NORTHWEST CLIMATE ADAPTATION SCIENCE CENTER

2025 Deep Dive: Too Hot to Handle? Managing the Ecological Impacts of Extreme Heat in the Northwest

This is one of three working group syntheses describing the state of the 1) biophysical science, 2) management and practice and 3) policy and human dimensions of the ecological impacts of extreme heat.

BIOPHYSICAL WORKING GROUP SYNTHESIS

In the summer of 2021, an extreme heat wave in the Pacific Northwest, popularly referred to as the "2021 heat dome", had dramatic impacts across a variety of organisms and ecosystems. In this report we synthesize information on those impacts, available management options and knowledge and capacity needs in anticipation of future extreme heat events of a similar magnitude in the region. In addition to serving as a case study of an extreme heat event, the ecological impacts and management of the 2021 Pacific Northwest heat wave may also provide insight into the impacts and management of other acute extreme events in the region.

Extreme heat and the 2021 Pacific Northwest heat wave

An unprecedented extreme heat event affected Washington, Oregon and parts of Idaho, British Columbia, Alberta and northern California from late June to early July 2021 (hereafter referred to as the "2021 PNW heat wave"). This event brought record summer temperatures to the region (Heeter et al., 2023), with maximum air temperatures over 43°C (109°F) and exceeding 49°C (120°F) in some locations (Loikith and Kalashnikov, 2023). Canopy foliage in the sun reached even greater temperatures (Still et al., 2023). The 2021 PNW heat wave is categorized as one of the most extreme heat events globally (Thompson et al., 2022). However, the likelihood (Bartusek et al., 2022; Chen et al., 2023) and extremity (Terray, 2023) of similar heat waves are expected to increase in the future as baseline temperatures increase.

This report synthesizes the ecological impacts of the 2021 Pacific Northwest heat wave and the region's vulnerability to extreme heat. Understanding the ecological impacts and efficacy of management responses to the 2021 PNW heat wave may help better prepare for and adapt to the impacts of potentially similar extreme terrestrial heat waves in the future. Terrestrial heat waves are defined as periods of "marked unusual hot weather (maximum, minimum and daily average temperature) over a region persisting for at least three consecutive days during the warm period of the year based on local climatological conditions, with thermal conditions recorded above given thresholds" (United Nations, 2022). We focus here on the direct and indirect impacts of the 2021 PNW heat wave and similar extreme terrestrial heat waves rather than marine heat waves (*sensu* Hobday et al., 2016).

The 2021 PNW heat wave's exceptional extremeness has been attributed to anomalous meteorological and atmospheric circulation patterns including a high pressure ridge ("heat dome") (Li et al., 2024; Loikith and Kalashnikov, 2023) and land-atmosphere feedback loops from increasing soil dryness (Bartusek et al., 2022; Li et al., 2024). Additionally, the 2021 PNW heat wave compounded the impacts of spring heat waves and early and record-breaking snowmelt rates to contribute to summer 2021 drought conditions (McEvoy and Hatchett, 2023; Reyes and Kramer, 2023). The dry and hot conditions of the 2021 PNW heat wave also contributed to an increase in 2021 burned area across the PNW and Western Canada (Jain et al., 2024; White et al., 2023). Although we focus on the parts of the Northwest Climate Adaptation Science Center's region most impacted by the 2021 PNW heat wave (Oregon, Washington and parts of Idaho), we leverage recent science from the Pacific Northwest of North America (Oregon, Washington and parts of Idaho, British Columbia, Alberta and northern California) and beyond to describe the short-term (months to years) and long-term (decades) effects of the 2021 PNW heat wave as well as management approaches, data and tools, and knowledge gaps.

Vulnerability: A framework for understanding the ecological impacts of extreme heat

The ecological impacts of extreme heat events like the 2021 PNW heat wave can be considered within a climate change vulnerability framework, wherein an organism, population or community's vulnerability to a given stressor is a factor of exposure, sensitivity and adaptive capacity (Foden et al., 2019; Thurman et al., 2020). Exposure, sensitivity and adaptive capacity can be defined in various ways, often depending on the scale of assessment, global change drivers, the systems being examined and the availability of information on key traits or processes being considered. **Exposure** is a multidimensional measure of the conditions and changes therein that an organism, population or community may experience. In the context of extreme heat, relevant aspects of exposure include the magnitude, timing, duration and frequency of extreme heat relative to historical conditions (Thurman et al., 2020). Sensitivity is the degree to which exposure directly or indirectly affects an organism, population or community. In this report, we focus on sensitivity to extreme heat exposure (Thurman et al., 2020). Finally, adaptive capacity is the ability of an organism, population, or community to cope with or adjust to climate change (IPCC, 2014). Adaptive capacity encompasses both intrinsic and extrinsic factors, as outside stressors such as anthropogenic activities can also limit the ability of organisms or ecosystems to respond to climate change (Beever et al., 2016). In this report, we focus discussion of adaptive capacity to the traits and processes that allow organisms, populations and ecosystems to cope with and minimize the ecological impacts of extreme heat. It should be noted that, at times, knowledge may overlap in one or more of these categories, particularly sensitivity and adaptive capacity (Thurman et al., 2020). Using the vulnerability framework, we structure the remainder of the report around (1) ecological impacts of the 2021 heat wave, (2) potential effectiveness of adaptation strategies, (3) tools and datasets available to inform management and (4) research and capacity-building needs.

1. What does science tell us about the ecological impacts of the 2021 heat wave and where, when and how similar extreme heat events may occur and impact ecosystems in the Northwest?

The documented short-term ecological impacts of the 2021 PNW heat wave are primarily negative to growth and/or survival of organisms but varied, ranging from minor physiological damage to large-scale mortality events. Variation in observed impacts could be a function of local exposure, sensitivity and adaptive capacity to extreme heat. More and longer-term impacts are anticipated as time unfolds.

1a. Documented impacts of the 2021 PNW heat wave

As only four years have elapsed since the 2021 heat wave, most observations of its ecological impacts are immediate and short-term, with most published research focusing on impacts to forests and intertidal shellfish (**Table 1**). Quickly following the 2021 heat wave, researchers, natural resource managers and the public at large noted ecological impacts such as shellfish dieoff (Raymond et al., 2022; Shivaram, 2021), tree scorch (Klein et al., 2022; Still et al., 2023; Williams, 2021), overheated wildlife (Grable, 2021), and pre-flight young birds jumping out of their nests to escape the heat (Knowles, 2021; Labbé, 2021; Morris and Bayard, 2021); many have been synthesized in Fleishman et al. (2025), though gaps remain for non-forest terrestrial ecosystems and freshwater organisms. As time goes on, additional and longer-term impacts are expected to emerge, though tracing these back to the 2021 PNW heat wave may prove difficult.

Table 1: A non-exhaustive assortment of ecological impacts linked to the 2021 PNW heat wave documented in the Northwest U.S. (Idaho, ID; Oregon, OR; and Washington, WA).

Habitat	Impact(s)	Source(s), peer- reviewed	Other sources
Terrestrial	Conifer trees (multiple species): Canopy scorch, seedling mortality, reduced diameter growth	Harrington et al., 2023 (OR and WA); Still et al., 2023 (OR and WA); Swanson et al., 2023 (WA)	Washington Natural History Program (WA); WADNR & USFS, 2021 (WA); ODF & USFS, 2021 (OR)
	Birds (multiple species): Nestling mortality	Sloane et al., 2022 (OR)	Dole, 2021 (OR); Morris and Bayard, 2021 (WA)
	Wildfire: Increased fire activity and burned area	Jain et al., 2024 (WA, OR, ID)	_
Intertidal	Shellfish (multiple species): Mortality, decreased density,	Miner et al., 2025 (WA); Raymond et al.,	_

	increased density, reduced size	2024 (WA), 2022 (WA)	
	Northern rockweed (Fucus distichus): Short-term (<1 year) dieback	Miner et al., 2025 (WA)	_
Freshwater	Stream temperatures: Increased hourly temperature records by 2.7°C; record high daily maximum temperatures	Déry et al., 2024 (OR, WA, MT, WY)	_
	Snowmelt: Early and record rapid melting of high elevation snowpack	Reyes and Kramer, 2023 (OR and WA)	_

Terrestrial impacts

Canopy scorch in conifers was documented across the region, and direct effects of heat (Still et al., 2023) and indirect effects of drought (Klein et al., 2022) have been implicated in foliar damage. Eddy covariance micrometeorology measurements (Lee et al., 2024) and individual tree (Harrington et al., 2023) measurements indicated reductions in ecosystem and tree productivity at least 1–2 years following the heat wave. This reduction in growth is in agreement with Ford et al. (2017), who previously observed that tree growth stops above ambient temperatures of 40°C during long summer photoperiods.

Local microsites, such as next to coarse woody debris (Swanson et al., 2023) or in forest understories (Brackett et al., 2024; John et al., 2024), buffered the conditions experienced during the heat event by lowering temperatures and increasing soil moisture availability. Such microclimate buffering is linked to lower seedling stress and greater survival and growth (Swanson et al., 2023), and could also prove less stressful for other organisms. Tree species varied in their sensitivity to the event. For example, ponderosa pine seedling survival through the 2021 PNW heat wave was greater than for Douglas-fir seedlings (Swanson et al., 2023).

Sustained extreme temperatures of the 2021 PNW heat wave appeared to increase and synchronize wildfire activity in the PNW and Western Canada, resulting in broad-scale tree mortality (Jain et al., 2024). Short-term effects of the 2021 PNW heat wave on trees that survived the primary effects of the 2020 Labor Day Fires in Oregon's Cascades did not result in unusually high delayed mortality levels (Dyer et al., 2025), likely due to the disproportionally high severity of these fire events. Short-term effects of the 2021 PNW heat wave in high elevations seemed relatively minor, as indicated by small changes in alpine snow algal blooms (van Hees et al., 2023) and minimal subalpine forest canopy scorch (Sibley et al. *in revision*).

Information on the 2021 PNW heat wave's impacts on terrestrial wildlife is limited, but includes nestling and fledgling bird mortality (Hindmarch and Clegg, 2024; Sloane et al., 2022). Microhabitat conditions may have also influenced sensitivity in these cases; for a small sample (n=8) of bushtit nests 0–244 m from water, 100% mortality in young during the 2021 PNW heat wave occurred at distances from water greater than 23 m (Sloane et al., 2022). More direct sunlight exposure during the event was associated with higher barn owl mortality (Hindmarch and Clegg, 2024).

Freshwater impacts

Few studies to date have investigated the ecological impacts of the 2021 PNW heat wave on freshwater organisms, despite observed changes in water temperatures and snowmelt timing. Across the Northwest, freshwater temperatures increased by an average of 2.7°C during the event, with less extreme temperature increases in upland snow- or glacial-fed rivers (Déry et al., 2024; Pelto et al., 2022). The 2021 PNW heat wave shifted high elevation snowpack melt from an expected late melt (due to La Niña and a relatively high snowpack in 2020–2021) to an earlier melt date more characteristic of warm, dry, El Niño years in Oregon and Washington (Reyes and Kramer, 2023). Although smaller heat events in the spring of 2021 prior to the heat wave also contributed to faster and earlier snowpack loss, Reyes and Kramer (2023) suggest that the 2021 PNW heat wave alone moved the time when 95% of snow was melted forward 9 days from the expected date. In the Skagit River Basin the June 2021 heat wave was linked to warm stream temperatures potentially offset by cool snowmelt water, but informal surveys did not find evidence of fish mortality in the two months following the heat wave (Maher and Veldhuisen, 2023). However, the authors hypothesized that mortality would have increased if a similar heat event had occurred later in the summer when streamflow is lower and snowpack is no longer a likely source of cooling runoff (Maher and Veldhuisen, 2023). Warming water temperatures are predicted to result in earlier emergence of salmonids with overall less biomass per yearling (Hawkins et al., 2020) and can also increase disease occurrence and susceptibility in salmonids (Chiaramonte et al., 2016). Freshwater ecosystems may respond to heat waves nonuniformly. While some freshwater wetlands, such as riparian areas, may buffer temperature increases and thus function as thermal refugia during heat waves, it is possible that open peatlands could have higher temperatures than surrounding areas due to their lack of tree canopy and relatively higher humidity (from conversation with Joe Roccio, WNHP). For example, Washington Natural History Program staff observed scorched western hemlock in some monitored peatlands in the Puget Lowlands.

Intertidal impacts

The 2021 PNW heat wave coincided with the lowest low tides of the year. The timing of the low tides coincided with the hottest times of day in some regions, such as inside the Puget Sound of Washington state (Raymond et al., 2022). Immediately following the heat wave, large die-offs of shellfish, barnacles and algae were observed in some locations (Miner et al., 2025; Raymond et al., 2022).

Overall, shellfish exhibited both increases and decreases in population density and reduced average size for some taxa (Raymond et al., 2024), possibly due to regional variation in timing of low tide and rapid population recovery over the course of the year (Miner et al., 2025). Sublethal impacts (for example, reduced clam fecundity) might not be detectable for several years after a heat event because of natural population variability (Raymond et al., 2024).

1b. Vulnerability to extreme heat

Existing research on factors influencing exposure, sensitivity and adaptive capacity to temperature extremes provides some guidance on which organisms and ecosystems are most vulnerable to future extreme heat events. **Exposure** to extreme heat depends on geographic patterns in the magnitude of temperature extremes as well as the duration and timing of such extremes. In terrestrial ecosystems, terrain (Dobrowski, 2011), tree canopy cover (Brackett et al., 2024; Davis et al., 2019; Wolff et al., 2020), canopy structural complexity (Frey et al., 2016) and other small-scale features (e.g., coarse woody debris; Swanson et al., 2023) can buffer and even decouple microclimatic conditions from the broader climate, thereby providing protection from extreme heat (i.e., refugia). Tree canopy cover can ameliorate soil surface temperatures (John et al., 2024), but this temperature-buffering effect is likely to diminish as soils become dryer (Davis et al., 2019). Freshwater ecosystems' exposure to extreme heat is likely mediated by hydrology and geology (e.g., Brinson, 1993). In the Columbia Plateau, studies have found that the water level and drying frequency of groundwater-driven wetlands are more impacted by changes in precipitation, whereas surface-water wetlands are more impacted by changes in temperature (Halabisky et al., 2017). Exposure to extreme air temperatures may also be buffered in streams and rivers fed primarily by snow- and glacier-melt due to heat-driven increases in cold meltwater (Maher and Veldhuisen, 2023; Piccolroaz et al., 2018; Reyes and Kramer, 2023).

The impacts of extreme heat are expected to vary not only with exposure but also with **sensitivity**, which can vary among and within species. Databases on thermal tolerances of terrestrial, freshwater, intertidal and marine organisms provide experimentally derived temperature thresholds for thousands of species (e.g., GlobTherm; Bennett et al., 2018), though these tolerances may differ in application due to differences in the duration of experimental exposure. Integrating magnitude and duration can provide a more realistic representation of exposure for identifying sensitivity thresholds (Cook et al., 2024; Neuner and Buchner, 2023; Rank et al., 2022). Heat tolerance can also vary among and within individuals of a given species depending on life stage and age. For example, Salómon et al. (2022) noted that the late summer heat wave of 2022 in Europe led to widespread stem dehydration but not growth impacts as most trees had already completed most of their growth for that season. Mature trees can tolerate a wider range of temperatures compared to juveniles (Dobrowski et al., 2015), and needle browning after the 2021 PNW heat wave decreased with tree age (Klein et al., 2022).

Conversely, the production of heat-protective heat stress proteins decreases with age in animals such as rainbow trout (*Oncorhynchus mykiss*) (Fowler et al., 2009), although juvenile animals may have lower adaptive capacity due to limited mobility (for example, mortality in fledglings unable to leave the nest during the 2021 PNW heat wave; Hindmarch and Clegg, 2024; Sloane et al., 2022).

Adaptive capacity enables individuals, populations, species or ecosystems to cope with or adjust to the impacts of extreme heat events at different spatial and temporal scales. For example, in the short term, mobile species can relocate to cooler microclimates or reduce internal temperatures by minimizing movement. Even in relatively sessile species, traits allowing organisms to access cooler habitats could reduce exposure to extreme heat, such as butter clams that burrow more deeply than some co-occurring bivalves (Raymond et al., 2022). Similarly, deep-rooted plants may be able to avoid heat damage to portions of their root systems, later replacing fine roots in surface soils (Aubin et al. 2016). These examples of behavioral flexibility are often considered a form of phenotypic plasticity, which reflects an organism's ability to modify behavior in response to changing conditions and can serve as a rapid-response mechanism to environmental variability (Beever et al., 2017). This behavioral dimension of plasticity is part of a broader suite of traits — including morphological, physiological and developmental plasticity — that may influence species' capacity to persist under climate change. While phenotypic plasticity is often favored in environments with predictable seasonal variability (Stotz et al., 2021), its adaptive value under increasing climate extremes remains uncertain. The benefits of plasticity depend on the reliability of environmental cues, the physiological limits of the trait in question and the degree to which the induced response remains adaptive under novel stress regimes. In some cases, plastic responses may be insufficient or maladaptive under extreme or rapidly changing conditions.

2. What can science tell us about the effectiveness of adaptation strategies for managing the ecological impacts of extreme heat?

Few strategies have been proposed, let alone evaluated, to reduce ecological vulnerability to extreme heat beyond general climate adaptation actions. However, the 2021 PNW heat wave's impacts may inform efforts to map exposure, reduce sensitivity and enhance adaptive capacity for future extreme heat events in the Northwest. Monitoring will be crucial to evaluate the effectiveness of actions to reduce vulnerability to extreme heat.

Few actions have been proposed to specifically manage the ecological impacts of extreme heat in Northwest ecosystems or elsewhere. In limited cases, logistically intensive actions have been taken to reduce or mitigate the impacts of extreme heat on priority organisms immediately prior to or during a heat event. For example, emergency action to save sockeye salmon from extreme heat has involved trucking individual fish from Washington reaches of the Snake River into the cooler Idaho waters (Read, 2021). Such emergency interventions still require evaluation of efficacy, however.

Given the limited applicability and feasibility of such actions, we focus here on informing proactive management to reduce vulnerability. Observed impacts of the 2021 PNW heat wave may inform predictions of species and areas that are more vulnerable to extreme heat. However, such predictions will vary in their accuracy without an understanding of the mechanisms underlying patterns of impact. In this section, we organize information around potential management actions into three categories:

- a. **Manage exposure** Information and actions to proactively identify, protect and cultivate areas of lower exposure to extreme heat.
- b. **Reduce sensitivity and enhance adaptive capacity** Actions to reduce the sensitivity and increase the adaptive capacity of organisms, species and ecosystems to extreme heat.
- c. **Monitor to inform management decisions** Monitoring and data collection before, during and after extreme heat events to inform ongoing and future management decisions.

2a. Manage exposure

Assessing past and potential extreme heat exposure can serve as a first step in preparing for future extreme heat events. The 2021 PNW heat wave was first forecast 8 days prior to the onset of the event and predicted to be an extreme heat wave by 5 days prior to its onset, a relatively long lead time from a meteorological perspective (White et al., 2023). Post-facto studies show that existing models could predict such an extreme event 2–3 weeks in advance (Lin et al., 2022). With regional warnings of an extreme heat event even just a few days in advance, measures and actions might be taken to mitigate negative effects and set up monitoring plans to assess impacts of exposure. Those actions would necessarily be small in scope as, realistically, a few weeks may not be enough time to apply broad-scale treatments to reduce exposure. Therefore, beyond general meteorological predictions, more localized variation in exposure to extreme heat can be considered when prioritizing sites for protection, restoration and microhabitat manipulation. While few tools exist for predicting exposure to extreme-heat at finer scales, Section 3 discusses tools and datasets that could approximate extreme heat exposure.

One proactive management approach could be to protect locations of lower extreme heat exposure and cultivate features known to reduce extreme heat exposure. Protecting climate change refugia (as proxies for extreme heat refugia) from anthropogenic disturbances (e.g., invasive species, harvest, development) could support their continued function (see Morelli et al., 2016 and 2020 for climate change refugia identification and protection suggestions). Refugia size matters. For example, larger fire refugia were more resistant to postfire delayed tree mortality than smaller (<60m radius) refugia following the 2020 Labor Day Fires and the 2021 PNW heat wave (Dyer et al., 2025). However, microhabitats can also serve as thermal refugia.

The buffering capacity of forest understory microclimates (Brackett et al., 2024; Davis et al., 2019; De Frenne et al., 2021; Frey et al., 2016) suggests that maintaining forest canopy cover and structural complexity may reduce understory temperature extremes. Retaining coarse woody debris can reduce extreme heat exposure for a range of organisms through shading and moisture retention, and has been shown to facilitate conifer seedling establishment and growth even under extreme heat wave conditions (Swanson et al., 2023). However, retaining canopy cover and coarse woody debris may conflict with other management goals, such as promoting species that require high-light environments (e.g., Douglas-fir seedlings), facilitating snow accumulation (Varhola et al., 2010) or fuel reduction. Therefore, considering these strategies in the context of other management goals, and monitoring their effects will be crucial to developing and refining effective management strategies.

In intertidal environments, aspect, inner or outer coast location, timing of the low tide relative to the time of the day and presence of cooling groundwater or meltwater appeared to mediate high temperature exposure during the 2021 heat wave (Raymond et al., 2022). Generally, sites with more solar irradiance experienced more intense extreme heat exposure. In the 2021 heat wave, artificially shaded plots proved effective in reducing barnacle (*S. cariosus*) mortality compared to unshaded plots (Hesketh and Harley, 2023). The same study showed that shellfish mortality rates were impacted primarily by temperature. Foundation species and key coastal habitats such as kelp forests and eelgrass meadows can also mitigate acute heat exposure by providing shade cover and reducing water evaporation, especially at high tidal elevations (Umanzor et al., 2017; Watt and Scrosati, 2013). However, because of the interacting variables that affect heat exposure in intertidal environments, responses to acute heat events in these environments may ultimately depend on the local temperature regime and other microclimate factors rather than the overall trend of the event (Mota et al., 2015).

2b. Reduce sensitivity and enhance adaptive capacity

When exposure to extreme heat is unavoidable, careful assessment of species' or populations' sensitivity and adaptive capacity may suggest and inform management actions to better enable organisms to withstand conditions in their current locations (Thurman et al., 2021). Limited management actions can be taken immediately preceding and during an event to reduce sensitivity and enhance adaptive capacity of focal species and organisms. Examples from the PNW of immediate response actions are rare (although see "Case Study: Mobilizing to Beat the Heat with the Shellfish Rapid Response Network"), but in Australia, thermal tolerances and temperature forecasts have been combined to predict heat-related flying fox mortality (Ratnayake et al., 2019).

Proactive options to reduce extreme heat sensitivity and promote adaptive capacity include manipulating community and population composition to increase heterogeneity and include more heat-tolerant species or genotypes, but knowledge and capacity gaps surround the efficacy and implementation of these strategies in general let alone during

extreme heat. Mixed forest management and promoting climate-adapted species has been associated with general risk reduction in a changing climate (Seidl et al., 2018). Terrestrial habitat managers and foresters might accept (sensu Schuurman et al., 2022) extreme heat driven changes to less heat-sensitive species, especially in areas with higher exposure such as south- and southwest-facing slopes, or direct these changes through replanting. For example, managers might consider planting more heat-tolerant trees than those that were historically prevalent in areas with the greatest potential exposure to extreme temperatures. However, the efficacy of specific planting prescriptions has not been widely tested. Conservation of low-mobilility, heat-sensitive species might focus on milder, northeast-facing slopes, cold air drainages or higher elevations. In areas with higher solar irradiance and more heat exposure, shellfish growers and managers may consider growing deeper-dwelling bivalve species that fared better after the 2021 PNW heat wave (Raymond et al., 2022), but such manipulations may be incompatible with management goals to promote certain species of cultural, economic or ecological importance.

In instances where manipulating community composition is not suitable, increasing intraspecific diversity may help reduce overall heat sensitivity (Zabin et al., 2022). In terrestrial ecosystems, planting a mix of genotypes with a range of heat tolerances may decrease a population's overall sensitivity to extreme heat. Although local populations and genotypes may be best adapted to current climates (Chaney et al., 2017; Germino et al., 2018), populations with limited genetic variability or mismatches between existing genomic variation and future conditions may be unable to survive and adapt to future conditions (Bay et al., 2018; Jones, 2013; Jordan et al., 2024). For example, in Colorado montane forests, sourcing tree seedlings from a downslope (~ 300 m below planting site), warmer seed zone (proxy for genetic variation) improved seedling survival compared to using restoration site's seed zone (Marshall et al., 2024). Climate-informed adaptation tools, such as the Seedlot Selection Tool and Climate Smart Adaptation Tool (St. Clair et al., 2022) can help managers select heat-tolerant population sources. Both tools include measures of extreme temperature in their climate characterizations, although it is not clear whether these tools designed for general climate change adaptation are effective at mitigating the effects of extreme heat events. Actions that reduce other stressors (e.g., removing invasive species, limiting habitat disturbance, planting pathogen-resistant genotypes) may also enhance an ecological community's ability to withstand and adapt to climate change and extreme heat events in the future (Colberg et al., 2024).

2c. Monitor to inform management decisions

Given how few extreme heat-specific management strategies exist and the dearth of information about these strategies' effectiveness, monitoring how well ongoing management practices mitigate the effects of extreme heat events will be crucial to inform future management recommendations. Ecological monitoring data (including not only *insitu* monitoring but also remote-sensing data, particularly when leveraged to measure productivity and plant cover) can also inform management by enabling comparison of the impacts of extreme heat relative to baseline conditions and other stressors.

However, existing long-term monitoring sites and methods may not be sufficient to capture the effects of extreme heat events, and therefore, the effectiveness of management approaches at mitigating such events. Members of the 2025 Deep Dive Biophysical Knowledge working group and 2025 Deep Dive workshop participants emphasized the importance of developing robust monitoring programs to establish ecological baselines against which the impacts of extreme heat and other stressors could be evaluated, to capture site- and population-specific variation and to evaluate the success or failure of management strategies. The Shellfish Rapid Response Network is one example of a group of scientists and practitioners collaborating to develop and implement monitoring that can capture the impacts of extreme events such as the 2021 PNW heat wave ("Case Study: Mobilizing to Beat the Heat with the Shellfish Rapid Response Network"). It should also be noted that even with solid long-term monitoring, long-term decision making may prove difficult as projections of future climate conditions, including extreme events, remain uncertain at scales relevant to managers.

3. What tools or datasets are available to inform the ecological management of extreme heat impacts in the Northwest?

Available tools and datasets can inform the ecological management of extreme heat impacts by providing proxies of exposure to extreme heat, evaluating the impacts of extreme heat on focal ecosystems and organisms and forecasting the occurrence and impacts of extreme heat. However, these tools and datasets often do not holistically consider vulnerability to extreme heat, and instead provide disparate estimates of exposure, sensitivity or adaptive capacity.

We discuss three main types of tools and datasets that address different aspects of extreme heat vulnerability: geospatial data, ecological monitoring data and predictive models. An informal survey by the 2025 Deep Dive's Management & Practice working group found that managers used many different types of resources, including technical data, community or place-based knowledge and in limited cases, decision-support tools and frameworks (Vieira et al., 2025). Limitations of these tools include issues of accessibility, usability and comprehensiveness; no tool incorporates all components of extreme heat vulnerability (exposure, sensitivity and adaptive capacity) at scales relevant to management. Climate change vulnerability assessments (e.g., Halofsky et al., 2022) offer a template for integrating our ecological understanding with these tools and datasets to support vulnerability assessments focused specifically on heat waves. Specific to the 2021 heat wave, responses were often opportunistic, suggesting that there might be a benefit to standardized, coordinated data collection efforts for future heat waves. To assist Northwest researchers, planners and policymakers in finding tools and datasets to predict and manage the impacts of extreme heat, we compiled relevant geospatial data, ecological data and predictive tools into a central database (Extreme Heat Tools & Resources).

3a. Spatial data can approximate exposure and impacts

Remote-sensing data has been used to determine large-scale forest impacts of the 2021 heat wave (WADNR & USFS 2021; ODF & USFS 2021), but current limits include spatial and temporal resolution. Fine grain surface temperature data collected via satellites, such as the ECOsystem Spaceborne Thermal Radiometer Experiment on Space Station (ECOSTRESS)'s semi-daily measurements, can provide information on general heat exposure. Such data may also be used to evaluate the impacts of management decisions. For example, ECOSTRESS data has provided preliminary evidence that tidal wetland restoration can cool surface water temperatures (Gustine et al., 2023).

Few extreme-heat-specific exposure estimates exist to our knowledge, but some climate exposure products and principles could be used as proxies to assess extreme heat exposure based on factors that contribute to maximum temperatures (e.g., mean temperatures, insolation, topography, etc.). Topography is strongly linked to local climate variation, and can be used to identify areas of low and high heat exposure. For example, in the Northern Hemisphere, north-facing slopes are often the coolest areas on the landscape, serving as thermal refugia by buffering or even decoupling local from ambient temperatures (Dobrowski, 2011; Morelli et al., 2016). Gridded climate data such as ClimateNA, TerraClimate, PRISM and others (Extreme Heat Tools & Resources) can be used to identify the warmest or most water-stressed areas on a landscape, which can be a proxy for heat exposure under extreme conditions. However, these data may be less-frequently updated than some coarser products, such as the ERA5-Land climatological data (Muñoz-Sabater et al., 2021). Topographic metrics such as continuous heat-insolation load index (CHILI, Theobald et al., 2015), an estimate of energy received by a location mid-day, can also serve as proxies for extreme heat exposure. Climdex offers reference period information specific to climate extremes.

Climate exposure estimates based on average climate data provided by most gridded climate datasets are likely coarse estimates of extreme heat exposure, which happens at a finer temporal scale (minutes, hours, days). Additionally, extreme heat may amplify the effects of other factors, such as light or drought, which would not be reflected in exposure datasets based on temporally aggregated data. Most of the products described in the above paragraph are available at a relatively coarse spatial resolution (800 m to 4 km), and would serve as approximations of heat exposure. Understanding how well these or other products identify extreme heat exposure, and developing extreme heat specific exposure products are emergent research needs. Mapping exposure and thermal refugia can also benefit from local microclimate monitoring, which would validate exposure mapping. Idaho's Multi-species Baseline Initiative is one example of this kind of effort (Lucid et al., 2016).

3b. Ecological monitoring data can be used to evaluate sensitivity, adaptive capacity and management efficacy

Data from pre-existing and ongoing monitoring protocols have opportunistically been used to evaluate the ecological impacts of the 2021 PNW heat wave (e.g., Déry et al., 2024; Hesketh and Harley, 2023; Sloane et al., 2022), but data collected for other purposes can pose challenges in detecting the independent or potentially synergistic impacts of an extreme event. For example, background variability made it difficult to use survey data from researchers and managers to determine the impacts of the 2021 PNW heat wave on intertidal bivalves (Raymond et al., 2024). Nonetheless, historical and long-term datasets can help provide baselines against which specific events such as the 2021 PNW heat wave can be compared while accounting for underlying variability. For example, Lloret and coauthors' approach (Lloret et al., 2011) to measuring tree resilience via metrics that consider growth and performance before and after stress could be used to assess the impacts of heat extremes (Andrus et al., 2024; Sterck et al., 2024). Knowing which species, populations or areas are more likely to withstand perturbations and recover from extreme heat events may inform restoration and efforts to improve ecosystem resiliency. There are multiple long-term monitoring initiatives in place within the Northwest with both aquatic and terrestrial focuses (e.g., WA DNR's ANeMoNe, NPS monitoring data, long-term ecological research projects such as the National Ecological Observatory Network, USDA Forest Service Forest Inventory and Analysis program, USDA Forest Service Experimental Forests and Ranges, and GLobal Observation Research In Alpine Environments), which could serve as starting points for establishing baselines and assessing the impacts of extreme events.

In Washington, several groups collect data on shellfish mortality through community reporting tools such as WDFW's Fish Carcass Reporting Form and the Pacific Shellfish Institute's Shellfish Mortality Reporting Form. A regional shellfish rapid response survey and reporting tool is also in development ("Case Study: Mobilizing to Beat the Heat with the Shellfish Rapid Response Network"). Existing ecological and environmental monitoring tools, including community science ("citizen science") programs such as Nature's Notebook and iNaturalist, might also be easily leveraged to collect data on baseline conditions and potential extreme heat event impacts. However, available and emerging data from various monitoring efforts will require analysis, processing and synthesis before it can be useful for informing management.

3c. Models and tools can predict vulnerability to extreme heat, but existing options are often inaccessible or difficult for managers to use

Predictive models of both exposure and response to extreme heat may help managers evaluate the risk of future heat wave impacts on their focal areas and organisms. The utility of predictions to support managers will depend on their temporal scale, with seasonal predictions helping to prepare for a likely event in the short-term, whereas decadal predictions would inform longer-term planning and management.

Various studies show potential for different methods, including machine learning, to better predict the 2021 heat wave and forecast where and when similar events may occur in the future (Emerton et al., 2022; Pons et al., 2024; Vonich and Hakim, 2024). Microclimate models could provide finer-scale predictions of which areas are more likely to serve as thermal refugia (Isaak et al., 2015; Meyer et al., 2023), which could also be more likely to serve as refugia during extreme heat events.

Functional traits have been suggested as a predictor of species' responses to marine heat waves (Harvey et al., 2022), and might be similarly useful for predicting terrestrial, freshwater and intertidal species' responses to atmospheric heat waves (Briscoe et al., 2023). Global datasets on functional traits such as thermal tolerances exist spanning terrestrial and aquatic habitats and multiple kingdoms (Araújo et al., 2013; Bennett et al., 2018; Hoffmann et al., 2013), but will require collating and filtering for Northwest species. Limitations to using functional traits to predict responses to extreme heat events include inconsistencies in how thermal tolerances are determined, differences in thresholds versus lethal amounts, intraspecific variability and adaptive capacity. Generally, more information is needed on species temperature tolerances in the PNW, although some data exists for tree seedlings (Marias et al., 2017) and fish (Isaak et al., 2015).

4. What are key science gaps around our knowledge of the ecological components of extreme heat impacts and adaptation in the Northwest?

There is limited research on the mechanisms and drivers of variation in the ecological impacts of the 2021 PNW heat wave, but additional controlled studies and monitoring could help disentangle responses from background variation. Few studies have evaluated the vulnerability of Northwest species and ecosystems to extreme heat, and few tools provide easily-accessible and spatially-explicit predictions of extreme heat exposure, sensitivity and adaptive capacity at scales relevant for management.

The 2025 Deep Dive Biophysical Knowledge working group identified several research and capacity-building needs to address knowledge gaps, summarized in the following two sections.

Research needs

- Quantify and synthesize the ecological effects of the 2021 PNW heat wave, including impacts in non-forest terrestrial and freshwater ecosystems, emerging longer-term responses and variation in individual, population, community and ecosystem-level responses.
- Understand the mechanisms and drivers of interspecific and intraspecific variation in sensitivity and adaptive capacity to extreme heat, including heat tolerance and underlying genetics and plasticity, especially for priority species in the Northwest.

- Characterize the interactive ecological effects of extreme heat and other anthropogenic, biotic and abiotic disturbances and stressors.
- **Develop and evaluate management and restoration actions** to address vulnerability to extreme heat events and co-occurring stressors.
- Assess and improve the effectiveness and accessibility of existing tools to measure and predict general and extreme heat exposure and impacts, including seasonal and long-term projections of the likelihood of heat events, and create new extreme-heat-specific tools as needed.

Capacity-building needs

- Support long-term and post-event rapid ecological and microclimate
 monitoring that generates data that is findable, accessible, interoperable and
 reusable (FAIR). These data can be used not only to establish ecosystem baselines
 and assess the effects of heat events and adaptation strategies, but also to test
 mechanistic understanding of ecological impacts and generate testable hypotheses
 for future experiments.
- Improve, operationalize and expand the accessibility of existing tools and datasets to better incorporate field observations and provide data and predictions at scales relevant to management and policy decisions.
- Develop spatially-explicit data and predictions on extreme heat vulnerability & resilience, including expanding climate exposure predictive tools to include extreme heat exposure.
- **Provide and synthesize guidance** on how to evaluate exposure risk and make informed decisions using available tools and datasets.
- **Facilitate preparation**, such as by establishing directories and procedures ahead of time for swift response during a potential future event.

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REFERENCES CITED

- Andrus, R.A., Peach, L.R., Cinquini, A.R., Mills, B., Yusi, J.T., Buhl, C., Fischer, M., Goodrich, B.A., Hulbert, J.M., Holz, A., Meddens, A.J.H., Moffett, K.B., Ramirez, A., Adams, H.D., 2024. Canary in the forest?—Tree mortality and canopy dieback of western redcedar linked to drier and warmer summers. J. Biogeogr. 51, 103–119. https://doi.org/10.1111/jbi.14732
- Araújo, M.B., Ferri-Yáñez, F., Bozinovic, F., Marquet, P.A., Valladares, F., Chown, S.L., 2013. Heat freezes niche evolution. Ecol. Lett. 16, 1206–1219. https://doi.org/10.1111/ele.12155
- Aubin, I., Munson, A.D., Cardou, F., Burton, P.J., Isabel, N., Pedlar, J.H., Paquette, A., Taylor, A.R., Delagrange, S., Kebli, H. and Messier, C., 2016. Traits to stay, traits to move: a review of functional traits to assess sensitivity and adaptive capacity of temperate and boreal trees to climate change. Environmental Reviews, 24(2), pp.164-186. https://doi.org/10.1139/er-2015-0072
- Bartusek, S., Kornhuber, K., Ting, M., 2022. 2021 North American heatwave amplified by climate change-driven nonlinear interactions. Nat. Clim. Change 12, 1143–1150. https://doi.org/10.1038/s41558-022-01520-4
- Bay, R.A., Harrigan, R.J., Underwood, V.L., Gibbs, H.L., Smith, T.B., Ruegg, K., 2018. Genomic signals of selection predict climate-driven population declines in a migratory bird. Science 359, 83–86. https://doi.org/10.1126/science.aan4380
- Beever, E.A., Hall, L.E., Varner, J., Loosen, A.E., Duham, J.B., Gahl, M.K., Smith, F.A., Lawler, J.J., 2017. Behavioral flexibility as a mechanism for coping with climate change. Front. Ecol. Environ. 15, 299–308. https://doi.org/10.1002/fee.1502
- Beever, E.A., O'Leary, J., Mengelt, C., West, J.M., Julius, S., Green, N., Magness, D., Petes, L., Stein, B., Nicotra, A.B., Hellmann, J.J., Robertson, A.L., Staudinger, M.D., Rosenberg, A.A., Babij, E., Brennan, J., Schuurman, G.W., Hofmann, G.E., 2016. Improving Conservation Outcomes with a New Paradigm for Understanding Species' Fundamental and Realized Adaptive Capacity. Conserv. Lett. 9, 131–137. https://doi.org/10.1111/conl.12190
- Bennett, J.M., Calosi, P., Clusella-Trullas, S., Martínez, B., Sunday, J., Algar, A.C., Araújo, M.B., Hawkins, B.A., Keith, S., Kühn, I., Rahbek, C., Rodríguez, L., Singer, A., Villalobos, F., Ángel Olalla-Tárraga, M., Morales-Castilla, I., 2018. GlobTherm, a global database on thermal tolerances for aquatic and terrestrial organisms. Sci. Data 5, 180022. https://doi.org/10.1038/sdata.2018.22

- Brackett, A.E., Still, C.J., Puettmann, K.J., 2024. Residual canopy cover provides buffering of near-surface temperatures, but benefits are limited under extreme conditions. Can. J. For. Res. 54, 1018–1031. https://doi.org/10.1139/cjfr-2023-0268
- Brinson, M., 1993. A hydrogeomorphic classification for wetlands (Technical Report No. WRP-DE-4), Wetlands Research Program technical report. U.S. Army Engineer Waterways Experiment Station. https://usace.contentdm.oclc.org/digital/collection/p266001coll1/id/7194/
- Briscoe, N.J., Morris, S.D., Mathewson, P.D., Buckley, L.B., Jusup, M., Levy, O., Maclean, I.M.D., Pincebourde, S., Riddell, E.A., Roberts, J.A., Schouten, R., Sears, M.W., Kearney, M.R., 2023. Mechanistic forecasts of species responses to climate change: The promise of biophysical ecology. Glob. Change Biol. 29, 1451–1470. https://doi.org/10.1111/gcb.16557
- Chaney, L., Richardson, B.A., Germino, M.J., 2017. Climate drives adaptive genetic responses associated with survival in big sagebrush (Artemisia tridentata). Evol. Appl. 10, 313–322. https://doi.org/10.1111/eva.12440
- Chen, Z., Lu, J., Chang, C.-C., Lubis, S.W., Leung, L.R., 2023. Projected increase in summer heat-dome-like stationary waves over Northwestern North America. Npj Clim. Atmospheric Sci. 6, 1–10. https://doi.org/10.1038/s41612-023-00511-2
- Chiaramonte, L.V., Ray, R.A., Corum, R.A., Soto, T., Hallett, S.L., Bartholomew, J.L., 2016. Klamath River Thermal Refuge Provides Juvenile Salmon Reduced Exposure to the Parasite Ceratonova shasta. Trans. Am. Fish. Soc. 145, 810–820. https://doi.org/10.1080/00028487.2016.1159612
- Colberg, E.M., Bradley, B.A., Morelli, T.L., Brown-Lima, C.J., 2024. Climate-Smart Invasive Species Management for 21st Century Global Change Challenges. Glob. Change Biol. 30, e17531. https://doi.org/10.1111/gcb.17531
- Cook, A.M., Rezende, E.L., Petrou, K., Leigh, A., 2024. Beyond a single temperature threshold: Applying a cumulative thermal stress framework to plant heat tolerance. Ecol. Lett. 27, e14416. https://doi.org/10.1111/ele.14416
- Davis, K.T., Dobrowski, S.Z., Holden, Z.A., Higuera, P.E., Abatzoglou, J.T., 2019. Microclimatic buffering in forests of the future: the role of local water balance. Ecography 42, 1–11. https://doi.org/10.1111/ecog.03836
- De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B.R., Zellweger, F., Aalto, J., Ashcroft, M.B., Christiansen, D.M., Decocq, G., De Pauw, K., Govaert, S., Greiser, C., Gril, E., Hampe, A., Jucker, T., Klinges, D.H., Koelemeijer, I.A., Lembrechts, J.J., Marrec, R., Meeussen, C., Ogée, J., Tyystjärvi, V., Vangansbeke, P., Hylander, K., 2021. Forest microclimates and climate change: Importance, drivers and future research agenda. Glob. Change Biol. 27, 2279–2297. https://doi.org/10.1111/gcb.15569

- Déry, S.J., Martins, E.G., Owens, P.N., Petticrew, E.L., 2024. Extreme hydrometeorological events induce abrupt and widespread freshwater temperature changes across the Pacific Northwest of North America. Commun. Earth Environ. 5, 1–13. https://doi.org/10.1038/s43247-024-01407-6
- Dobrowski, S.Z., 2011. A climatic basis for microrefugia: the influence of terrain on climate. Glob. Change Biol. 17, 1022–1035. https://doi.org/10.1111/j.1365-2486.2010.02263.x
- Dobrowski, S.Z., Swanson, A.K., Abatzoglou, J.T., Holden, Z.A., Safford, H.D., Schwartz, M.K., Gavin, D.G., 2015. Forest structure and species traits mediate projected recruitment declines in western US tree species. Glob. Ecol. Biogeogr. 24, 917–927. https://doi.org/10.1111/geb.12302
- Dyer, A.S., Busby, S., Evers, C., Reilly, M., Zuspan, A., Holz, A., 2025. Post-fire delayed tree mortality in mesic coniferous forests reduces fire refugia and seed sources. Landsc. Ecol. 40, 101. https://doi.org/10.1007/s10980-025-02111-2
- Emerton, R., Brimicombe, C., Magnusson, L., Roberts, C., Di Napoli, C., Cloke, H.L., Pappenberger, F., 2022. Predicting the unprecedented: forecasting the June 2021 Pacific Northwest heatwave. Weather 77, 272–279. https://doi.org/10.1002/wea.4257
- Fleishman, E., Rupp, D.E., Loikith, P.C., Bumbaco, K.A., O'Neill, L.W., 2025. Synthesis of publications on the anomalous June 2021 heat wave in the Pacific Northwest, United States and Canada. https://doi.org/10.1175/BAMS-D-24-0188.1
- Foden, W.B., Young, B.E., Akçakaya, H.R., Garcia, R.A., Hoffmann, A.A., Stein, B.A., Thomas, C.D., Wheatley, C.J., Bickford, D., Carr, J.A., Hole, D.G., Martin, T.G., Pacifici, M., Pearce-Higgins, J.W., Platts, P.J., Visconti, P., Watson, J.E.M., Huntley, B., 2019. Climate change vulnerability assessment of species. WIREs Clim. Change 10, e551. https://doi.org/10.1002/wcc.551
- Ford, K.R., Harrington, C.A., St. Clair, J.B., 2017. Photoperiod cues and patterns of genetic variation limit phenological responses to climate change in warm parts of species' range: Modeling diameter-growth cessation in coast Douglas-fir. Glob. Change Biol. 23, 3348–3362. https://doi.org/10.1111/gcb.13690
- Fowler, S.L., Hamilton, D., Currie, S., 2009. A comparison of the heat shock response in juvenile and adult rainbow trout (Oncorhynchus mykiss) implications for increased thermal sensitivity with age. Can. J. Fish. Aquat. Sci. 66, 91–100. https://doi.org/10.1139/F08-192
- Frey, S.J.K., Hadley, A.S., Johnson, S.L., Schulze, M., Jones, J.A., Betts, M.G., 2016. Spatial models reveal the microclimatic buffering capacity of old-growth forests | Science Advances. Sci. Adv. 2. https://doi.org/DOI: 10.1126/sciadv.1501392

- Germino, M.J., Moser, A.M., Sands, A.R., 2018. Adaptive variation, including local adaptation, requires decades to become evident in common gardens. Ecol. Appl. 29, e01842. https://doi.org/10.1002/eap.1842
- Grable, J., 2021. Climate-Fueled Heat Waves Spell Danger for Wildlife. Sierra.

 https://www.sierraclub.org/sierra/climate-fueled-heat-waves-spell-danger-for-wildlife
- Gustine, R.N., Nickles, C.L., Lee, C.M., Crawford, B.A., Hestir, E.L., Khanna, S., 2023. Evaluating Habitat Suitability and Tidal Wetland Restoration Actions With ECOSTRESS. J. Geophys. Res. Biogeosciences 128, e2022JG007306. https://doi.org/10.1029/2022JG007306
- Halabisky, M., Lee, S.-Y., Hall, S.A., Rule, M., 2017. Can we conserve wetlands under a changing climate? Mapping wetland hydrology across an ecoregion and developing climate adaptation recommendations, Report prepared for Great Northern Landscape Conservation Cooperative. https://www.sciencebase.gov/catalog/item/55e07c5fe4b0f42e3d040f3e
- Halofsky, J.E., Peterson, D.L., Gravenmier, R.A., 2022. Climate change vulnerability and adaptation in southwest Oregon. Gen Tech Rep PNW-GTR-995 Portland US Dep. Agric. For. Serv. Pac. Northwest Res. Stn. 445 P 995, 1–445. https://doi.org/10.2737/PNW-GTR-995
- Harrington, C.A., Gould, P.J., Cronn, R., 2023. Site and provenance interact to influence seasonal diameter growth of Pseudotsuga menziesii. Front. For. Glob. Change 6. https://doi.org/10.3389/ffgc.2023.1173707
- Harvey, B.P., Marshall, K.E., Harley, C.D.G., Russell, B.D., 2022. Predicting responses to marine heatwaves using functional traits. Trends Ecol. Evol. 37, 20–29. https://doi.org/10.1016/j.tree.2021.09.003
- Hawkins, B.L., Fullerton, A.H., Sanderson, B.L., Steel, E.A., 2020. Individual-based simulations suggest mixed impacts of warmer temperatures and a nonnative predator on Chinook salmon. Ecosphere 11, e03218. https://doi.org/10.1002/ecs2.3218
- Heeter, K.J., Harley, G.L., Abatzoglou, J.T., Anchukaitis, K.J., Cook, E.R., Coulthard, B.L., Dye, L.A., Homfeld, I.K., 2023. Unprecedented 21st century heat across the Pacific Northwest of North America. Npj Clim. Atmospheric Sci. 6, 1–9. https://doi.org/10.1038/s41612-023-00340-3
- Hesketh, A.V., Harley, C.D.G., 2023. Extreme heatwave drives topography-dependent patterns of mortality in a bed-forming intertidal barnacle, with implications for associated community structure. Glob. Change Biol. 29, 165–178. https://doi.org/10.1111/gcb.16390

- Hindmarch, S.R., Clegg, D., 2024. Extreme Weather Events: The Hottest, Wettest, and Coldest Year Coincides with a Decline in Barn Owl Productivity in Southwestern Canada. J. Raptor Res. 58, 121–124. https://doi.org/10.3356/JRR-23-11
- Hobday, A.J., Alexander, L.V., Perkins, S.E., Smale, D.A., Straub, S.C., Oliver, E.C.J., Benthuysen, J.A., Burrows, M.T., Donat, M.G., Feng, M., Holbrook, N.J., Moore, P.J., Scannell, H.A., Sen Gupta, A., Wernberg, T., 2016. A hierarchical approach to defining marine heatwaves. Prog. Oceanogr. 141, 227–238. https://doi.org/10.1016/j.pocean.2015.12.014
- Hoffmann, A.A., Chown, S.L., Clusella-Trullas, S., 2013. Upper thermal limits in terrestrial ectotherms: how constrained are they? Funct. Ecol. 27, 934–949. https://doi.org/10.1111/j.1365-2435.2012.02036.x
- IPCC, 2014. Climate change 2014: Synthesis Report. Contribution of Working Groups I, II, and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. (No. AR5). IPCC (Intergovernmental Panel on Climate Change), Geneva, Switzerland. https://www.ipcc.ch/report/ar5/syr/
- Isaak, D.J., Young, M.K., Nagel, D.E., Horan, D.L., Groce, M.C., 2015. The cold-water climate shield: delineating refugia for preserving salmonid fishes through the 21st century. Glob. Change Biol. 21, 2540–2553. https://doi.org/10.1111/gcb.12879
- Jain, P., Sharma, A.R., Acuna, D.C., Abatzoglou, J.T., Flannigan, M., 2024. Record-breaking fire weather in North America in 2021 was initiated by the Pacific northwest heat dome. Commun. Earth Environ. 5, 1–10. https://doi.org/10.1038/s43247-024-01346-2
- John, A., Pradhan, K., Case, M.J., Ettinger, A.K., Hille Ris Lambers, J., 2024. Forest canopy cover affects microclimate buffering during an extreme heat event. Environ. Res. Commun. 6, 091015. https://doi.org/10.1088/2515-7620/ad7705
- Jones, T.A., 2013. When local isn't best. Evol. Appl. 6. https://doi.org/10.1111/eva.12090
- Jordan, R., Harrison, P., Breed, M., 2024. The eco-evolutionary risks of not changing seed provenancing practices in changing environments. Ecol. Lett. 27. https://doi.org/DOI:10.1111/ele.14348
- Klein, T., Torres-Ruiz, J.M., Albers, J.J., 2022. Conifer desiccation in the 2021 NW heatwave confirms the role of hydraulic damage. Tree Physiol. 42, 722–726. https://doi.org/10.1093/treephys/tpac007
- Knowles, H., 2021. 'Hawkpocalypse': Baby birds of prey have leaped from their nests to escape West's extreme heat. Wash. Post. https://www.washingtonpost.com/nation/2021/07/17/heat-wave-baby-hawks/

- Labbé, S., 2021. Birds jumped out of their nests to escape the June heat wave [WWW Document]. Pique Newsmag. https://www.piquenewsmagazine.com/must-reads/birds-jumped-out-of-their-nests-to-escape-the-june-heat-wave-4183127 (accessed 3.17.25).
- Lee, S.-C., Meyer, G., Foord, V.N., Spittlehouse, D.L., Burton, P.J., Jassal, R.S., Black, T.A., 2024. Disruption and recovery of carbon dioxide and water vapour exchange over British Columbia forests after natural and human disturbance. Agric. For. Meteorol. 355, 110128. https://doi.org/10.1016/j.agrformet.2024.110128
- Li, X., Mann, M.E., Wehner, M.F., Rahmstorf, S., Petri, S., Christiansen, S., Carrillo, J., 2024. Role of atmospheric resonance and land–atmosphere feedbacks as a precursor to the June 2021 Pacific Northwest Heat Dome event. Proc. Natl. Acad. Sci. 121, e2315330121. https://doi.org/10.1073/pnas.2315330121
- Lin, H., Mo, R., Vitart, F., 2022. The 2021 Western North American Heatwave and Its Subseasonal Predictions. Geophys. Res. Lett. 49, e2021GL097036. https://doi.org/10.1029/2021GL097036
- Lloret, F., Keeling, E.G., Sala, A., 2011. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. Oikos 120, 1909–1920. https://doi.org/10.1111/j.1600-0706.2011.19372.x
- Loikith, P.C., Kalashnikov, D.A., 2023. Meteorological Analysis of the Pacific Northwest June 2021 Heatwave. Mon. Weather Rev. 151, 1303–1319. https://doi.org/10.1175/MWR-D-22-0284.1
- Lucid, M., Robinson, L., Ehlers, S., 2016. Multi-species Baseline Initiative Project Report: 2010-2014. Idaho Fish & Game, Coeur d'Alene, Idaho. https://idfg.idaho.gov/sites/default/files/campaigns/MBI_Report_Chapter1_Overview.pdf
- Maher, S., Veldhuisen, C., 2023. Stream Temperature Monitoring in Forested Tributaries of the Skagit River Basin 15-year Update and Analysis. https://skagitcoop.org/wp-content/uploads/Maher-Veldhuisen.-Forested-tributaries-temperature-analysis-and-report-2008-2022.pdf
- Marias, D.E., Meinzer, F.C., Woodruff, D.R., McCulloh, K.A., 2017. Thermotolerance and heat stress responses of Douglas-fir and ponderosa pine seedling populations from contrasting climates. Tree Physiol. 37, 301–315. https://doi.org/10.1093/treephys/tpw117
- Marshall, L.A.E., Fornwalt, P.J., Stevens-Rumann, C.S., Rodman, K.C., Chapman, T.B., Schloegel, C.A., Stevens, J.T., 2024. What influences planted tree seedling survival in burned Colorado montane forests? For. Ecol. Manag. 572, 122321. https://doi.org/10.1016/j.foreco.2024.122321

- McEvoy, D.J., Hatchett, B.J., 2023. Spring heat waves drive record western United States snow melt in 2021. Environ. Res. Lett. 18, 014007. https://doi.org/10.1088/1748-9326/aca8bd
- Meyer, A.V., Sakairi, Y., Kearney, M.R., Buckley, L.B., 2023. A guide and tools for selecting and accessing microclimate data for mechanistic niche modeling. Ecosphere 14, e4506. https://doi.org/10.1002/ecs2.4506
- Miner, C.M., Berry, H.D., Bohlmann, H., Dethier, M.N., Fradkin, S.C., Gaddam, R., Raymond, W.W., Raimondi, P.T., 2025. Location and natural history are key to determining impact of the 2021 atmospheric heatwave on Pacific Northwest rocky intertidal communities. Front. Mar. Sci. 12. https://doi.org/10.3389/fmars.2025.1503019
- Morelli, T.L., Barrows, C.W., Ramirez, A.R., Cartwright, J.M., Ackerly, D.D., Eaves, T.D., Ebersole, J.L., Krawchuk, M.A., Letcher, B.H., Mahalovich, M.F., Meigs, G.W., Michalak, J.L., Millar, C.I., Quiñones, R.M., Stralberg, D., Thorne, J.H., 2020. Climate-change refugia: biodiversity in the slow lane. Front. Ecol. Environ. 18, 228–234. https://doi.org/10.1002/fee.2189
- Morelli, T.L., Daly, C., Dobrowski, S.Z., Dulen, D.M., Ebersole, J.L., Jackson, S.T., Lundquist, J.D., Millar, C.I., Maher, S.P., Monahan, W.B., Nydick, K.R., Redmond, K.T., Sawyer, S.C., Stock, S., Beissinger, S.R., 2016. Managing Climate Change Refugia for Climate Adaptation. PLOS ONE 11, e0159909. https://doi.org/10.1371/journal.pone.0159909
- Morris, J., Bayard, T., 2021. Mortality Event at West Seattle Caspian Tern Colony [WWW Document]. Audubon Wash. https://wa.audubon.org/news/mortality-event-west-seattle-caspian-tern-colony (accessed 3.17.25).
- Mota, C.F., Engelen, A.H., Serrão, E.A., Pearson, G.A., 2015. Some don't like it hot: microhabitat-dependent thermal and water stresses in a trailing edge population. Funct. Ecol. 29, 640–649. https://doi.org/10.1111/1365-2435.12373
- Muñoz-Sabater, J., Dutra, E., Agustí-Panareda, A., Albergel, C., Arduini, G., Balsamo, G., Boussetta, S., Choulga, M., Harrigan, S., Hersbach, H. and Martens, B., 2021. ERA5-Land: A state-of-the-art global reanalysis dataset for land applications. Earth system science data, 13(9), pp.4349-4383. https://doi.org/10.5194/essd-13-4349-2021
- Neuner, G., Buchner, O., 2023. The dose makes the poison: The longer the heat lasts, the lower the temperature for functional impairment and damage. Environ. Exp. Bot. 212, 105395. https://doi.org/10.1016/j.envexpbot.2023.105395
- Pelto, M.S., Dryak, M., Pelto, J., Matthews, T., Perry, L.B., 2022. Contribution of Glacier Runoff during Heat Waves in the Nooksack River Basin USA. Water 14, 1145. https://doi.org/10.3390/w14071145
- Piccolroaz, S., Toffolon, M., Robinson, C.T., Siviglia, A., 2018. Exploring and Quantifying River

- Thermal Response to Heatwaves. Water 10, 1098. https://doi.org/10.3390/w10081098
- Pons, F.M.E., Yiou, P., Jézéquel, A., Messori, G., 2024. Simulating the Western North America heatwave of 2021 with analogue importance sampling. Weather Clim. Extrem. 43, 100651. https://doi.org/10.1016/j.wace.2024.100651
- Rank, R., Maneta, M., Higuera, P., Holden, Z., Dobrowski, S., 2022. Conifer Seedling Survival in Response to High Surface Temperature Events of Varying Intensity and Duration. Front. For. Glob. Change 4. https://doi.org/10.3389/ffgc.2021.731267
- Ratnayake, H.U., Kearney, M.R., Govekar, P., Karoly, D., Welbergen, J.A., 2019. Forecasting wildlife die-offs from extreme heat events. Anim. Conserv. 22, 386–395. https://doi.org/10.1111/acv.12476
- Raymond, W.W., Barber, J.S., Dethier, M.N., Hayford, H.A., Harley, C.D.G., King, T.L., Paul, B., Speck, C.A., Tobin, E.D., Raymond, A.E.T., McDonald, P.S., 2022. Assessment of the impacts of an unprecedented heatwave on intertidal shellfish of the Salish Sea. Ecology 103, e3798. https://doi.org/10.1002/ecy.3798
- Raymond, W.W., Tobin, E.D., Barber, J.S., Hayford, H.A., Raymond, A.E.T., Speck, C.A., Rogers, D., Brown, R., 2024. Short-term effects of an unprecedented heatwave on intertidal bivalve populations: fisheries management surveys provide an incomplete picture. Front. Mar. Sci. 11. https://doi.org/10.3389/fmars.2024.1390763
- Read, R., 2021. Instead of swimming up the too-warm Snake River, endangered salmon take the highway upstream in a pickup truck. Anchorage Dly. News. https://www.adn.com/nation-world/2021/07/26/instead-of-braving-the-too-warm-snake-river-endangered-salmon-take-the-highway-in-a-pickup-truck/
- Reyes, L., Kramer, M.G., 2023. High-elevation snowpack loss during the 2021 Pacific Northwest heat dome amplified by successive spring heatwaves. Npj Clim. Atmospheric Sci. 6, 1–12. https://doi.org/10.1038/s41612-023-00521-0
- Salómon, R.L., Peters, R.L., Zweifel, R., Sass-Klaassen, U.G., Stegehuis, A.I., Smiljanic, M., Poyatos, R., 2022. The 2018 European heatwave led to stem dehydration but not to consistent growth reductions in forests. Nat. Commun. 13. https://doi.org/10.1038/s41467-021-27579-9
- Schuurman, G.W., Cole, D.N., Cravens, A.E., Covington, S., Crausbay, S.D., Hoffman, C.H., Lawrence, D.J., Magness, D.R., Morton, J.M., Nelson, E.A., O'Malley, R., 2022.

 Navigating Ecological Transformation: Resist–Accept–Direct as a Path to a New Resource Management Paradigm. BioScience 72, 16–29.

 https://doi.org/10.1093/biosci/biab067

- Seidl, R., Albrich, K., Thom, D., Rammer, W., 2018. Harnessing landscape heterogeneity for managing future disturbance risks in forest ecosystems. J. Environ. Manage. 209, 46–56. https://doi.org/10.1016/j.jenvman.2017.12.014
- Shivaram, D., 2021. Heat Wave Killed An Estimated 1 Billion Sea Creatures, And Scientists Fear Even Worse. NPR. https://www.npr.org/2021/07/09/1014564664/billion-sea-creatures-mussels-dead-canada-british-columbia-vancouver
- Sloane, S.A., Gordon, A., Connelly, I.D., 2022. Bushtit (Psaltriparus minimus) nestling mortality associated with unprecedented June 2021 heatwave in Portland, Oregon. Wilson J. Ornithol. 134, 155–162. https://doi.org/10.1676/21-00080
- St. Clair, J.B., Richardson, B.A., Stevenson-Molnar, N., Howe, G.T., Bower, A.D., Erickson, V.J., Ward, B., Bachelet, D., Kilkenny, F.F., Wang, T., 2022. Seedlot Selection Tool and Climate-Smart Restoration Tool: Web-based tools for sourcing seed adapted to future climates. Ecosphere 13, e4089. https://doi.org/10.1002/ecs2.4089
- Sterck, F., Song, Y., Poorter, L., 2024. Drought- and heat-induced mortality of conifer trees is explained by leaf and growth legacies. Sci. Adv. 10. https://www.science.org/doi/10.1126/sciadv.adl4800
- Still, C.J., Sibley, A., DePinte, D., Busby, P.E., Harrington, C.A., Schulze, M., Shaw, D.R., Woodruff, D., Rupp, D.E., Daly, C., Hammond, W.M., Page, G.F.M., 2023. Causes of widespread foliar damage from the June 2021 Pacific Northwest Heat Dome: more heat than drought. Tree Physiol. 43, 203–209. https://doi.org/10.1093/treephys/tpac143
- Stotz, G.C., Salgado-Luarte, C., Escobedo, V.M., Valladares, F., Gianoli, E., 2021. Global trends in phenotypic plasticity of plants. Ecol. Lett. 24, 2267–2281. https://doi.org/10.1111/ele.13827
- Swanson, M.E., Magee, M.I., Nelson, A.S., Engstrom, R., Adams, H.D., 2023. Experimental downed woody debris-created microsites enhance tree survival and growth in extreme summer heat. Front. For. Glob. Change 6. https://doi.org/10.3389/ffgc.2023.1224624
- Terray, L., 2023. A Storyline Approach to the June 2021 Northwestern North American Heatwave. Geophys. Res. Lett. 50, e2022GL101640. https://doi.org/10.1029/2022GL101640
- Theobald, D.M., Harrison-Atlas, D., Monahan, W.B., Albano, C.M., 2015. Ecologically-Relevant Maps of Landforms and Physiographic Diversity for Climate Adaptation Planning. PLOS ONE 10, e0143619. https://doi.org/10.1371/journal.pone.0143619

- Thompson, V., Kennedy-Asser, A.T., Vosper, E., Lo, Y.T.E., Huntingford, C., Andrews, O., Collins, M., Hegerl, G.C., Mitchell, D., 2022. The 2021 western North America heat wave among the most extreme events ever recorded globally. Sci. Adv. 8, eabm6860. https://doi.org/10.1126/sciadv.abm6860
- Thurman, L.L., Gross, J.E., Mengelt, C., Beever, E.A., Thompson, L.M., Schuurman, G.W., Hoving, C.L., Olden, J.D., 2021. Applying assessments of adaptive capacity to inform natural-resource management in a changing climate. Conserv. Biol. 36, e13838. https://doi.org/10.1111/cobi.13838
- Thurman, L.L., Stein, B.A., Beever, E.A., Foden, W., Geange, S.R., Green, N., Gross, J.E., Lawrence, D.J., LeDee, O., Olden, J.D., Thompson, L.M., Young, B.E., 2020. Persist in place or shift in space? Evaluating the adaptive capacity of species to climate change. Front. Ecol. Environ. 18, 520–528. https://doi.org/10.1002/fee.2253
- Umanzor, S., Ladah, L., Calderon-Aguilera, L.E., Zertuche-González, J.A., 2017. Intertidal macroalgae influence macroinvertebrate distribution across stress scenarios. Mar. Ecol. Prog. Ser. 584, 67–77. https://doi.org/10.3354/meps12355
- van Hees, D., Hanneman, C., Paradis, S., Camara, A.G., Matsumoto, M., Hamilton, T., Krueger-Hadfield, S.A., Kodner, R.B., 2023. Patchy and Pink: Dynamics of a Chlainomonas sp. (Chlamydomonadales, chlorophyta) algal bloom on Bagley Lake, North Cascades, WA. FEMS Microbiol. Ecol. 99, fiad106. https://doi.org/10.1093/femsec/fiad106
- Varhola, A., Coops, N.C., Weiler, M., Moore, R.D., 2010. Forest canopy effects on snow accumulation and ablation: An integrative review of empirical results. J. Hydrol. 392, 219–233. https://doi.org/10.1016/j.jhydrol.2010.08.009
- Vonich, P.T., Hakim, G.J., 2024. Predictability Limit of the 2021 Pacific Northwest Heatwave From Deep-Learning Sensitivity Analysis. Geophys. Res. Lett. 51, e2024GL110651. https://doi.org/10.1029/2024GL110651
- Watt, C.A., Scrosati, R.A., 2013. Bioengineer effects on understory species richness, diversity, and composition change along an environmental stress gradient: Experimental and mensurative evidence. Estuar. Coast. Shelf Sci. 123, 10–18. https://doi.org/10.1016/j.ecss.2013.02.006
- White, R.H., Anderson, S., Booth, J.F., Braich, G., Draeger, C., Fei, C., Harley, C.D.G., Henderson, S.B., Jakob, M., Lau, C.-A., Mareshet Admasu, L., Narinesingh, V., Rodell, C., Roocroft, E., Weinberger, K.R., West, G., 2023. The unprecedented Pacific Northwest heatwave of June 2021. Nat. Commun. 14, 727. https://doi.org/10.1038/s41467-023-36289-3

- Williams, K., 2021. Experts detail Oregon forest damage in aftermath of June heat dome; long term effects unknown. The Oregonian.

 https://www.oregonlive.com/environment/2021/11/experts-detail-oregon-forest-damage-in-aftermath-of-june-heat-dome-long-term-effects-unknown.html
- Wolff, C.L., Demarais, S., Brooks, C.P., Barton, B.T., 2020. Behavioral plasticity mitigates the effect of warming on white-tailed deer. Ecol. Evol. 10, 2579–2587. https://doi.org/10.1002/ece3.6087
- Zabin, C.J., Jurgens, L.J., Bible, J.M., Patten, M.V., Chang, A.L., Grosholz, E.D., Boyer, K.E., 2022. Increasing the resilience of ecological restoration to extreme climatic events. Front. Ecol. Environ. 20, 310–318. https://doi.org/10.1002/fee.2471