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Vegetation stability and the habitat associations of the endemic taxa of the Olympic Peninsula, Washington, USA

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Abstract. Explanations for areas of endemism often involve relative climatic stability, or low climate velocity, over time scales ranging from the Pleistocene to the late Cenozoic. Given that many narrowly endemic taxa in forested landscapes display discrete habitat associations, habitat stability should be similarly important for endemic persistence. Furthermore, while past climate variability is exceedingly difficult to quantify on millennial time scales, past distributions of habitats may be robustly inferred from paleoecological records. The Olympic Peninsula, Washington, supports a biota with several insular features including 29 endemic plant and animal taxa. Here I present the geographic distribution and habitat of the endemic taxa, and then examine the vegetation stability of the past 14,300 years from five pollen records associated with discrete vegetation zones on the peninsula. I show that 11 endemics have distributions centered on dry alpine scree and rock in the northeastern quadrant of the peninsula, and nine occur in shaded riparian forests in the southwest. Vegetation turnover during the post-glacial period was smallest in these areas. However, another long pollen record from the western peninsula reveals existence of shrub tundra and greatly reduced forest cover, indicating southward displacement of shaded riparian habitats by perhaps as much as 100 km. Although this study supports an association of post-glacial vegetation stability with endemism, records spanning the glacial maximum indicate widespread tundra during long periods of the late Pleistocene and therefore suggest southern displacement of forest-associated endemics. While some of the alpine scree-associated endemics may have persisted *in situ*, many others likely arrived via a variety of dispersal trajectories. These histories include dispersal from southern refugia towards ocean barriers preventing further northward dispersal, contraction from more widespread distributions, and recent divergence from sister taxa. This study shows that paleoecological records can cast strong doubt on the inference that areas of endemism necessarily imply *in situ* glacial survival.

Keywords. Allochthonous endemism, pollen records, community rate of change, multidimensional scaling.

Introduction

Explanations for areas of endemism often invoke climatic stability over time scales ranging from the Pleistocene to the late Cenozoic. Mountainous areas frequently harbor areas of endemism possibly because such areas have a low climate velocity due to steep climatic gradients and strong topoclimatic effects, resulting in lower migration requirements on Quaternary (10,000–100,000 year) time scales (Sandel et al. 2011). However, quantifying climatic stability is fraught with a range of difficulties related to paleodistribution modeling including uncertainty in simulations of paleoclimates and statistical downscaling of those simulations to fine-scale topography (Gavin et al. 2014). Another approach to address historical explanations for modern endemism is to assess habitat stability from paleoecological records (Hájková et al. 2015). Pollen and other fossil assemblages can reveal past environments at resolutions finer than the biome, such as the particular vegetation types and habitats within which endemic taxa are concentrated. Thus, paleoecological records may be a first-order means of assessing the persistence of potentially suitable habitat over long time scales. For example, paleoecological studies conducted in areas assumed to be a glacial refugium can indicate whether environmental conditions were regionally suitable for such refugia (Holmgren et al. 2014).

In this study, I assess whether habitats that support narrowly distributed endemics were indeed stable on glacial time scales and then I address the implications of such stability, or lack thereof, on the origin of endemism. A recent origin of such habitats would imply either that the endemic taxa have recently dispersed into an area (i.e. allochthonous endemics) or that there has been recent niche evolution of particular functional traits. The traits that tie narrowly distributed endemics to particular habitats (characterized by attributes such as canopy openness, edaphic moisture, lithology, etc.) are likely conserved over Quaternary time scales (Wiens and Graham 2005), suggesting that dispersal rather than recent niche evolution is more likely. Therefore, examining paleoecological records with respect to the coarse habitat requirements of endemic taxa should test the assumption that regional-scale areas of endemism necessarily imply local persistence (i.e. refugia) over Quaternary time scales.

The Olympic Peninsula of northwest Washington State presents an excellent opportunity to address the endemism-stability association (Figure 1). The Olympic Peninsula lies adjacent to the maximum extent of the Cordilleran Ice Sheet, and therefore remained partially unglaciated through the late Quaternary. The peninsula is marked by several insular features including 29 taxa currently known to be endemic to the peninsula and areas immediately to the south (Houston et al. 1994, Gavin and Brubaker 2015). The endemic taxa include ten vascular plants, one amphibian, five mammals, one fish, 11 arthropods, and one mollusk (Table 1; Gavin and Brubaker 2015). This endemism, as well as other disjunctions, has led some to conclude that the Olympic Mountains served as a refugium close to the ice sheets, allowing rapid recolonization of the Puget Lowlands (Buckingham et al. 1995). This hypothesis has not been scrutinized in light of the palynological record. Several pollen records provide a coarse environmental context for this area of endemism. Specifically, five lake-sediment pollen records exist spanning the broad environmental gradient from high precipitation on windward mountain ranges, up to 2400 m above sea level, to the rain shadow in the northeast which receives less than 10% of the rainfall of the wettest locations (Figure 1c). Most lake basins in the region, including the five focal sites this study, were formed during deglaciation between 14.5 ka and 12 ka (thousands of years ago) and thus do not reveal vegetation during the severe climates of the late Pleistocene. Another long pollen record from the southwest extends to before the Last Glacial Maximum (LGM, spanning 24–19 ka) and provides evidence of lowland environments almost to the last interglacial or roughly 90,000 years ago (Heusser et al. 1999).

Recent distribution mapping of 608 occurrence observations of the endemic plants and animals revealed a general association with two of the six major potential natural vegetation zones (Gavin and Brubaker 2015). Specifically, endemic richness on a 4-km grid shows a major center of endemism of subalpine and alpine specialists in the northeastern peninsula and less distinct endemism associated with the large rivers of the western peninsula (Figure 1b). Published observations indicate at least qualitative habitat associations of the endemic taxa. Eleven taxa occur within the subalpine fir forests or higher elevations in the north or northeast; eight of these are species-level endemics while three are subspecies or varieties. These taxa are found mainly on scree slopes or rocky sites which are common in the dry subalpine and alpine zones (Rehn 1952, Buckingham et al. 1995). Another nine taxa are endemic to shaded riparian sites on the western peninsula; eight of these are species-level endemics. This endemism suggests stability of perennial streams and moist understory habitat in Sitka spruce (*Picea sitchensis*) forests (Gavin and Brubaker 2015).

In this study I compare rates of vegetation turnover, a proxy for habitat stability, between endemic-rich and endemic-poor habitats. I use five pollen records and I assume each record represents the vegetation dynamics in its potential natural vegetation zone. I predict greater stability through time in the endemic-rich areas compared to endemic-poor areas. I also predict that the vegetation change in the longer 90 ka record is much greater than any of the post-glacial records, with implications for interpreting the local persistence of endemism through the LGM.

Table 1. Endemic taxa of the Olympic Peninsula and their habitat associations. Several taxa with southern extents south of the peninsula are included and noted. The list does not include fish varieties endemic to recently formed lakes.

Species	Common name	Southern range limit	Reference
Subalpine and alpine scree and rocky sites, north and northeastern peninsula			
Astralagaus cottonii	Olympic Mountain milkvetch	47° 57'	Buckingham et al. (1995)
Campanula piperi	Piper's bellflower	47° 47'	Buckingham et al. (1995)
Erigeron flettii	Flett's fleabane	47° 31'	Buckingham et al. (1995)
Hesperia comma hulbirti	Hulbirt's skipper	47° 56'	Lindsey (1939)
Nebria danmanni	Mann's gazzelle beetle	47° 48'	Kavanaugh (1981)
Nisquallia olympica	Olympic grasshopper	47° 31'	Rehn (1952)
Oeneis chryxus valerata	Olympic arctic butterfly	47° 56'	Yake (2005)
Petrophytum hendersonii	Olympic rock mat	47° 24'	Buckingham et al. (1995)
Senecio neowebsteri	Olympic Mountain groundsel	47° 46'	Buckingham et al. (1995)
Synthyris pinnatifida var. *lanuginosa*	Olympic Mountain synthyris	47° 49'	Buckingham et al. (1995)
Viola flettii	Flett's violet	47° 31'	Buckingham et al. (1995)
Subalpine and parkland meadows and forest			
Marmota olympus	Olympic marmot	47° 42'	Edelman (2003)
Scapanus orarius (Olympic clade)	coast mole	46° 09'	Welch (2008)
Tamias amoenus caurinus	Olympic yellow-pine chipmunk	47° 56'	Sutton (1992), Demboski and Sullivan (2003)
Thomomys mazama melanops	Olympic Mazama pocket gopher	47° 58'	Verts and Carraway (2000)
Lowland to montane streams and riparian understory			
Acuclavella makah	Makah harvestman	47° 40'	Richart and Hedin (2013)
Bryelmis rivularis	riffle beetle	44° 28'	Barr (2011)
Hemphillia burringtoni	arionid jumping slug	46° 35'	Burke (2005)
Leonardesmus injucundus	millipede	46° 30'	Shelley and Shear (2006)
Microlympia echina	millipede	47° 49'	Shear and Leonard (2003)
Nebria acuta quileute	Quileute gazelle beetle	47° 59'	Kavanaugh (1979)
Novumbra hubbsi	Olympic mudminnow	46° 39'	McPhail (1967)
Rhyacotriton olympicus	Olympic torrent salamander	47° 10'	Adams and Bury (2002)
Tubaphe levii	Olympic peninsula millipede	47° 34'	Causey (1954)
Lowland to montane bogs and partial shade			
Corallorhiza maculata var. *ozettensis*	spotted coral root	48° 10'	Tisch (2001)
Erigeron peregrinus ssp. *peregrinus* var. *thompsonii*	Thompson's wandering fleabane	n.a. (SW peninsula)	Buckingham et al. (1995)
Erythronium quinaultense	Quinault fawn lily	47° 31'	Allen (2001)
Sand dunes and deflation plains			
Cicindela bellissima frechini	Pacific coast tiger beetle	48° 19'	Leffler (1979)
Throughout			
Mustela erminea olympica	Olympic ermine	47° 34'	Hall (1945)

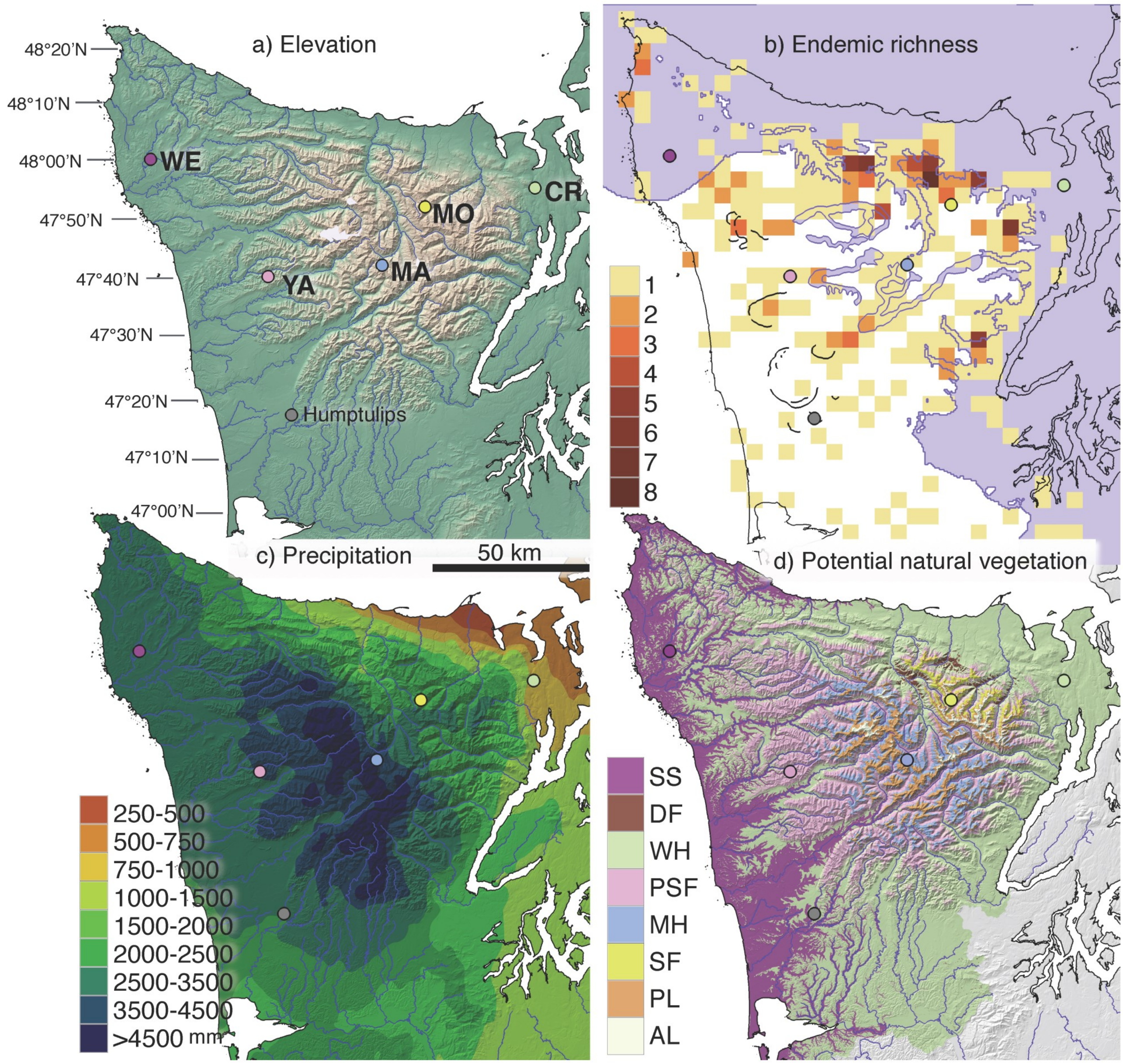


Figure 1. (a) Shaded relief elevation map of the Olympic Peninsula. Sites of pollen records are marked (Table 2). **(b)** Richness of the 29 Olympic Peninsula endemics mapped onto a 4-km grid. Modified from Gavin and Brubaker (2015). Blue shading and blue lines indicate the approximate maximum limits of Cordilleran ice (to the north and east) and valley glaciers (to the west) in the Lateglacial period (ca. 17 ka). Thick black lines indicate earlier Pleistocene moraines of valley glaciers. **(c)** Mean annual precipitation, 1970-1999 (Daly et al. 2002). **(d)** Potential natural vegetation zones based on the late-successional dominant species or vegetation formation (Henderson et al. 2011). SS = Sitka spruce; DF = Douglas-fir; WH = western hemlock; PSF = Pacific silver fir; MH = mountain hemlock; SF = subalpine fir; PL = parkland; AL = alpine.

Methods

The five pollen records used in this study (Table 2) were recently discussed in Gavin and Brubaker (2015). The five pollen records are associated with distinct forest zones: Wentworth Lake in the Sitka Spruce Zone on the west coast, Yahoo Lake in the Pacific Silver Fir (*Abies amabilis*) Zone at middle elevations mainly on the west side of the peninsula, Martins Lake in the Mountain Hemlock (*Tsuga mertensiana*) Zone in high-snowpack parkland settings, Moose Lake in the Subalpine Fir (*Abies lasiocarpa*) Zone in dry parkland settings, and Crocker Lake in the Western Hemlock (*Tsuga heterophylla*) Zone, dominating at lower elevations especially on the east side (Figure 1). I examined the rate of pollen turnover at these sites in three ways. First, I calculated palynological rate of change using the chord distance (i.e. Euclidean

Table 2. Pollen records from the Olympic Peninsula used in this study.

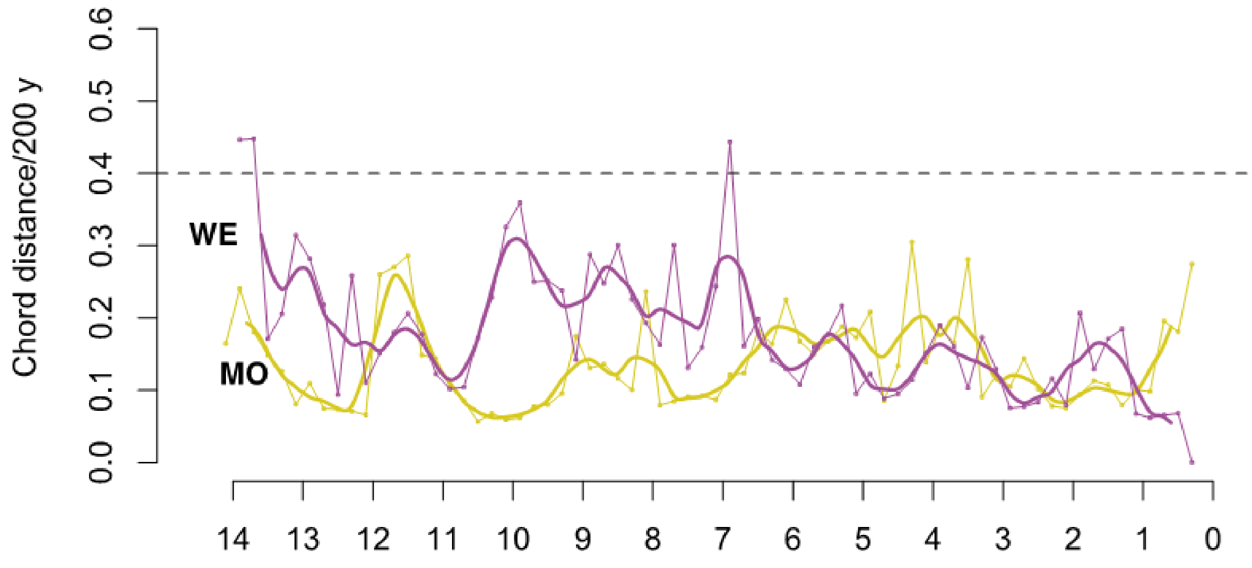
Site name	Vegetation zone	Location	Elevation (m)	Number of radiocarbon dates and tephras[1]	Core length (cm) and maximum age (ka)	Number of pollen samples and mean sample interval (years)	References
Wentworth Lake (WE)	Sitka Spruce	48° 01' N 124° 32' W	47	6	937 (13.9)	53 (260)	Gavin and Brubaker (2015)
Yahoo Lake (YA)	Pacific Silver Fir	47° 41' N 124° 01' W	717	6	430 (14.6)	50 (285)	Gavin et al. (2013)
Martins Lake (MA)	Mountain Hemlock	47° 43' N 123° 32' W	1423	3 (1)	277 (13.0)	47 (280)	Gavin et al. (2001)
Moose Lake (MO)	Subalpine Fir	47° 53' N 123° 21' W	1544	3 (1)	708 (14.2)	42 (347)	Gavin et al. (2001)
Crocker Lake (CR)	Western Hemlock	47° 56' N 122° 53' W	54	4 (1)	1181 (12.3)	49 (255)	McLachlan and Brubaker (1995)
Humptulips (H1)	Sitka Spruce	47° 17' N 123° 55' W	120	8	770 (ca. 90)	155 (–)	Heusser et al. (1999)

1. Does not include rejected dates. Parentheses show the number of additional pollen-stratigraphic ages assigned based on the regional pine decline.

distance applied to square-root transformed pollen proportion data) between consecutive samples after interpolating the pollen data to 200-year intervals (close to the mean sample interval). The chord distance is the square root of the commonly used squared-chord-distance applied to pollen data, but is linearly correlated with the Bray distance (r = 0.96). The rates of change were calculated from the 29 pollen and spore types that occurred in at least two samples at three of the five sites. Second, trajectories of palynological change were visualized using non-metric multidimensional scaling (NMDS) applied to pollen assemblages interpolated to 100 years for the common period of 12.3–0.5 ka. Combining data from the five sites in a single ordination reveals the relative trajectories of change and the overall compositional turnover within sites. While ordinations are normally based upon modern vegetation gradients, this approach does not constrain the ordination space to modern vegetation gradients. Interpolating pollen data to 100 years shows more details in the trajectories than would a coarser interpolation. NMDS was performed with the chord distance applied to the same 29 pollen types using the metaMDS function in the `vegan` package for `R` (Faith et al. 1987, Oksanen et al. 2015). Third, I used modern analog analysis to examine whether vegetation zones shifted elevationally through time and to identify periods of no-analog pollen assemblages. Modern pollen assemblages were from surface sediments of a set of 67 lakes across the peninsula (Gavin et al. 2005). Analogs were computed using the chord distance applied to ten pollen types (nine arboreal and the sum of herbaceous pollen). Chord distances from fossil to modern assemblages were interpreted using thresholds specific to each vegetation zone, as determined by within-zone versus between-zone distances (Gavin et al. 2005). These thresholds were 0.56 for Sitka Spruce, 0.40 for Pacific Silver Fir, 0.37 for Mountain Hemlock, 0.50 for Subalpine Fir, and 0.44 for Western Hemlock.

I tested for significant differences of the rate of change (i.e. serial dissimilarity) and the overall compositional turnover (i.e. all pairwise comparisons) between sites. To focus on the highest rates of change among sites, I used a nonparametric test that compared the 90th percentiles of the distributions of rate-of-change values or overall compositional turnover. This bootstrap test was run using the Harrell-Davis quantile estimator with 2000 simulations (`qcomhd` function in the `WRS` package for `R`; Wilcox et al. 2014).

a) Endemic-rich sites



b) Endemic-poor sites

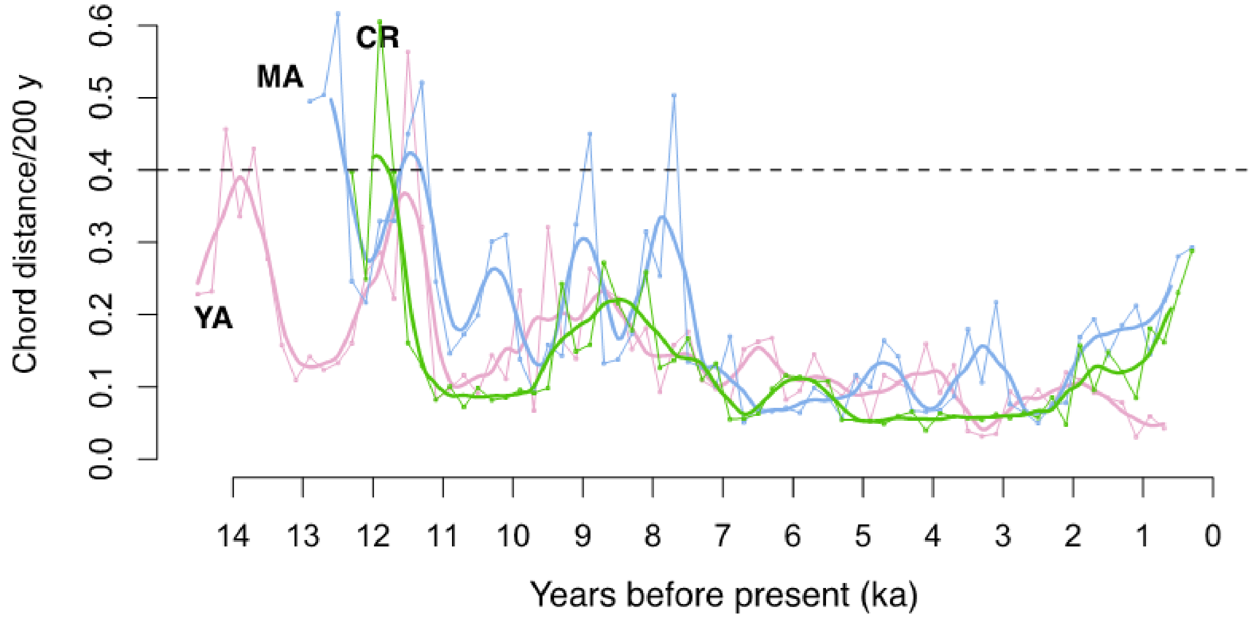


Figure 2. Palynological rate of change at two sites within **(a)** endemic-rich vegetation zones (Wentworth and Moose) and **(b)** three endemic-poor vegetation zones (Yahoo, Martins, and Crocker). Pollen assemblages were interpolated to 200-year intervals and the chord distance was calculated between assemblages across each time interval. The smoothed line is a LOESS fit in 500-year windows. Dashed lines show the general criterion for assessing vegetation analogs, suggesting that the endemic-poor sites were experiencing turnover at the scale of coarse vegetation zones within 200-year intervals.

To examine vegetation turnover during the late Pleistocene, I applied modern analog analysis to a long pollen record from the Humptulips River area on the southwestern peninsula (Heusser et al. 1999). The chronology of this record is not constrained before the limit of radiocarbon dating (50 ka), but features fluctuating arboreal pollen abundances that suggest the core reaches the latter stages of the last interglacial (Heusser et al. 1999, Gavin and Brubaker 2015). Pollen data were obtained from digitizing the published pollen diagram.

Results

The rate of palynological change was generally greater in the Lateglacial and the early Holocene periods (Figure 2). At the endemic-rich sites, the rates of palynological change were high at 13 ka and 10–7 ka (Wentworth) or 12–11 ka (Moose). At the three endemic-poor sites, rates of change were synchronously high at 12–11 ka and 9–7.5 ka, after which they declined to low values until ca. 2 ka. For the period common to all five records (12.3–0.5 ka), the 90th percentile did not differ significantly among sites except for an indication that Moose might have a lower rate of palynological change than Martins ($P = 0.12$). If limited to the early Holocene (>7 ka), the 90th percentile at Wentworth was significantly lower than at Martins ($P = 0.01$) and Moose was lower than all other sites ($P < 0.05$ for each comparison) except for Crocker ($P = 0.08$). Results did not differ appreciably for other quantiles tested between 0.75 and 0.9.

The NMDS ordination revealed relative amounts of palynological change over the common period of 12.3–0.5 ka (Figure 3a). The convex hulls delimiting each site, summarizing the overall palynological turnover, showed that the endemic-rich sites (Wentworth and Moose) span, on average, only 36% of the area of the hulls at the non-endemic sites. Statistical tests of the 90th percentile of chord distances of all pairwise within-site comparisons showed that Martins had significantly greater, and Moose had significantly lower, values than all other sites ($P < 0.01$).

The NMDS ordination also revealed distinctly different palynological trajectories through time among the sites (Figure 3b). Species scores in the ordination space revealed that axis 1 reflects changing moisture levels, with disturbance-adapted dry-site taxa at low values and shade-tolerant moist-site taxa at high values. Axis 2 is reflecting changing mean temperature, from riparian and coastal tree taxa to high (cold) tree and meadow taxa. Most sites showed a trajectory towards warmer and drier taxa from 12–10 ka, then a trajectory towards wetter taxa up to ca. 7 ka, after which there was generally little change. Two

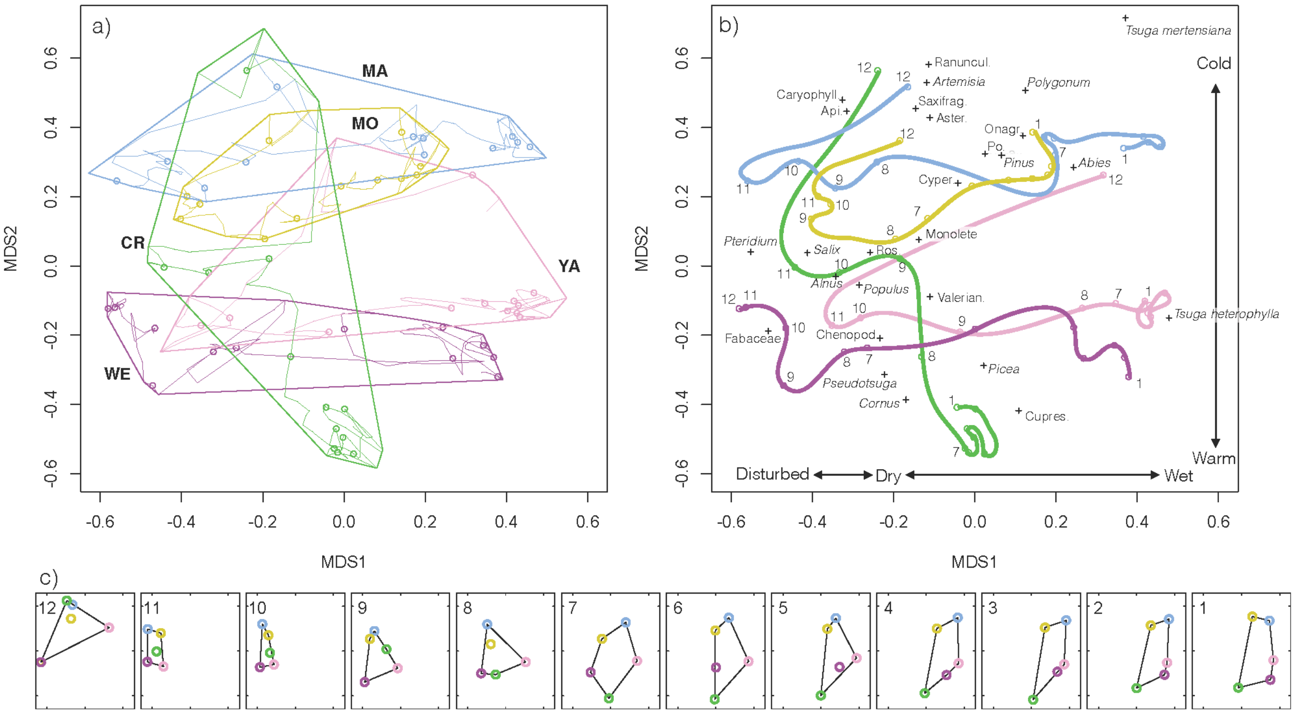


Figure 3. Non-metric multidimensional scaling (NMDS) applied to five pollen records simultaneously. Pollen assemblages at each site were interpolated to 100-year intervals within the common period of the five sites (12.3 to 0.5 ka). **(a)** Thin lines show the trajectories of palynological change (vertices are 100-year pollen samples) and the thick lines show the convex hull for each site. Circles show millennia (12 to 1 ka). **(b)** Simplified NMDS figure showing smoothed vegetation trajectories between labeled millennia samples. Species scores are shown by plus signs; the 'aceae' in family names are abbreviated. **(c)** Convex hulls of all five sites calculated in millennial time steps.

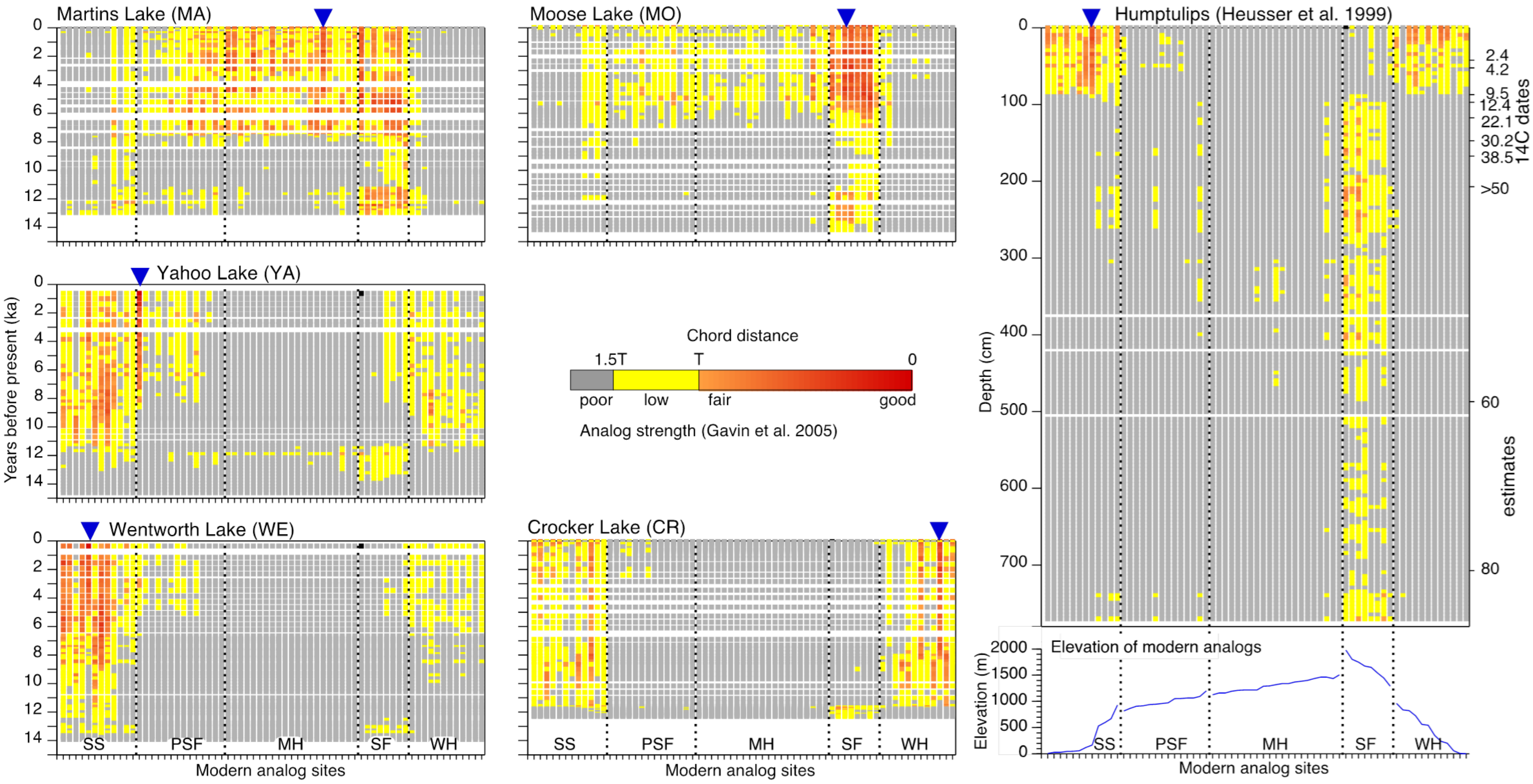


Figure 4. Modern analog analysis of six pollen records using a reference set of 67 modern pollen analogs collected from areas of undisturbed vegetation on the Olympic Peninsula. The modern pollen analogs are arrayed along the x-axis sorted by elevation within the vegetation zones (Figure 1d); dashed lines separate vegetation zones. Blue triangles indicate the columns corresponding to the sites of the pollen records, whose core-top samples are included in the modern analog set. Chord-distance thresholds (T) are specific for vegetation zone as described in the methods. Age estimates on the long Humptulips record are based on published radiocarbon dates (Heusser et al. 1999) and, below 250 cm, correlation with the northern Greenland isotope record (Gavin and Brubaker 2015).

exceptions to this pattern were Crocker (in the rain shadow) in which the major trajectory was towards warmer conditions and Wentworth (on the coast) in which there was only a minor early Holocene excursion toward warm/dry taxa. If plotted in time slices (Figure 3c), the ordination revealed similar composition of the dry-side sites at 12 ka, overall greater similarity through the early Holocene (10–9 ka), and differentiation and stabilization of the relative positions among the five sites by 6 ka.

The modern analog analysis generally confirmed patterns revealed in the NMDS ordination (Figure 4). For each site, strong modern analogs were identified within the same vegetation zone for at least the last 7000 years. During the early Holocene, the high-elevation sites (Martins and Moose) had no-analog pollen assemblages, lower-elevation sites (Wentworth and Crocker) had similar or somewhat higher-elevation analogs, and the mid-elevation site (Yahoo) had lower-elevation analogs. During the Lateglacial (>12 ka) all sites except Wentworth had some analog to the Subalpine Fir Zone.

The long pollen record from Humptulips revealed distinct analog and no-analog patterns (Figure 4). The Holocene period was contained in the top 80 cm of this core, and had strong analogs to sites in the low-elevation Sitka Spruce and Western Hemlock zones. The LGM and Lateglacial, limited to the next 30 cm of core, was likely marked by sedimentation hiatuses and the few pollen assemblages there have no analogs identified. Extensive periods earlier in the Pleistocene had analogs with the Subalpine Fir vegetation zone, while other periods before 60 ka were no-analog pollen assemblages. The no-analog pollen assemblages both during the LGM and earlier were marked by high grass pollen (>30%; not shown).

Discussion

Post-glacial and LGM environments in endemic-rich habitats

The pollen record representing the most endemic-rich vegetation zone (Moose Lake in the Subalpine Fir Zone) had lower palynological rates of change compared to other pollen records. This was true especially for the time of rapid vegetation change at the Younger Dryas to Holocene transition at 11.6 ka. At Moose Lake, subalpine fir was consistently present in the sediment record suggesting the climate was cold and continental since the Lateglacial (Gavin et al. 2001). Moose Lake also had the least amount of overall palynological turnover during the last 12,000 years. Similarly, the pollen record representing the other endemic-rich vegetation zone (Wentworth Lake in the Sitka Spruce Zone) consistently supported Sitka spruce suggesting moderated cool maritime climate since the Lateglacial (Gavin and Brubaker 2015).

The two endemic-rich vegetation zones occur at the extremes of the environmental gradient on the Olympic Peninsula: the highly moderated Pacific coast and the dry rainshadow parkland and alpine environments of the northeastern mountain ranges. The relative stability of post-glacial vegetation in these zones may be explained by how maritime and topographic effects operated on millennial time scales and with respect to the climatic niche of the dominant tree species. Along the coast, the climate was likely continuously maritime but with increasing available moisture through the Holocene. Wentworth Lake continuously supported Sitka spruce and other warm-adapted taxa yet never supported subalpine taxa (e.g. mountain hemlock) over the period of record. The ordination of pollen data shows a trajectory from disturbed and fairly dry to wetter conditions, but always at the warm end of axis 2 (Figure 3). This is plausible as onshore flow, which moderates summer temperature, may have acted to counter-balance the effect of increasing insolation in the early Holocene (Briles et al. 2008). In the northeast mountains, the conditions also remained cold and fairly dry and within the climatic niche of subalpine fir. Increasing moisture during the late Holocene had only moderate effect at Moose Lake, resulting in pollen assemblages at 1 ka not substantially different from those at 12 ka. At dry low-elevation Crocker Lake, the palynological trajectory is orthogonal to that at the coast (Wentworth Lake); this is likely the result of the rain shadow suppressing the increased moisture of the late Holocene, but temperatures warmed rapidly through the early Holocene (Figure 3b). Thus, moderated temperatures characterize the coastal climate while suppressed rainfall characterizes the interior northeastern climate. These two modes of moderation of climate may have been important over longer periods than only the last 14,000 years.

No endemic taxa have a strong association with upland old-growth forest habitats that historically dominated the western peninsula and which are well represented within the Olympic National Park. This is surprising given the great environmental complexity provided by old-growth western hemlock/Douglas-fir (*Pseudotsuga menziesii*) forest. Old growth trees in this area reach ages over 500 years, heights from 60 to 75 m, and diameters of 2 m. In the context of the paleoecological record, however, this lack of endemism makes sense. High pollen percentages of shade-tolerant western hemlock and western redcedar (*Thuja plicata*) did not occur until ca. 6500 years ago; prior to that time the early Holocene supported frequent fire and high abundances of alder (*Alnus*) pollen and bracken fern (*Pteridium*) spores (Brubaker 1991). Old growth forest, as a widespread forest type, dates to only the mid Holocene (Hebda and Whitlock 1997). Fire refugia likely existed in the most topographically protected locations such as riparian gallery forests, and this habitat is indeed the one harboring modern endemics. One caveat to the claim of low upland-forest endemism is that canopy arthropods in coastal temperate rainforests, such as on the Olympic Peninsula, remain little explored.

The vegetation stability described above may have been essential for continuously providing suitable habitat for the endemic taxa during the post-glacial period. However, lake basins that are suitable for high quality vegetation records normally do not span the LGM, as such basins were formed by glacial recession. Fortunately, older sites do exist on the western coastal plain where early Pleistocene terminal moraines impounded bogs that contain sediments spanning the LGM. If we are to assume that at least some of the Olympic Peninsula endemics are autochthonous, resulting from *in situ* evolution, then consideration of ecosystem stability over time spans longer than the post-glacial period is required.

Endemism patterns in the context of LGM environments

Could the northeastern subalpine and alpine endemic taxa have persisted *in situ* through the LGM? Substantial ice-free areas occurred in the area. Cirque lakes in the northeast occur at an elevation of 1500–1700 m in south-facing valleys (close to most ridgelines) and 1300–1400 m in north-facing valleys. The Vashon lobe of the Cordilleran Ice Sheet reached a maximum elevation of 1000 m at 17 ka (Porter and Swanson 1998). These ice-free areas are steep and were affected by periglacial processes, and likely dominated by scree slopes. Indeed, nearly all of the endemic taxa restricted to the north and northeastern peninsula occur on scree or open rocky sites, with the exception of four mammals such as the Olympic marmot that depend on productive meadows and soils sufficiently deep for hibernacula. The talus and scree in the area today, however, do not have permafrost and likely differ in many respects from the LGM environments. The closest large glaciers occur in the central peninsula (the Mount Olympus massif) where few endemics occur. Furthermore, many Lateglacial pollen assemblages throughout the peninsula show analog conditions to the dry Subalpine Fir Zone, and the Humptulips pollen record also has Subalpine Fir Zone analogs before the LGM (Figure 4). Taken together, these facts are consistent with an allochthonous origin of the northeastern alpine endemics, likely with a wider past distribution that has contracted into the northeast and against the dispersal barrier of the lowland forests and the Strait of Juan de Fuca to the north. As glacial populations likely existed in the more moderated maritime climates, it is reasonable to assume that several taxa migrated northward only onto the peninsula and not concurrently up the Cascade Range, followed by extirpation on their trailing edge and resulting in endemism on the penin-

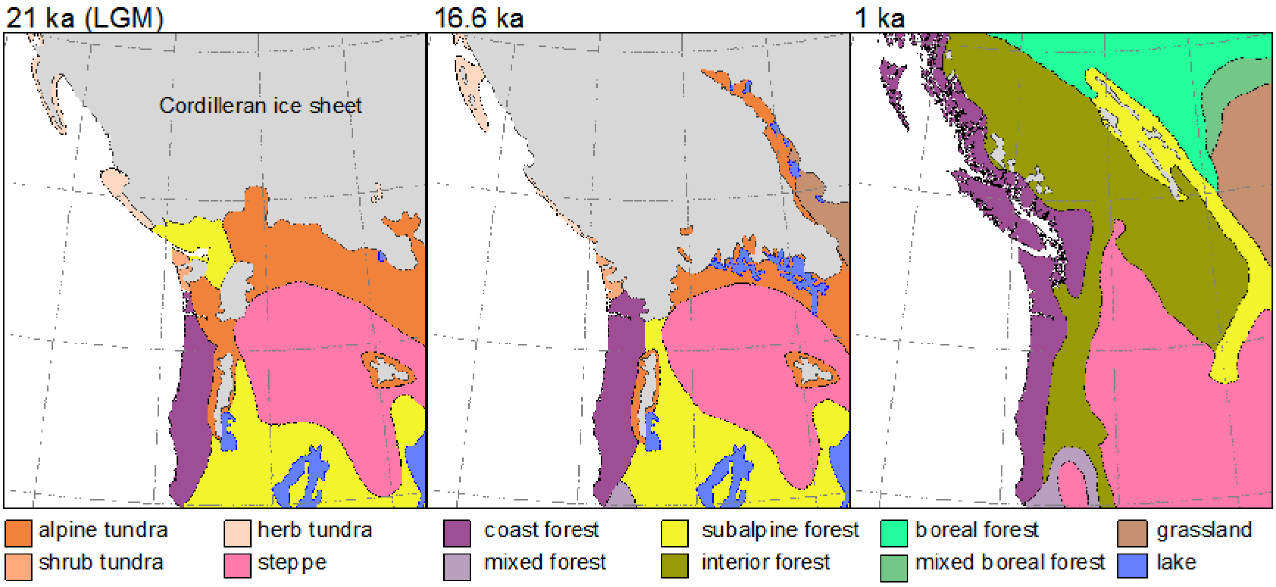


Figure 5. Biome and ice sheet reconstructions for the southern Cordilleran Ice Sheet region (Dyke 2005).

sula. A similar explanation has been proposed for endemism patterns on the Yucatan Peninsula with distributions driven by changing moisture through the Pleistocene (Lee 1980).

Could the southwestern lowland endemic taxa have persisted *in situ* through the LGM? This region includes a large coastal plain that would have been larger by hundreds of square kilometers during lower sea levels of the Late Pleistocene. The Humptulips bog pollen record clearly shows that the coastal vegetation was not stable through the LGM. Two main lines of evidence indicate that tundra predominated for long periods of time (millennia) on the western peninsula. First, in addition to Humptulips bog, several pollen records from moraine-dammed bogs on the western peninsula that span the LGM show high herbaceous and grass pollen and only brief periods of mountain hemlock forest (Heusser 1977, 1978). Hiatuses in sedimentation during the LGM until about 15 ka suggest conditions were too dry and cold for organic matter to accumulate in the bogs (Gavin and Brubaker 2015). These results are reflected in regional biome reconstructions that show shrub tundra predominating on the western Olympic Peninsula at both 21 ka and 16.6 ka (Figure 5; Dyke 2005). Second, global climate model simulations for 21 ka are consistent with a maritime tundra climate; modern climate analogs to these simulations are found on the Aleutian Islands of Alaska (Gavin and Brubaker 2015).

Long periods of tundra vegetation would create very challenging conditions for the lowland endemics. Taxa that rely on shaded riparian environments, such as the Olympic mudminnow (*Novumbra hubbsi*), likely could not survive a tundra environment. It is more reasonable to suspect these taxa were restricted to the closest forested settings. The nearest pollen records that suggest continuous forested conditions through the LGM occur in the southwest Washington foothills, 100 km or more to the south (Grigg and Whitlock 2002, Jiménez-Moreno et al. 2010). While pollen records cannot rule out the existence of forest "microrefugia" within a treeless landscape, the Humptulips bog site and other LGM-age sites (e.g. Heusser 1978) occur at fairly low elevation and close to large rivers; such sites are most likely to be the warmest and wettest through a cold-dry glacial maximum. Some taxa not strictly endemic to the western lowlands of the Olympic Peninsula have ranges extending to northwest Oregon (e.g., *Bryelmis rivularis*) that may be the result of northward expansion from a more southern coastal refugium. In addition, lower sea level during the LGM period resulted in a broader extent of coastal lowlands by 20–40 km in southwest Washington and northwest Oregon.

The above interpretation of periglacial landscapes stands in contrast to inferences from some genetic analyses. For example, though not an endemic to the peninsula, seaside juniper (*Juniperus *maritima*) has a distribution and genetic structure suggestive of a northeastern Olympic Peninsula refugium; extant populations there are ancestral to populations beyond the peninsula (Adams et al. 2010). Similarly, many amphibian species have distinct Olympic Peninsula clades, and while coalescent times are poorly constrained many are believed to date to older than the LGM (Monsen and Blouin 2003). However, using such genetic data, it is often difficult to discern between a spatially dynamic refugium that migrated latitudinally (with extinction at the trailing edge) versus a static *in situ* refugium (Graham et al. 2010). For example, another detailed comparative phylogeographic study of two salamander species with coastal (including the Olympic Peninsula) clades revealed long-term isolation between the Cascade Range and the coastal (Olympic) range, but persisting populations near the Columbia River appear to be the source for northward dispersal onto the peninsula (Steele and Storfer 2007). Such an inference would not have been possible had there been extinction of the trailing edge during the northward dispersal.

Conclusions

Several authors have posited that the endemism of the Olympic Peninsula provides strong support for it functioning as a refugium during the LGM and longer (Houston et al. 1994, Buckingham et al. 1995, Adams et al. 2010). These arguments are based upon co-occurrence of lineages and very rarely invoke paleoecological information to support claims of refugia. This study aims to show how pollen records can provide coarse information on the persistence of habitats that are strongly associated with modern endemism. While there is support for an endemism-stability relationship on the Olympic Peninsula inferred from post-glacial pollen records, longer pollen records indicate extensive tundra and therefore periglacial conditions during the coldest periods of the late Pleistocene. This places significant doubt on the existence of an Olympic Mountain refugium that supported all 29 known endemics prior to 14,500 years ago. Rather, a range of alternate explanations and incongruent biogeographic histories may be invoked to best fit the available data. For taxa recently diverged from their sister groups (e.g., the five mammals), post-glacial colonization and divergence may be supported once coalescent phylogeographic studies are undertaken. Lowland taxa of the western Olympic Mountains may have found refugia in coastal areas to the south where forest persisted. Of the endemics adapted to scree slopes of the northeastern Olympic Mountains, some may have persisted *in situ* while others may have had a larger geographic distribution for most of the Pleistocene but are now relict in a much smaller interglacial refugium. Additional fossil records will be essential to inform on these alternate histories. In summary, this study has shown that the supposition that areas of modest levels of endemism necessarily imply *in situ* glacial persistence can fall apart once fossil records and paleoenvironmental interpretations are invoked.

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