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Commentary

Causes of widespread foliar damage from the June 2021 Pacific Northwest Heat Dome: more heat than drought

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This scientific commentary refers to 'Conifer desiccation in the 2021 NW heatwave confirms the role of hydraulic damage' by Klein et al. (doi: 10.1093/treephys/tpac007).

Most of the Pacific Northwest (PNW, USA) and British Columbia experienced extraordinarily high air temperatures during an extreme heat wave event ('Heat Dome') in the late June of 2021 (Neal et al. 2022, Qian et al. 2022). In many locations, all-time record high air temperatures (T_{air}) exceeding 40–45 °C were observed during the Heat Dome. Within days of the event, widespread foliar damage was observed in many locations of this region along with some reports of tree mortality. As the frequency of coincident heat waves and drought has increased and is expected to continue to increase (Alizadeh et al. 2020), understanding the environmental drivers, biophysical and physiological mechanisms, and ecological consequences of heat damage incurred by forests is of broad relevance. Indeed, there is an increasing recognition that forest vulnerabilities to heat waves can lead to widespread growth reductions and even mortality (Breshears et al. 2021).

A recent paper (Klein et al. 2022) used this extraordinary event to link mechanisms of drought-induced plant mortality (hydraulic failure) to the observed foliar damage. Klein et al. related photographic observations of foliar damage from a variety of tree species and cultivars growing in a botanic garden near Seattle, WA, to hydraulic parameters from other studies of the same species. They found relationships between the degree of damage and literature-derived values of P50—the xylem pressure at which a 50% loss of conductivity occurs. Specifically, Klein et al. found no damage in species with a P50 value below −5 MPa, as well as age-related patterns, with younger trees experiencing more damage. Based on this evidence, Klein et al. concluded that drought-induced hydraulic damage was the mechanism responsible for the observed foliar damage. This analysis is compelling, and no doubt the hydraulic properties of trees played a role in forest impacts observed throughout the region. However, in what follows, we argue that framing this event as an opportunity to test drought sensitivity, with the foliar damage driven by dehydration and hydraulic failure, fails to consider the role of extreme heat as a primary mechanism of foliar damage.

While Klein et al. focus on the Heat Dome as a driver of drought and its impacts on plant hydraulic function, it was among the most extreme heat waves ever recorded globally and the most intense in the observational record for the PNW region (Thompson et al. 2022). There is a clear distinction in the climate and hydrometeorological literature between droughts and heat waves, and distinguishing vegetation impacts from each is important. Heat waves are not just associated with droughts, as is commonly assumed, but are increasing in frequency during both wet and dry conditions (Hao et al. 2013, Teskey et al. 2015). While hydraulic damage is a well-established mechanism underlying drought-induced plant mortality (Brodribb and Cochard 2009, Hammond et al. 2019, Sapes et al. 2019), the exceptional temperatures experienced by trees during the Heat Dome must be considered, as extreme heat can be lethal to leaf tissues even with short exposure times (Bigras 2000, Teskey et al. 2015, O'sullivan et al. 2017, Lancaster and Humphreys 2020). Extreme heat can also dramatically increase the plant water loss at branch (Billon et al. 2020), tree (Drake et al. 2018) and ecosystem scales (Krich et al. 2022). While in many areas of the PNW, the Heat Dome was superimposed atop varying levels of drought, ranging across categories classified by the US Drought Monitor from 'abnormally dry' to 'extreme' to 'exceptional drought', the area around the botanic garden where foliar browning was observed by Klein et al. was classified in the lowest category of drought ('abnormally dry') during the week before the Heat Dome occurred (Figure 1A, see magenta circle for garden location). For an event as wide-ranging as the Heat Dome, a broad-scale view reveals extensive areas of foliage scorch following the event. Aerial detection surveys documented > 90,000 ha of foliar damage following the Heat Dome, with the most extensive impacts in coastal Douglas-fir and western hemlock plantation forests of western Oregon and Washington that were experiencing only abnormally dry or moderate drought conditions at the time of the Heat Dome (Figure 1A and B). By contrast, many forests around the Willamette Valley and western slopes of the Cascades were experiencing severe to exceptional drought at the time of the Heat Dome (Figure 1A, brown, orange and red colors for drought severity) and experienced less foliar damage.

It is similarly unclear if the responses observed at the botanic garden were representative of the foliage damage recorded at many locations in the PNW. When the mechanism of conifer foliage browning is drought-induced hydraulic failure, the lag between the onset of hydraulic failure and visually apparent foliar browning has been observed to take several months (Blackman et al. 2019, Hammond et al. 2019) and not days as occurred following the Heat Dome. Furthermore, while Klein et al. refer to foliar damage as 'needle desiccation', in some sense presupposing the cause of damage, needles can discolor for many reasons. Given that Klein et al.'s study did not directly measure the hydraulic failure or needle water content of the plants under study, it cannot be concluded that needle desiccation (or dehydration) following hydraulic failure was the sole or even primary cause of foliar browning. Indeed, a conference that gathered researchers, foresters and stakeholders to share post-Heat Dome analyses included an observation that Christmas tree farms irrigated before and during the event also suffered from considerable scorch damage (https://www.forestry.oregonstate.edu/heat-dome). The widely observed damage (Figure 1) appears, in quality and timing, most similar to the fire scorching of foliage, and 'foliage scorch' is the term that was widely applied by foresters and botanists, throughout the PNW region, to the damage observed at many locations.

Notably, the observed scorch had distinctive spatial and temporal patterns that suggest heat was the primary driver of foliar damage. Across multiple landscapes with damaged foliage, aspect was frequently noted. Trees located on south- and west-facing slopes and on exposed edges near roadsides typically had the greatest foliar scorch, and opposite sides of the same trees, or same hillsides, exhibited little to no scorch (Figure 1C and D). In addition, we noted that trees in cooler coastal areas with later dates of budburst (Figure 2; Ford et al. 2016) tended to have greater scorch than trees in warmer and more inland and southern areas where earlier budburst would have resulted in foliage that had hardened off prior to the heat event. Klein et al. did not include any information on aspect, nor did they provide information on where their photographed trees occurred relative to sun and wind exposure, or how their damage estimates were determined, so it is difficult to discern the causes of foliar scorching at the botanic garden; however, we did note that foliage damage on two short plants shown in Klein et al. (Figure 3) appeared to be in close proximity to rocks or pavers, which may have increased the temperatures for low-lying foliage.

While the extreme heating of foliage during fire has been observed to impart rapid losses of stored water pools, sufficient to drive vascular systems to the point of hydraulic failure (Hoffmann et al. 2021), whether heatwaves in the fire's absence can similarly drive hydraulic failure remains unknown. While some hydraulic segmentation is possible in trees (Johnson et al. 2016), it is generally between varied tissues (leaves vs stems) and not between sunlit vs shaded foliage. Indeed, drought impacts on tree crowns typically form slowly across a season, are patchier across a given stand and usually affect the entire crown and not just sun-exposed foliage, and often become noticeable later in the growing season when the soil moisture is lower (Hinckley et al. 1978, Andrew et al. 2016). By contrast, the Heat Dome damage occurred rapidly (within days) following the event and was often uniform on exposed foliage (Figure 1C). Thus, an explanation beyond desiccation and the role of drought is necessary to explain the widespread observations of damaged foliage.

Together, the rapidity of foliar scorching (hours to days) and the prevalence of foliar scorching in sunlit foliage challenge the hypothesis that drought combined with hydraulic failure was a primary cause of foliar damage. The aspect effect noted above (and shown over broad landscape scales in Figure 1D) is telling, as this is consistent with heat damage when the midday and afternoon sun coincided with the highest air temperatures of the event. Similarly, forests near the coast experienced the greatest scorch (Figure 1B; note the concentration of scorch damage, shown in red). Coastal and near-coastal forests are typically

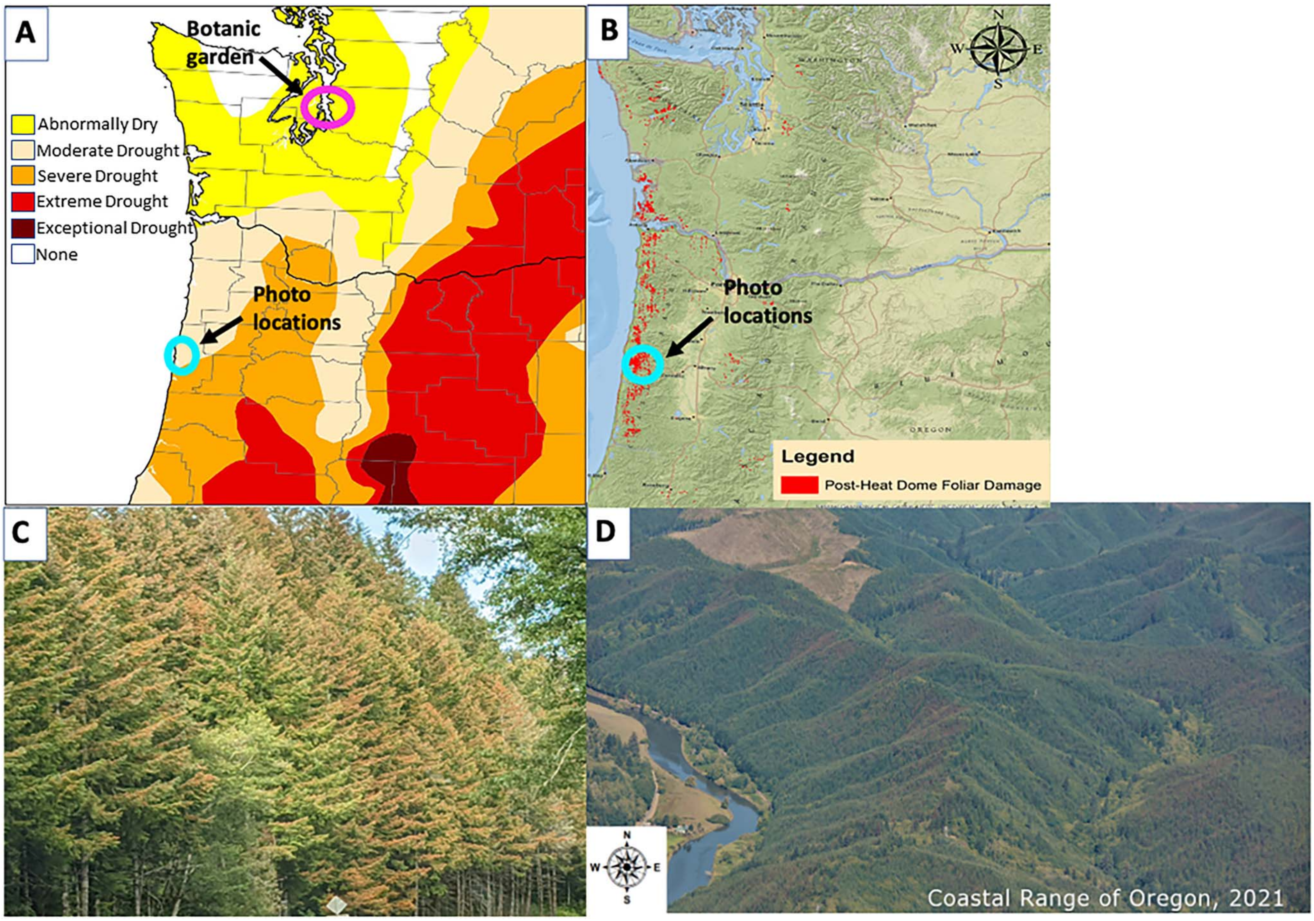

Figure 1. (A) Drought monitor map of the US PNW for 22 June 2021 and (B) polygons of post-Heat Dome foliar damage from US Forest Service aerial detection surveys collected between 26 July and 29 October 2021 in collaboration with the Oregon Department of Forestry and Washington Department of Natural Resources. Examples of Douglas-fir foliage scorch on south-facing coastal stands and west-facing hillsides are shown in panels (C) and (D), respectively; approximate photo locations are shown in cyan circles in panels (A) and (B). Photo credits: Adam Sibley and Daniel DePinte.

buffered from extreme temperatures and lag inland areas in phenological development due to marine layer cooling (Figure 2). This landscape-scale pattern also implies that anomalous heat—rather than drought and hydraulic failure alone—was the primary cause for foliar damage.

Anomalous heat impacts on foliage might be expected based on well-known leaf temperature (T_{leaf}) patterns (Jones 2013). Leaves frequently exceed air temperature (T_{air}), especially when leaves are in the sun, when they can be 5–15 °C hotter than air (e.g., Aubrecht et al. 2016, Still et al. 2019). High temperature and high irradiance in combination—as occurred during the Heat Dome—can be especially damaging to leaves (Berry and Bjorkman 1980, Bongi and Long 1987, Teskey et al. 2015). Notably, the 2021 PNW Heat Dome coincided with the longest photoperiod and greatest solar insolation of the year, driving sunlit T_{leaf} well above T_{air}. For example, at the H.J. Andrews Experimental Forest in Oregon, T_{air} measured at the long-term climate station (at standard height of 1.5 m) broke all-time records on the hottest day of 28 June 2021 (when peak T_{air} was ~44 °C). Microclimate measurements made in the upper crown (56 m aboveground) of a nearby old-growth Douglas-fir tree recorded a similar peak T_{air}; sunlit foliage temperatures measured with a thermal camera at that same height were as much as 12 °C above adjacent T_{air} (Figure 3). The duration of foliage temperatures $\geq$40 °C was at least 26 hours across the entire Heat Dome event, and likely longer than this, as the camera was not operating for most of the daylight h on 27 June. By comparison, shielded and aspirated air temperatures equaled or exceeded 40 °C for just over 11 h during the event, and an unshielded thermistor on a south-facing branch exceeded 40 °C for 14.5 h. The afternoon heat was likely amplified by stomatal closure in response to extremely high air vapor pressure deficits (VPDs), which reached values exceeding 8 kPa during the hottest conditions and around 10 kPa for leaf-specific VPD. Stomatal closure would reduce transpiration and its cooling benefits under extreme conditions (Birami et al. 2018, Drake et al. 2018, Still et al. 2019), particularly in tree species that typically close their stomata earlier in response

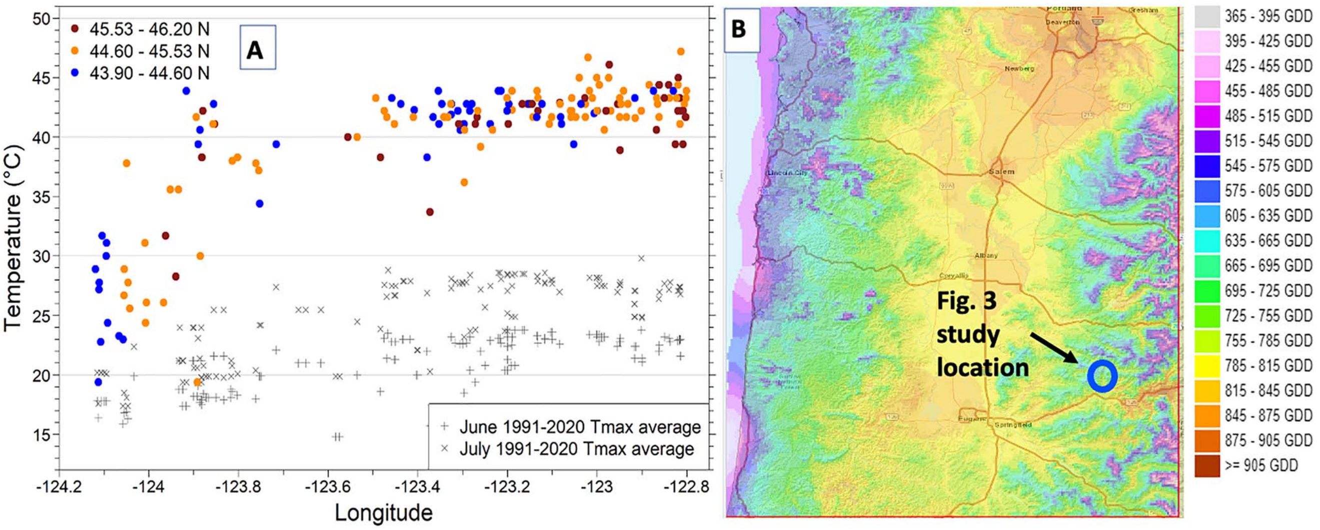

Figure 2. (A) Climatological T_{max} in June and July (plus and cross mark symbols) and T_{max} on 27 June 2022 (filled circles) shown as a function of latitude and longitude for weather stations in western Oregon. (B) Map of accumulated growing degree days in western Oregon above a 5 °C base temperature (GDD) between the approximate start of the growing season and the beginning of the heat dome (1 April–26 June 2021) with approximate location of study site in Figure 3 shown in dark blue circle.

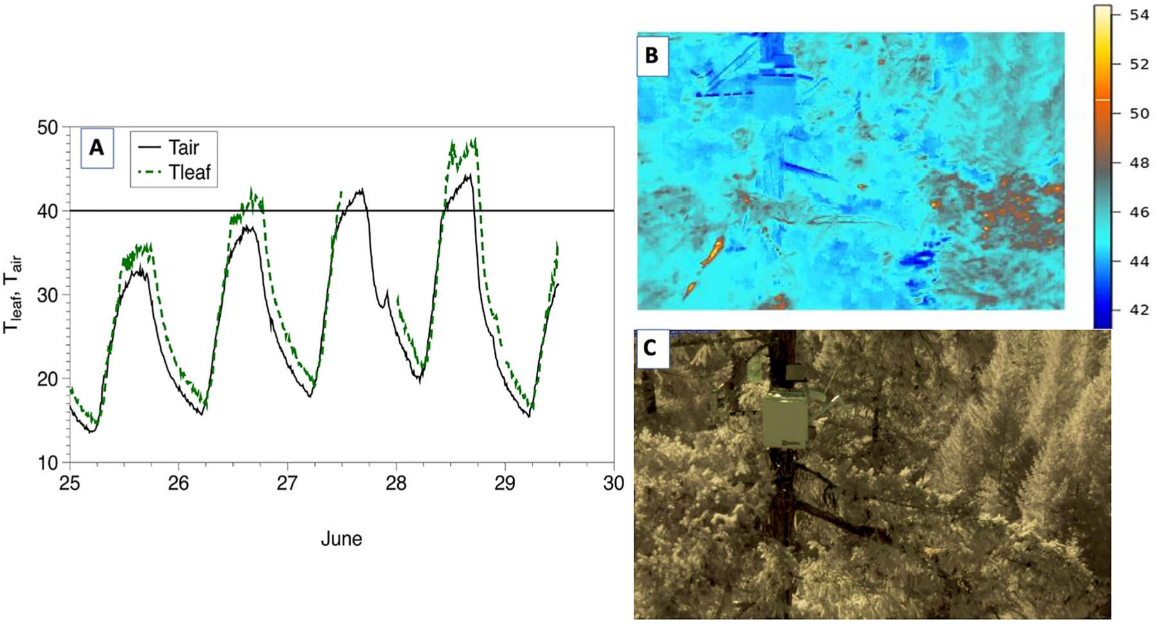

Figure 3. (A) Time series of leaf temperature data (dashed line) that were extracted from the thermal images of a foliage-dominated region of interest along with air temperature data from an aspirated temperature sensor in a radiation shield located at the same height (56 m aboveground) in the upper-canopy of a Douglas-fir tree at the HJ Andrews experimental Forest near Blue River, Oregon. Thermal images were taken by a FLIR SC220 thermal camera. (B) Example thermal image of the bole and foliage taken on the locally hottest day of the Heat Dome (collected at 12:30 PDT on 28 June 2022). (C) Visible image of same crown area taken at a different time to illustrate features seen in the thermal image.

to higher VPD, such as those with less negative P50 values. Such high absolute leaf temperatures are near or above known damaging and possibly lethal thresholds for leaf tissues of many species (Teskey et al. 2015, Marias et al. 2017, Lancaster and Humphreys 2020). The impacts of excessive heat on leaf structure and function are manifold and include damage to enzymatic activity, increased photooxidation, and loss of membrane stability (Hueve et al. 2011, Guha et al. 2018). Indeed, earlier experimental warming on two of the species exhibiting damage in Klein et al. (*Picea mariana* and *Picea glauca*) suggested that needle browning occurred relatively quickly (Colombo et al. 1992, Bigras 2000): a 30-min exposure to 48 °C produced 50% foliar damage in *P. glauca* compared with 100% foliar damage in *P. mariana* (Teskey et al. 2015).

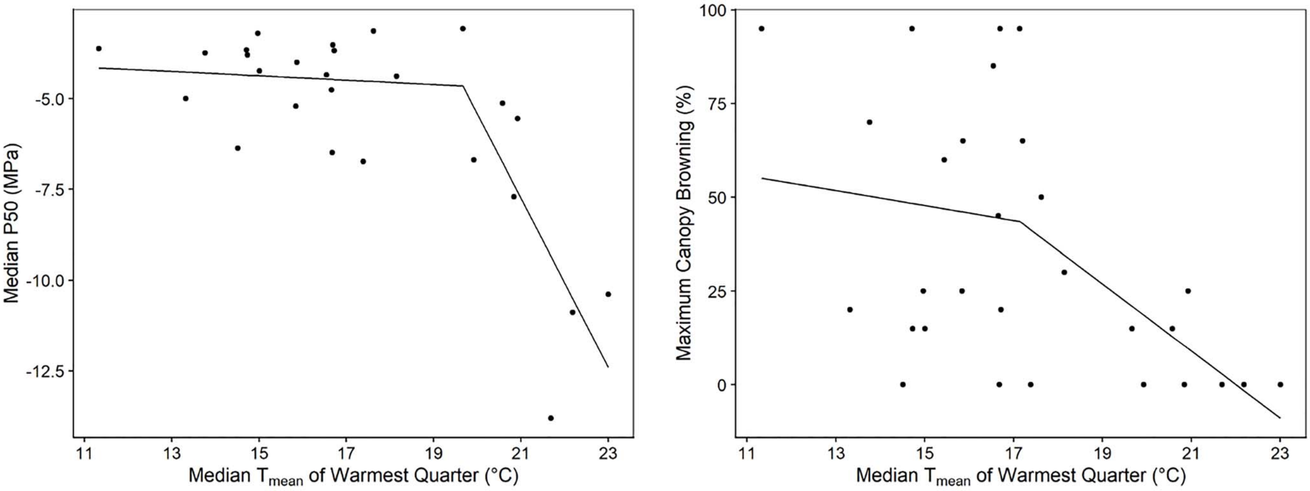

Figure 4. Relationships between species P50 (left panel) and maximum canopy browning % (right panel) from Klein et al. and median T_{air} of the warmest quarter from Bioclim for those same species in both cases fitted with segmented-regression models. Median P50 was calculated from all values provided for each species by Klein et al.; maximum canopy Browning (%) was determined by taking the maximum value of all observations for each species in the database of Klein et al.

Table 1. Mean elevation of occurrence for species from for available species with at least 50% of maximum canopy browning in the database of Klein et al. (2022). Elevation data were obtained from the WorldClim V2 database (Fick and Hijmans 2017) using species distribution data derived from GBIF occurrence data (derived dataset, GBIF.org, 13 May 2022).

Species	Mean elevation of occurrence (m)
Abies concolor	2075
Abies alba	2075
Abies lasiocarpa	1880
Abies veitchii	1638
Picea abies	274
Picea glauca	356
Picea orientalis	1417
Picea pungens	2085
Picea rubens	476
Pinus mugo	1197
Pinus strobiformis	2463

Finally, there are strong taxonomic and biogeographic patterns for the species with significant foliar damage reported in Klein et al. that hint at mechanisms of foliar damage (significant damage is taken here as ≥50% maximum canopy browning, as the browning patterns were variable within species). These patterns suggest that temperature deviations from the thermal niches of species were also important drivers of foliar damage. At a family level, no species in Cupressaceae were found in that study to have significant foliar damage, while all of the species with significant damage are in the Pinaceae family. These lineages are distinct in many ways and diverged at least 250 MYA (Leslie et al. 2012), so it is perhaps not surprising that foliar damage would be expressed differently within them. The primary genera in the Pinaceae family for which Klein et al. reported extensive damage were *Abies*, *Picea* and *Pinus*. Notably, 8 of the 11 conifer species with significant foliar damage in Klein et al.'s database occur naturally at mean elevations above 1000 m (Table 1). Species growing at higher elevations experience on average lower mean, maximum and minimum air temperatures. Several of the species with maximum canopy browning of at least 20% observed by Klein et al. occur in climates with a cooling marine layer influence. For example, the three species in Cupressaceae that Klein et al. reported as having experienced at least 20% maximum canopy browning (*Sequoia sempervirens*, 30%; *Thuja plicata*, 25%; and *Fitzroya cupressoides*, 20%) occur naturally only in the coastal and mountainous regions of North and South America. Of course, P50 values may be correlated with the temperature regime of species in their natural habitats. To examine the correlations among P50, canopy browning and species thermal niches, we compared Klein et al.'s canopy browning observations to the spatial bioclimatic data for each species native distribution using species occurrence data from the Global Biodiversity Information Facility (GBIF; http://www.gbif.org). Species with more negative P50 values were found to be distributed in warmer environments, with an apparent breakpoint just above a median T_{air} of the warmest quarter of 20 °C (Figure 4). Similarly, species from the warmest environments did not experience high percentages of canopy browning, whereas species from cooler environments exhibited a much larger range of canopy browning responses (Figure 4). Therefore, the correlation between P50 and canopy browning demonstrated by Klein et al. cannot be taken as a direct evidence of the role of hydraulic vulnerability to cavitation in the canopy scorch experienced in the Heat Dome event.

In conclusion, multiple lines of evidence imply that extreme heat stress was a primary driver of foliar damage, particularly under high solar irradiance. Heat damage best explains crown- and landscape-scale scorch patterns observed across the PNW, along with the swift browning of canopies, though it does not exclude associated hydraulic damage as a contributor to the foliage scorch and especially to the subsequent mortality observed in some trees. One of the most certain predictions of climate models is an increase in the frequency, duration and intensity of heat waves with climate warming. The likelihood that extreme heat led to widespread foliar scorch and other tree impacts, from this event, argues for a renewed emphasis on understanding heat tolerance and the underlying physiological and biophysical mechanisms leading to greater heat resilience in tree species. Novel avenues that should be pursued include exploring connections between hydraulic properties and thermotolerance, such as safety margins (O'sullivan et al. 2017), the importance of evolutionary lineages in structuring traits and environmental responses to heat (Anderegg et al. 2022), and whether forest canopies actually maintain canopy temperatures below damaging thresholds (Still et al. 2022).

Species occurrence and climate extraction methods

Species occurrence data were downloaded from the GBIF using the 'rgbif' package (Chamberlain and Boettiger 2017) in R version 4.0.1 (R Core Team 2020). Occurrence data were cleaned using the 'CoordinateCleaner' package (Zizka et al. 2019) and were filtered to retain only specimens collected after 1945 to ensure that coordinates were accurate. Occurrence data were additionally filtered by country code to remove points outside of their native distribution; for species present within the USA, data were additionally filtered using longitude. Derived data were uploaded to Zenodo and were registered with GBIF (Derived dataset GBIF.org 2022). Point data for each species were then converted to a presence/absence grid (0.5° spatial resolution) and were used to extract the climate data for each species' distribution. Gridded (0.5°) bioclimatic ('Bioclim') layers were obtained from the WorldClim Version 2 database (Fick and Hijmans 2017). Segmented regression analysis was used to test for correlations among P50 and canopy browning data from Klein et al. and species' thermal niche data derived from GBIF using the 'segmented' package (Muggeo 2008).

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