et al. 1994). We note that both the alpine northeastern mountains and southwestern peninsula contained substantial unglaciated areas during the

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