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Correspondence

Correspondence regarding "The problem of conifer species migration lag in the Pacific Northwest region since the last glaciation" by Elias, S.A., (2013), Quaternary Science Reviews 77, 55–69

The velocity of species dispersal post-last glacial maximum (LGM) is an interesting question from both paleo-historical and contemporary perspectives. The apparent time lag between a location's climate becoming suitable for a given species and that species' arrival at that location has important implications for our understanding of the relationship between climate variables such as temperature and moisture and the dispersal ability of plants. Our knowledge of species dispersal rates underlies assumptions required for the interpretation of pollen and sediment records, biogeochemical reconstructions, and other endemic species distributions.

From a contemporary perspective, our expectation of future species distributional shifts in response to a warming climate can be informed by historic range expansion since the LGM. Thus it is important to correctly estimate those dates and rates. Elias (2013) attempts to calculate tree species dispersal rates along the northwestern North American coast post-LGM. This area – the largest contiguous temperate rainforest ecosystem on the planet – was extensively glaciated during the LGM and is currently experiencing important transformations due to climate change. Elias concludes that tree species migration in this region, originating from the south, was rapid: 2–4 times the rate of similar species in eastern North America. Unfortunately, the Elias (2013) review and analysis does not consider localized refugia for those species, or their ecology, within southeast Alaska during the LGM; these considerations would likely change the conclusions. Evidence for local refugia comes from a variety of fields, and while the geographic extent and biological communities of these cryptic refugia are still under study, it is important to consider them when reconstructing historical migration rates.

1. Geologic and geographic evidence

The basis for conclusions of rapid migration is the assumption that there were no refugia available in coastal areas north of the Queen Charlotte Islands (also known as Haida Gwaii) during the last major glaciation (~26,000–13,000 years BP); "…this entire region was buried by the Cordilleran Ice Sheet during the last glaciation" (Elias, 2013). Recently, however, geologic and geographic studies have explored the possibility of non-glaciated areas in or near the Alexander Archipelago of southeast Alaska during the LGM. Numerous probable refugia have been identified based on geologic characteristics and mapped along the southeast Alaskan coast (north of Haida Gwaii) from Dixon Entrance in the south to Lituya Bay in the northern portion of the region (southern Alexander Archipelago map, Carrara et al., 2003; regionally summarized in Carrara et al., 2007). These postulated refugia occur not only on islands outside the extent of the ice sheet, but also on unglaciated ocean-facing slopes, nunataks (exposed peaks above the glaciers), and parts of the inner continental shelf exposed by the lowered sea level and glacial forebulges (Baichtal and Carlson, 2010). Geologic evidence of glaciation, such as glacial till and erratics, are likewise missing from large portions of the outer islands (Carrara et al., 2003), and freshwater diatoms and shell-bearing deposits indicate that the portions of the area were both non-glaciated and above sea level (Barron et al., 2009; Addison et al., 2010). This evidence indicates that local glacial distributions left large areas exposed even at the height of the LGM.

2. Genetic support

Exposed, un-glaciated land does not necessarily equate to viable populations of flora and fauna. However, molecular evidence from a variety of plant and animal subpopulations and endemic subspecies suggests that communities did persist through the LGM on refugia along the outer coast of the Alexander Archipelago, north of Haida Gwaii (Fleming and Cook, 2002; Shafer et al., 2010; Cook and MacDonald, 2013; Dawson et al., 2013). Fossil remains in cave formations in the southern portions of the archipelago also imply continuous habitation by various large terrestrial mammals before and after the LGM, as well as marine mammals and small terrestrial mammals during the LGM (Heaton and Grady, 2003). Thus there is evidence for glacial refugia from molecular and cave fauna data, although these materials and sites need to be explored further.

3. Tree populations: biogeography and biology

Tree population persistence in the Alexander Archipelago during the LGM has been less studied, but it would be inappropriate to completely discount that possibility given the strong evidence for exposed land and the molecular data indicating that animal populations also persisted in the region. The biogeography of two tree species also suggests post-glacial colonization from nearby coastal refugia. Subalpine fir (*Abies lasiocarpa*) has several disparate populations in the southern Alexander Archipelago which may be descendant from coastal populations (Harris, 1965; Carrara et al., 2007; see Worley and Jaques (1974) for alternate hypothesis). The discontinuous presence of yellow-cedar (*Callitropsis nootkatensis*)

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in the eastern portions of the Alexander Archipelago, which align geographically with the proposed coastal refugia (to the west; Carrara et al. (2007)), also supports this hypothesis if one assumes a slow rate of dispersal eastwards and a low reproductive capacity (Hennon et al., 2012). Unfortunately, much of the landscape that could provide pollen data and tree macrofossils to support/refute the coastal refugia hypothesis is now below sea level. Elias does cite palynological and fossil tree data in his biogeographical reconstructions, but there are a variety of studies that were not included in the review which suggest alternate conclusions. For example, a study on Pleasant Island, near Glacier Bay, found near contemporaneous establishment of lodgepole pine and mountain hemlock (*Tsuga mertensiana*) after glaciation, and concluded that there were likely nearby refugia (Hansen and Engstrom, 1996). Other authors' data were misinterpreted; Heusser's review (1985) is heavily cited by Elias throughout, but Heusser applied his dated chronology of vegetation history from Juneau to the undated records from Ketchikan (a distance south of ~400 km) for summary purposes. In another case, the fossil spruce stump from Copper River basin discussed by Ager (1989), and cited by Elias (2013) as support for the Sitka spruce timeline, is not actually Sitka spruce, but rather white spruce (*Picea glauca*), a boreal species (Ager, 1989).

Colonization of recently deglaciated terrain depends on precipitation, temperature, competition, and other factors, as outlined by Elias (2013). However, some of the environmental requirements are not as stringent as Elias assumes. For example, citing Chapin et al. (1994), Elias states that a lack of appropriate seedbeds essentially precludes Sitka spruce (*Picea sitchensis*) "from playing a pioneering role on the landscape." Yet Lawrence (1950), and several other studies in the region, recognized that spruce can establish in the open, within a decade of deglaciation, and work in Glacier Bay by Fastie (1995) and Chapin et al. (1994) documents spruce establishment without facilitation from other tree species. Sitka spruce is also a common pioneer on uplifted beaches in the area (Griffith, 1992; Motyka, 2003). Overall, it is unlikely that there is a particular successional sequence required for spruce establishment, a similar conclusion reached by others (e.g. Johnson and Miyanishi, 2008). Furthermore, in conditions not favorable to sexual reproduction and/or seedling establishment, many of these species (Sitka spruce, western hemlock (*Tsuga heterophylla*), mountain hemlock, western redcedar (*Thuja plicata*) and yellow-cedar; Burns and Honkala 1990) can maintain populations asexually via layering. Vegetative reproduction has two consequences: first, there is potential for these species to have maintained populations in marginal habitat in periglacial areas during the LGM if conditions for seedling establishment were not favorable, and second, there may be a genetic signal of those periods present in the phylogeography of current populations that could be examined to test this hypothesis. The location of potential refugia would explain some of the discordance between the pollen/macrofossil dating sites and the reconstructed range maps in Elias (2013), which show dates for pine and spruce which are more conducive to northern coastal refugia than dispersal from southern refugia. For example, in Fig. 5 of Elias (2013), the oldest spruce pollen records are from the Fairweather region north of the Alexander Archipelago, which was identified as a potential refugium by Carrara et al. (2007).

As in the molecular and fossil data, the evidence for forests in coastal refugia is not conclusive, but the strong indirect evidence means one cannot discount the possibility. Rather than only spreading north from British Columbia as assumed, tree species could actually be spreading east, and from more local sources. The likely presence of refugia undermines Elias's key conclusions, that the rate of spread of these species was surprisingly rapid (4× the rate of spruce dispersal in Eastern North America, for example). Given the refugia proposed by Carrara et al. (2007), dispersal rates were potentially slower, in line with estimates from other regions, explaining some of the incongruities in Elias' dispersal timing maps. It is also worth noting that the current distributional patterns of tree species – both to the north and the east – as well as the molecular evidence from faunal species, might represent the combination of migration from multiple refugia (Cook et al., 2006); these two potential refugia patterns (small areas in situ and larger areas further south) are not mutually exclusive, and may have played different roles for different species.

4. Conclusions

The possibility of glacial refugia on the coastal margins of the Alexander Archipelago must be considered in any rate-of-migration estimates, and the lack of consideration in Elias (2013) of the geologic, genetic, and full pollen record is unfortunate, as is the inaccurate understanding of the ecology. If refugia were indeed present, as the physical and biological evidence suggests, then dispersal rates for tree species were likely slower and other mechanisms may have played a role in limiting their dispersal success, such as tectonic instability or disturbance frequency (Sykes and Prentice, 1996; Johnstone and Chapin, 2003). Truly conclusive evidence (e.g. a tree macrofossil dated from the height of the LGM) has yet to be found, and fluctuations in sea level make investigations difficult. Genetic analysis of these species throughout their geographic range would provide important insights into their origins and migration pathways. But the potential for refugial populations cannot be discounted given the geologic evidence of available land and the genetic and archaeological suggestions of persistent floral and faunal populations. Previous work in the region has considered the possibility of coastal refugia in southeast Alaska in addition to southern refugia only (e.g. Harris, 1965; Peteet, 1991; Hansen and Engstrom, 1996; Carrara et al., 2007; Ager et al., 2010; Shafer et al., 2010; Hennon et al., 2012); as geologic and molecular evidence accumulates for this alternate hypothesis, it remains an important part of any discussion on species dispersal in the region. These considerations are important for at least two reasons. First, an overestimate of species dispersal rates hinders our understanding of the historical record, and could lead to incorrect conclusions about the environment at the time of the LGM. This is important both to reconstructions of regional climate and habitat for fauna inhabiting the coastal refugia. Second, this phenomenon of extremely slow (and in some cases ongoing) dispersal post-LGM is a valuable proxy for tree migration in the era of a warming climate – the same factors that have driven slow migration rates historically are likely to limit species around the world as they migrate to higher latitudes to maintain equilibrium with climate in the future. Therefore getting this issue "correct" is vital to informing our attempts to understand how other species will move in a warming climate (e.g. Nathan et al., 2011). This is not only important from an ecological perspective, but also for forest management programs aimed at climate adaptation that rely on understanding natural migration rates for their planning. Although there is no "smoking gun" as yet demonstrating the presence or lack of forests in glacial refugia along the southeast Alaskan coast (identified by Carrara et al., 2007), a large body of indirect evidence from geologic/geographic research, molecular data, and species biogeography strongly suggests this possibility. Further work is required to confirm or refute this hypothesis, which has important implications for both historical interpretation and the contemporary issue of climate change.

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References

Addison, J.A., Beget, J.E., Ager, T.A., Finney, B.P., 2010. Marine tephrochronology of the Mt. Edgecumbe volcanic field, Southeast Alaska, USA. Quat. Res. 73, 277–292.

Ager, T.A., Carrara, P.E., Smith, J.L., Anne, V., Johnson, J., 2010. Postglacial vegetation history of Mitkof Island, Alexander archipelago, southeastern Alaska. Quat. Res. 73, 259–268.

Ager, T.A., 1989. History of the late Pleistocene and Holocene vegetation in the Copper River basin, south-central Alaska. In: Carter, L.D., Hamilton, T.D., Galloway, J.P. (Eds.), Late Cenozoic History of the Interior Basins of Alaska and the Yukon, USGS Circular, vol. 1026, pp. 89–92.

Baichtal, J.F., Carlson, R.J., 2010. Development of a model to predict the location of Early-Holocene habitation sites along the western coast of Prince of Wales island and the outer islands, southeast Alaska. Curr. Res. Pleistocene 27, 64–66.

Barron, J., Bukry, D., Dean, W., Addison, J., Finney, B., 2009. Paleoceanography of the Gulf of Alaska during the past 15,000 years: results from diatoms, silicoflagellates, and geochemistry. Mar. Micropaleontol. 72, 176–195.

Burns, R.M., Honkala, B.H., 1990. Silvics of Forest Trees of the United States. In: Conifers. USFS Agricultural Handbook, vol. 1, p. 654.

Carrara, P.E., Ager, T.A., Baichtal, J.F., Van Sistine, D.P., 2003. Map of Glacial Limits and Possible Refugia in the Southern Alexander Archipelago, Alaska, During the Late Wisconsin Glaciation. U.S. Geological Survey Miscellaneous Field Studies Map MF-2424. U.S. Geological Survey, Denver, Colorado. Available at: http://pubs.usgs.gov/mf/2003/mf-2424/.

Carrara, P.E., Ager, T.A., Baichtal, J.F., 2007. Possible refugia in the Alexander Archipelago of southeastern Alaska during the late Wisconsin glaciation. Can. J. Earth Sci. 44, 229–244.

Chapin III, F.S., Walker, L.R., Fastie, C.L., Sharman, L.C., 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. Ecol. Monogr. 64, 149–175.

Cook, J.A., Dawson, N.G., MacDonald, S.O., 2006. Conservation of highly fragmented systems: the north temperate Alexander Archipelago. Biol. Conserv. 133, 1–15.

Cook, J.A., MacDonald, S.O., 2013. Island life: coming to grips with the insular nature of North Pacific Coastal Forests. In: Orians, G.H., Schoen, J.W. (Eds.), Conservation of North Pacific Coastal Forests. University of Washington Press, Seattle, pp. 19–42.

Dawson, N.G., Hope, A.G., Talbot, S.L., Cook, J.A., 2013. A multi-locus evaluation of ermine (Mustela erminea) across the Holarctic, testing hypotheses of Pleistocene diversification in response to climate change. J. Biogeogr.. http://dx.doi.org/10.1111/jbi.12221.

Elias, S.A., 2013. The problem of conifer species migration lag in the Pacific Northwest region since the last glaciation. Quat. Sci. Rev. 77, 55–69.

Fastie, C.L., 1995. Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. Ecology 76 (6), 1899–1916.

Fleming, M.A., Cook, J.A., 2002. Phylogeography of endemic ermine (*Mustela erminea*) in southeast Alaska. Mol. Ecol. 11, 795–808.

Griffith, R.S., 1992. Picea sitchensis. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/.

Hansen, B.C.S., Engstrom, D.R., 1996. Vegetation history of Pleasant Island, southeastern Alaska, since 13,000 yr. BP. Quat. Res. 46, 161–175.

Harris, A.S., 1965. Subalpine fir on Harris ridge near Hollis, Prince of Wales island, Alaska. Northwest Sci. 39 (4), 123–128.

Heaton, T.H., Grady, F., 2003. The Late Wisconsin Vertebrate history of Prince of Wales island, southeast Alaska. In: Schubert, B.W., Mead, J.I., Graham, R.W. (Eds.), Ice Age Cave Faunas of North America. Indiana University Press, pp. 17–53.

Hennon, P.E., D'Amore, D.V., Schaberg, P.G., Witter, D.T., Shanley, C.S., 2012. Shifting climate, altered niche, and a dynamic conservation strategy for yellow-cedar in the North Pacific coastal rainforest. BioScience 62, 147–158.

Heusser, C.J., 1985. Quaternary pollen records from the Pacific Northwest coast: Aleutians to the Oregon-California boundary. In: Bryant, V.M., Holloway, R.G. (Eds.), Pollen Records of Late-quaternary North American Sediments. American Association of Stratigraphic Palynologists Foundation, Austin, Texas, pp. 141–165.

Johnson, E.A., Miyanishi, K., 2008. Testing the assumptions of chronosequences in succession. Ecol. Lett. 11, 419–431.

Johnstone, J.F., Chapin, F.S., 2003. Non-equilibrium succession dynamics indicate continued northern migration of lodgepole pine. Glob. Change Biol. 9, 1401–1409.

Lawrence, D.B., 1950. Glacier fluctuation for six centuries in southeastern Alaska and its relation to solar activity. Geogr. Rev. 40 (2), 191–223.

Motyka, R.J., 2003. Little Ice Age subsidence and post Little Ice Age uplift at Juneau, Alaska, inferred from dendrochronology and geomorphology. Quat. Res. 59, 300–309.

Nathan, R., Horvitz, N., He, Y., Kuparinen, A., Schurr, F.M., Katul, G.G., 2011. Spread of North American wind-dispersed trees in future environments. Ecol. Lett. 14, 211–219.

Peteet, D.M., 1991. Postglacial migration history of lodgepole pine near Yakutat, Alaska. Can. J. Bot. 69, 786–796.

Shafer, A.B.A., Cullingham, C.I., Cote, S.D., Coltman, D.W., 2010. Of glaciers and refugia: a decade of study sheds new light on the phylogeography of northwestern North America. Mol. Ecol. 19, 4589–4621.

Sykes, M.T., Prentice, I.C., 1996. Climate change, tree species distributions and forest dynamics: a case study in the mixed conifer/northern hardwoods zone of northern Europe. Clim. Change 34, 161–177.

Worley, I.A., Jaques, D., 1974. Subalpine fir in coastal western North America. Northwest Sci. 47 (4), 265–273.

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