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Response

I thank these authors (Buma et al., 2014), for their interest in my paper. The topic of postglacial tree migration has always been a controversial one, so it is not surprising that my review of the evidence for the postglacial establishment of Pacific Northwest forest species in southern Alaska would generate some additional controversy. Burma et al. are perfectly correct in their statement that I did not consider localized refugia for these tree species within southeast Alaska during the LGM. However, I take exception to their statement that I did not consider the ecology of these trees in my reconstruction of regional events during the last glacial maximum (LGM). On the contrary, a consideration of the ecological requirements of these PNW tree species is precisely the reason I excluded the possibility of their survival in southeast Alaska during the height of the last glaciation, as explained below.

I was aware of the work of my colleagues, Paul Carrara and Tom Ager (USGS, Denver) in southeast Alaska, and I have no argument with their conclusions about the likelihood of ice-free regions on some of the islands of the Alexander Archipelago and adjacent continental shelf regions. I should have stated this in my article. I also heartily agree with their statement (Carrara et al., 2007), 'Exposed, unglaciated land does not necessarily equate to viable populations of flora and fauna.' Having made that statement, they immediately go on to defend the idea that unglaciated patches of southeastern Alaska *did* provide suitable habitats for the regional biota. This concept is at the heart of Buma et al.'s argument. However, even if parts of the Alexander Archipelago remained ice-free during the last glaciation, would these periglacial regions have provided suitable habitat for PNW trees? Since we have no suitable proxy evidence from these hypothesized refugia, how can we tell what the conditions were like there during the LGM: the climatic bottleneck through which all high latitude biota had to pass, if they survived *in situ* in refugia?

Carrara et al. (2007) carried out an extensive survey of the Quaternary geology of the Alexander Archipelago, searching for regions that were ice-free during the LGM. While they did find a lack of evidence for glaciation on parts of six islands and adjacent continental shelf regions, they apparently also failed to find even a single pond, lake or bog with a basal age predating the end of the last glaciation in southeast Alaska. I would gladly accept the authors' hypothesis about the existence of a glacial refugium for PNW forest in southeast Alaska, if the following conditions were met: (1) If one or more sedimentary archives (pond, lake or bog) are found in the potential refugial regions that have undisturbed basal sediments yielding a ^{14}C age greater than 13,000 ^{14}C yr BP; (2) if those glacial-age sediments were found to yield pollen and plant macrofossil remains of PNW forest species. If these two conditions were met, then we could say definitively that this region formed a glacial refugium for PNW tree species. Unless and until such reliably dated fossil tree evidence is found, the hypothesis that parts of southeast Alaska formed a refuge for PNW trees will remain speculation.

Having said that, there is some fossil evidence for the presence of some kind of biotic refugium in southeast Alaska, at least towards the end of the last glaciation. For instance, a brown bear skeleton dated 11,630 ± 120 ^{14}C yr BP was found on the west side of Coronation Island (Heaton and Grady, 2003). Its presence on the island has been used by Carrara et al. (2007) as evidence of a nearby refugium. Similarly, brown bear remains from a cave on Prince of Wales Island, dated 12,295 ± 120 ^{14}C yr BP, have been used as evidence for a nearby refuge. It cannot be denied that these bear fossils present a very strong case for the presence of *some* nearby refuge, i.e., an unglaciated ecosystem that provided sufficient food to support these bears. The question remains, however, was this ecosystem PNW forest? Brown bears (*Ursus arctos*) are generalist feeders, and the species is found today in a wide range of habitats outside the PNW forest regions, including tundra regions (Eide et al., 1994).

The other line of evidence invoked by Buma et al. is based on modern populations of various vertebrate species in southeast Alaska, and speculations on their phylogenetic history. Phylogenetics can be a powerful tool in the development of our understanding of the origins of modern species, but inferences based solely on modern distributions must ultimately be confirmed by fossil data. The molecular evidence, while compelling, is not unequivocal. For instance, one of the sources quoted by Buma et al., Fleming and Cook (2002), concluded in their paper that the 'Island clade' of ermines, while the best candidate among mammals for a North Pacific coastal refugium, might well prove to have been part of a wider island clade that would have included islands southward on the Pacific coast (e.g., Haida Gwaii). They went on to say that such issues would not be resolved until sampling of genotypes across North American populations takes place. The most recent summary of the modern evidence for biotic refugia on the Alexander Archipelago is by Cook and MacDonald (2013). In this paper, the authors state that extant organisms may have persisted in glacial refugia on the outer continental shelf, '… *or they may have first colonized this region of the coast along a tidewater route*' (emphasis mine). In the absence of fossil data, it is impossible to say which of these two competing hypotheses (or some other alternative) is correct. They go on to say that the genetic evidence shows that a suite of periglacial species persisted in coastal refugia during the LGM, and then recolonized the outer islands in the early Holocene. I agree that ice-free regions along the western edge of the Alexander Archipelago may well have provided refuge to periglacial species. However, the cold, harsh conditions associated with periglacial landscapes are far from conducive to the establishment, growth and reproduction of PNW forest trees.

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Table 1
Climatic parameters associated with the modern ranges of Pacific Northwest tree species (data from Thompson et al., 2006).

Species	TMAX range (°C)	TMIN range (°C)	MAP range (mm/yr)
Sitka spruce	8–20	−15 to 3	900–5000
Western hemlock	7.5–19	−11 to 3	800–5000
Mountain hemlock	7.5–22	−13 to 3	700–6000
Shore pine	10.5–15	−8 to 3	1000–5000
Nootka cypress	10–14	−7 to 3	1500–6000

What degree of ice-proximal cooling affected any exposed land on the Alexander Archipelago during the LGM? A 30-year study of temperature and precipitation at an ice-proximal site adjacent to Wolverine Glacier, about 40 km northeast of Seward, Alaska, showed that summer air temperatures near the ice margin are about 4.5 °C cooler than those at Seward (adjusted for elevation by a lapse rate of 0.2 °C per 100 m), and mean January temperatures were 3 °C cooler (USGS, 2014). The modern mean July temperature (TMAX) in the Alexander Archipelago region (based on data from Port Alexander: NOAA, 2002) is about 13 °C. Modern mean January temperature (TMIN) is 1 °C. We have no paleoclimate reconstructions for the last glacial maximum interval in southeast Alaska, precisely because of the lack of fossil sites from this interval. Insect fossil evidence from interior Alaska (Elias, 2000) suggests that mean July temperatures were about 4 °C cooler than today at sites that were well away from the chilling effects of glacial ice, and mean January temperatures were about 8 °C cooler. Taken in combination, LGM temperatures in southeast Alaska were considerably cooler than modern, being depressed by a combination of cold LGM climates in the northern high latitudes and the influence of local climatic cooling due to proximity to glacial ice. As a crude estimate, then, we might infer that mean July temperatures on any unglaciated (but certainly ice-proximal) landscapes on the Alexander Archipelago were as much as 8.5 °C cooler than modern values, and mean January temperatures were about 11 °C cooler than today. Using this estimate of LGM regional cooling, we arrive at a mean July temperature of 4.5 °C and a mean January temperature of −10 °C. This summer temperature estimate is well below the known thermal tolerances of PNW forest tree species (Table 1). The six main PNW tree species of southeast Alaska all require TMAX values of at least 7.5 °C, and two of them require TMAX values of 10 °C or more (Thompson et al., 2006). The estimated TMIN value of −10 °C is too cold for both shore pine and Nootka cypress (Table 1).

In summary, I did not consider that PNW forest tree species persisted in southeast Alaska through the last glaciation for two main reasons: (1) There is no fossil evidence (i.e., pollen, plant macrofossils or stomata) for the presence of these trees during the last glaciation; (2) Our best estimates of LGM climatic conditions for ice-proximal sites in this region indicate that summer temperatures were simply too cold to support the growth and reproduction of these tree species. So until we have the fossil evidence to test Buma et al.'s assertions about an LGM refugium for PNW tree species in southeastern Alaska, this particular kind of refugium seems quite unlikely.

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