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Microclimate Refugia Are Transient in Stable Old Forests, Pacific Northwest, USA

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Abstract An issue of global concern is how climate change forcing is transmitted to ecosystems. Forest ecosystems in mountain landscapes may demonstrate buffering and perhaps decoupling of long-term rates of temperature change, because vegetation, topography, and local winds (e.g., cold air pooling) influence temperature and potentially create microclimate refugia (areas which are relatively protected from climate change). We tested these ideas by comparing 45-year regional rates of air temperature change to unique temporal and spatial air temperature records in the understory of regionally representative stable old forest at the H.J. Andrews Experimental Forest, Oregon, USA. The 45-year seasonal patterns and rates of warming were similar throughout the forested landscape and matched regional rates observed at 88 standard meteorological stations in Oregon and Washington, indicating buffering, but not decoupling of long-term climate change rates. Consideration of the energy balance explains these results: while shading and airflows produce spatial patterns of temperature, these processes do not counteract global increases in air temperature driven by increased downward, longwave radiation forced by increased anthropogenic greenhouse gases in the atmosphere. In some months, the 45-year warming in the forest understory equaled or exceeded spatial differences of air temperature between the understory and the canopy or canopy openings and was comparable to temperature change over 1,000 m elevation, while in other months there has been little change. These findings have global implications because they indicate that microclimate refugia are transient, even in this forested mountain landscape.

Plain Language Summary To walk into a forest on a warm sunny day is to be impressed by the relatively cool environment under the forest compared to openings. This study examined how the processes that govern air temperature within the forest may influence how forests are experiencing anthropogenic climate change. Drawing on a unique set of climate studies in the Andrews Forest, Oregon, USA, over the past half century, this study demonstrates how a forested mountain landscape influences heat through shading, winds, and other processes, leading to persistent spatial patterns of temperature in the landscape. Nevertheless, air temperature in the forest understory is changing at similar rates and with similar seasonal patterns as at standard meteorological stations throughout the Pacific Northwest (Oregon and Washington). In months with the most rapid warming (July and August), temperature increase over the past 45 years in the forest understory equals or exceeds the spatial differences of air temperature within the forest, or between the forest and openings, and it is comparable to the temperature differences over 1,000 m elevation. These findings are important because they indicate that forests are not protected from climate change, and season-specific changes may control ecosystem response.

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Key Points:

- Spatial variation in temperature (microclimates) persisted for 45 years in the understory of stable, old conifer forests
- Forest understories are buffered, but not decoupled, from regional temperature trends
- In some months, 45-year forest understory warming equaled or exceeded temperature variation over ~1,000 m elevation

Supporting Information:

Supporting Information may be found in the online version of this article.

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1. Introduction

An issue of global concern is how climate change forcing is transmitted to ecosystems. From a spatial perspective, researchers have asked, are there locations where climate remains persistently cooler, and/or is changing less rapidly, than other areas? If so, how can these areas be identified and protected? From a temporal perspective, researchers have asked, how rapidly is climate changing in a given area, and at what times of year or times of day are changes most rapid? How do these rates and timing compare to the ability of populations or communities to tolerate conditions, adapt or migrate?

Research examining spatial aspects of climate change has focused on concepts of buffering, decoupling, and microclimate refugia (or microrefugia). Buffering in the context of climate change refers to differences among locations in the intercepts of linear regressions fitted to time series of temperature, whereas decoupling refers to

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differences among locations in the slopes of the regressions (Lenoir et al., 2017). Microclimate refers to localized surface climate, in other words conditions in the places and at the scales relevant to organisms such as plants and animals (Geiger et al., 2009; Rosenberg et al., 1983). Microclimate is strongly influenced by the planetary boundary layer, the portion of the atmosphere in contact with Earth's surface (Oke, 2002). Microclimate refugia are defined as areas that are relatively protected from contemporary climate change (Morelli et al., 2020), typically interpreted as having lesser extremes or lesser rates of change of temperature.

Research examining the timing of climate change has focused on concepts of climate velocity and seasonality of climate change. Climate velocity refers to the expected speed of spatial displacement (e.g., km yr^{-1}) necessary in order for organisms to maintain constant temperature conditions over time (Loarie et al., 2009). The seasonality of temperature change is important because life histories, and hence ecological processes, are tied to specific, seasonal temperature cues and thresholds (e.g., Ernakovich et al., 2014; Winslow et al., 2017). Long-term ecological research indicates that ecosystem response to climate change depends on the seasonal timing of change across a wide range of ecosystem types (Jones & Driscoll, 2022).

In order for two locations to have consistently different temperature (i.e., different microclimates), they must have different energy balances. The energy balance of a location depends on net radiation (longwave and shortwave) as well as energy exchanges via advection, phase changes of water (latent heat fluxes) and sensible heat fluxes (Oke, 2002). One location may have a lower temperature than another if it is more shaded (reduced net shortwave radiation reaching the soil surface), has higher evaporation rates (latent heat), or is cooled by sensible heat exchanges, including wind or currents (advection). For example, X. Lee et al. (2011) used an energy balance framework to explain why air temperature differed above the forest canopy versus nearby canopy openings.

Over time, increased greenhouse gas emissions from human activities drive the greenhouse effect, which increases net longwave radiation and heats Earth's atmosphere. Because this process affects only the longwave energy term in the energy balance, two locations with differing initial temperature located within the same climate region would be expected to experience similar long-term rates of change in temperature (buffering). In order for rates of temperature change to differ between two locations in the same climate region (decoupling), a component of the energy balance in addition to net longwave radiation must also change (Geiger et al., 2009; Oke, 2002). For example, one location might become more shaded over time, or experience long-term increases in moisture, evaporation, or transpiration. Also, the frequency of regional weather patterns or increased atmospheric CO2 concentrations might alter cold air pooling at some locations (Daly et al., 2009; Rupp et al., 2021).

To our knowledge no studies have evaluated evidence of buffering or decoupling within forested ecosystems using observational records collected over the past half century of climate change. Long-term records of climate within ecosystems are rare, because records used to measure climate change, such as those from the US Historical Climate Network (USHCN) (Menne et al., 2009), are recorded at consistent locations on generally flat, open sites that are relatively free from effects of vegetation disturbance and succession. Published studies also have not linked rates of climate change to the spatial variation in temperature produced by vegetation, topography, and elevation. This study addresses these gaps.

To test these ideas, we drew on unique long-term meteorological records and climate studies from the H.J. Andrews Experimental Forest (64 km^2, hereafter "Andrews Forest"), a forested mountain landscape in Oregon, USA, as well as temperature records from 88 standard meteorological stations in the US Historical Climatology Network (USHCN) in a wide range of locations spanning rainforests to deserts in Oregon and Washington (>500,000 km^2) over the period 1979–2023. Data from the Andrews Forest included air temperature measured for nearly 50 years in the understory of tall, old forests, which experienced minimal disturbance and associated energy balance changes during the study period. These old forest sites span >1000 m of elevation and occur in varied landscape positions. Vegetation and topography affect energy balance components such as net solar radiation and advection (including cold air drainage and pooling) in this landscape (Drake et al., 2022; Rupp et al., 2020; Wolf et al., 2021). Distinct vegetation communities identified in the 1970s in these old forests were associated with temperature (Zobel et al., 1976), implying that microclimates have shaped old forest communities for centuries.

The objectives of the study were to determine season-specific rates of change in forest understory air temperature, to test whether they were consistent with the concepts of buffering or decoupling, and to compare rates of temperature change to spatial variation in a forested mountain landscape. Overall, the study aims to reveal how climate change forcing is transmitted to mountain forest ecosystems generally. The study asked the following questions:

1. How do air temperatures and rates of air temperature change in the understory of stable old forests over the period 1979–2023 differ by landscape position and elevation?
2. How do rates of air temperature change in the forest understory compare with rates at standard meteorological stations in the region?
3. How do rates of temperature change compare to the spatial patterns of temperature produced by vegetation, topography, and elevation?

2. Methods

2.1. Conceptual Approach

It has long been known that forests influence air temperature, wind, and moisture (Anders, 1882; Kittredge, 1948; R. Lee, 1978). However, less is known about how climate change is occurring within forested landscapes. Rates of air temperature change over time at two locations may have different intercepts but the same slope ("buffering" (**A**, Figure 1a)) or they may have different slopes ("decoupling") (**A′**, Figure 1b). If buffering prevails, temperature differs among locations, but the rate of temperature change is the same at all locations (Figure 1b). If decoupling occurs, cooler areas may experience lesser changes, potentially retaining temperatures within hypothetical tolerance limits (blue shading, Figure 1b). Buffering and decoupling have been linked to effects of vegetation (**B′–B**, **C′–C**, Figure 1c), topography, (**D′–D**, Figure 1d) and elevation (**E′–E**, Figure 1d).

Using this framework (Figure 1), we quantified spatial differences in temperature resulting from effects of vegetation, topography, and elevation in the Andrews Forest (Figures 1c and 1d). To determine whether climate change is buffered or decoupled within forests (Figures 1a and 1b), we compared 45-year average temperatures and rates of temperature change among locations in the understory of stable old forest in the Andrews Forest and at standard meteorological stations in the USHCN network in Oregon and Washington. We compared rates of change over time to spatial variation in air temperature associated with vegetation, topography, and elevation (Figure 1).

2.2. Study Site

The study area includes the Andrews Forest (64 km^2) and the states of Oregon and Washington (>500,000 km^2) in the Pacific Northwest region of the United States. Regional ecosystems span rainforests to deserts and include much of the remaining old-growth forest in the US (DellaSala et al., 2022; Pelz et al., 2023; Spies & Franklin, 1988; USDA Forest Service, 2023a, 2023b), of which the Andrews Forest is a prime example (J. F. Franklin & Dyrness, 1973).

The Andrews Forest, established in 1948, is a mountain watershed located on the western slope of the Cascade Range in Oregon (Figure 2). It spans 430 to >1,600 m elevation with steep (30%–60%) slopes shaped by glacial, deep earthflow, debris flow, and fluvial processes (Goodman et al., 2022; Swanson & James, 1975). The quasi-Mediterranean or marine west coast climate has mild, moist winters and warm, dry summers. Deeply incised valleys and steep slopes create a landscape of highly variable solar radiation exposure and promote the frequent formation of cold air pools in valley bottoms (Figure 1d, Rupp et al., 2020). Vegetation is primarily old-growth forest dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) below 1,000 m and sub-alpine forest above 1,000 m. These forests established after widespread fires of ∼1500 CE and the mid 1800s (J. F. Franklin et al., 1981; Morrison & Swanson, 1990; Tepley et al., 2013, 2014; Weisberg & Swanson, 2003).

2.3. Data Sources and Data Analysis

This analysis draws upon regional air temperature data from the Office of the Washington State Climatologist (2024) and multiple unique climate studies in the Andrews Forest over the past 65 years (Figure 2, Table S1 in Supporting Information S1). Climate stations (meteorological stations) were established starting in 1958, and air temperature measurements in the understory of old-growth forest reference stands began in 1970 (Figure 2, Daly et al., 2024, 2019). The reference stands represent regionally representative mature and old-growth forest in plant associations with varied temperature and moisture conditions, that is, microclimates (Table S2 in Supporting

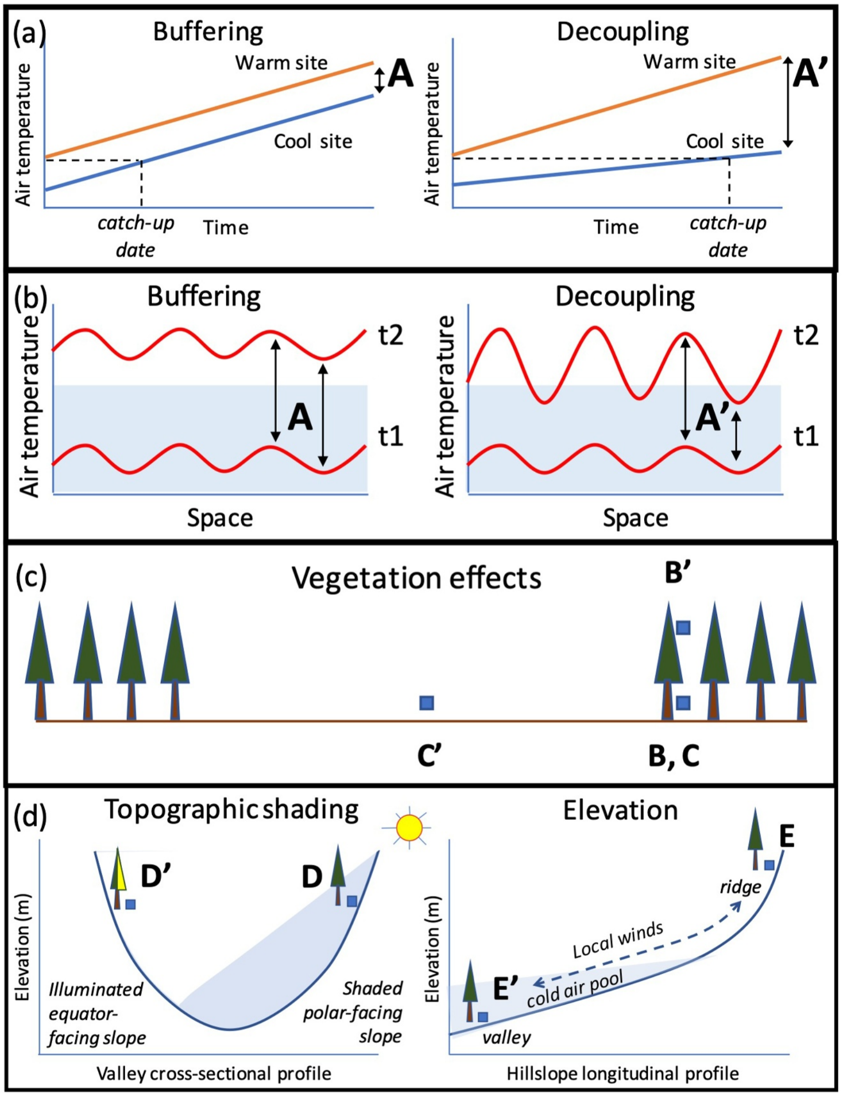

Figure 1. Concepts about temporal change in temperature and factors influencing spatial patterns of temperature. (a) Buffering (**A**) and decoupling (**A′**) in time. (b) Buffering (**A**) and decoupling (**A′**) in space, relative to some hypothetical tolerance limits (blue shading). (c) Vegetation effects produce differences between the forest canopy and the understory (**B′–B**) and between canopy openings and the forest understory (**C′–C**). (d) Effects of topography, that is, illuminated-versus shaded (blue shading) slopes (**D′–D**) and elevation, including air temperature decline as elevation increases and cold air pooling produced by local winds (blue shading) (**E′–E**).

Information S1, Acker et al., 1998; Dyrness et al., 1974; J. F. Franklin & Dyrness, 1973; Hawk et al., 1978; Zobel et al., 1976). Periodic measurements (J. Franklin et al., 2024) have established that vegetation has been stable in these stands from 1970 to 2023 (e.g., Acker et al., 2002, 2023). Towers (Bond, 2012; Thomas, 2013, 2017) and old-growth trees (Frey & Jones, 2020; C. Still, 2023) were vertically instrumented starting in the early 2000s. A distributed temperature sensor network in the forest understory was established in 2009 (Schulze et al., 2023, Table S1 in Supporting Information S1).

2.3.1. Temporal Change in Air Temperature

As the primary source for climate trends in the region, average monthly maximum and minimum air temperature (hereafter, T_{max} and T_{min}) for all USHCN stations throughout Oregon ($n = 40$) and Washington ($n = 44$) was obtained from the Office of the Washington State Climatologist (2024) for the period 1979 to 2023. As a secondary check on whether local weather station trends were consistent with statewide averages, monthly average

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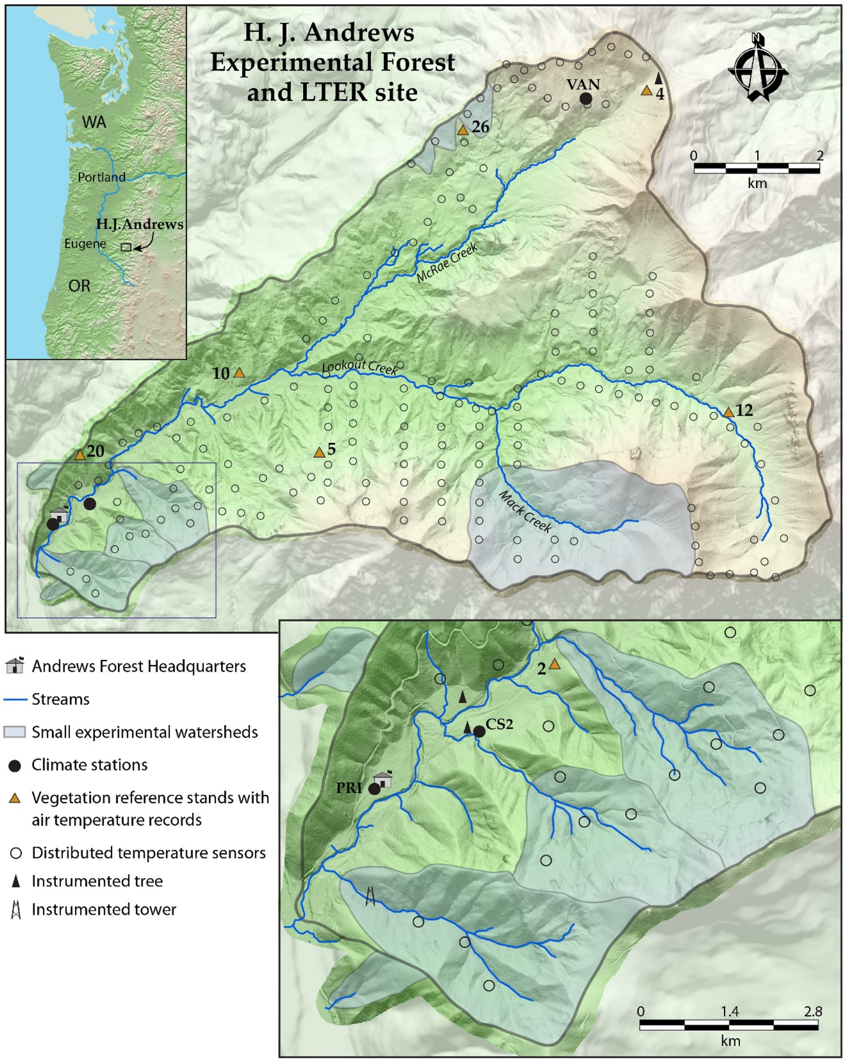

Figure 2. Location of the H.J. Andrews Experimental Forest and climate records used in this study, including meteorological stations, reference stands (numbered triangles), distributed temperature sensors (open circles), vertically instrumented trees (black triangles), and instrumented tower (See Table S1 in Supporting Information S1 for data set characteristics).

T_{max} and T_{min} data also were obtained from four National Weather Service COOP stations near the Andrews Forest: Leaburg (50 km WSW, ID 354811, 206 masl), Lookout Point (65 km SW, ID 355050, 217 masl), Foster Dam (40 km NW, ID 353047, 168 masl), and Belknap Springs (5 km SSE ID 350652, 656 masl) (Menne et al., 2012). USHCN records have been homogenized for climate trend estimation, but COOP station records have not (Menne et al., 2009, 2012); hence results from nearby COOP stations were used merely to confirm that local stations generally followed the same patterns as the statewide homogenized data and are shown only in Supporting Information S1.

Air temperature data from 1979 to 2023 were obtained from sensors located in the understory of mature and old-growth forest reference stands in the Andrews Forest (Daly et al., 2024, Figure 2, Tables S1 and S2 in Supporting Information S1). From 1979 to 1990, sensors were installed at 1 m height above the ground in summer and raised above the snowpack in winter. After 1990, sensors were permanently raised to 1 m above average winter snowpack. Air temperature rarely varies more than 1°C between 1.5 and 10 m height in a vertically instrumented tree (C. Still, 2023). Daily T_{max} and T_{min} have been measured from 1979 to the present at seven reference stands (triangles labeled 2, 4, 5, 10, 12, 20, and 26, Figure 2, hereafter referred to as RS02, etc.). Elevation of the reference stands ranges from 450 to >1,300 masl and landscape positions include toeslope/valley (RS02, RS12), midslope (RS05, RS10), and upper slope/ridge (RS04, RS20, RS26) with various topographic shading (Figure 2,

Table S2 in Supporting Information S1). Monthly T_{max} and T_{min} were calculated from daily values for all months with >25 days of data (Table S3 in Supporting Information S1) for all years and for the 45-year period at each reference stand. Monthly precipitation data from the CS2 meteorological station and T_{max} and T_{min} from the PRI and VAN meteorological stations were obtained for the period 1979 to 2023 (Figure 2, Daly et al., 2019); vegetation succession and disturbance around those stations precluded trend estimation.

In our analysis, we compared air temperature in the forest understory at the Andrews Forest to statewide averages for a large number of stations in OR and WA (USHCN data). Comparisons with homogenized data from many stations in OR and WA (USHCN) provide strength in numbers and more consistent data quality. Rates of change of T_{max} and T_{min} were determined for each month of the year for 1979–2023 using linear regression at the seven reference stands and the statewide averages for USHCN stations in Oregon and Washington (and for subsets of USHCN stations in Oregon, data not shown). Temperature data were checked for normality prior to analysis; regression residuals were normally distributed. The significance of differences in rates was determined based on the 95% confidence intervals around the regression slope coefficients. Bivariate correlations were calculated for T_{max}, T_{min}, and rates of temperature change for each month over the period 1979–2023, among all seven reference stands in the Andrews Forest and the statewide averages for Oregon and Washington. As a check, rates of change of T_{max} were also calculated by season (winter [December–February], spring [March–May], summer [June–August], fall [September–December]).

2.3.2. Spatial Patterns of Air Temperature

We quantified four types of spatial patterns in the forested landscape (Figure 1). Spatial patterns associated with vegetation effects were determined from two vertically instrumented old-growth trees (a tree ∼750 m SW of RS02 [PC002, 488 m elevation] and a tree within 100 m of RS04 [PC017, 1,301 m elevation]) and from three sensors each at PRI (1.5 km SW of RS02) and VAN (1 km W of RS04) meteorological stations (locations in Figure 2). Spatial differences in T_{max} and T_{min} were calculated between 36.5 m above ground in the canopy versus 1.5 m at the base of instrumented trees (B′-B, Figure 1) and between 1.5 m height at meteorological stations in openings versus 1.5 m height at the base of a nearby instrumented tree (C′-C, Figure 1) for each month in 2017 (Table S1 in Supporting Information S1, Daly et al., 2019; Frey & Jones, 2020). Spatial differences of mean monthly T_{max} and T_{min} associated with topography (D′-D, Figure 1d) and elevation (E′-E, Figure 1d, °C/1,000 m) were determined for the period 2008 to 2009 from 168 sensors at 1.5 m height in the forest understory in a distributed sensor network in the Andrews Forest (Schulze et al., 2023, open circles in Figure 2, Table S1 in Supporting Information S1).

2.3.3. Local Winds

To illustrate how forest canopy heating and cooling influence air temperature and local winds, data also were obtained for air temperature, wind speed, and wind direction at the base and the top of the forest canopy at a 56-m instrumented old-growth tree (C. Still, 2023) and a 37-m tower at the mouth of a 1 km^2 tributary watershed (Bond, 2012; Thomas, 2017) located near the mouth of the Andrews Forest watershed (Figure 2, Table S1 in Supporting Information S1). These data were recorded at 5–15-min resolution for periods of weeks to several years. To illustrate effects of local winds on seasonal and landscape patterns of air temperature, hourly data on wind speed and wind direction were obtained from meteorological stations at near-ridge (VAN, 1,263 m) and valley bottom (PRI, 436 m) locations from 2015 to 2018 (Daly et al., 2019) (Figure 2, Table S1 in Supporting Information S1). The number of hours per month with upslope and downslope winds at the near-ridge and valley bottom stations and at the top and the base of the canopy of the instrumented tree was calculated and expressed as a percent of total hours per month.

3. Results

3.1. Buffering, Not Decoupling, of Long-Term Rates of Temperature Change

Rates of change of mean monthly T_{max} and T_{min} did not differ among reference stands in the Andrews Forest or with the statewide average at USHCN stations in Oregon and Washington (Figure 3, Table S3 in Supporting Information S1). Rates of change were highly correlated among reference stands and with USHCN stations in Oregon and Washington (Table S4 in Supporting Information S1). Rates of temperature change in the forest understory at the Andrews Forest and in Oregon and Washington were highest in typically dry summer months

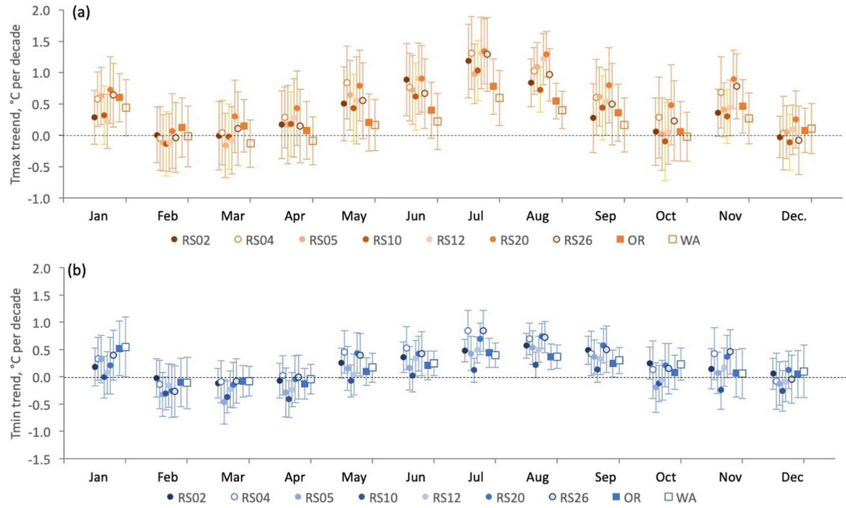

Figure 3. Rates of change of (a) mean monthly maximum air temperature (T_{max}) and (b) mean monthly minimum air temperature (T_{min}) (°C/decade) at reference stands in the Andrews Forest and for statewide average temperature at all USHCN stations in Oregon and Washington ($n = 84$), 1979–2023. Error bars are the 95% confidence interval around the slope term from a linear regression. Symbol colors indicate low to high elevation, left to right, dark to light shades (see Table S2 in Supporting Information S1 reference stand site characteristics). Numbers in Table S3 in Supporting Information S1. Data sources: Daly et al. (2024), Menne et al. (2012), Office of the Washington State Climatologist (2024).

(July and August) and not significantly different from zero in February, March, April, October, and December (Figure 3, Table S3 in Supporting Information S1). Rates in the forest understory were not different for the study period (1979–2023) versus other time periods (start dates of 1970, 1979 and end dates of 2011, 2015, 2019, 2023, data not shown).

The coolest sites in the landscape were RS04 (1,310 m) and RS12 (1,010 m), in a N-trending valley prone to cold air pooling (Rupp et al., 2020, Table S2 in Supporting Information S1) and the warmest site was RS20 (683 m, equator-facing). In months with the most rapid warming rates (July, August), temperature change over less than four decades at the coolest sites (RS04, Jul T_{max} and RS12, Aug T_{min}) had surpassed 1979 temperatures at the warmest site (RS20, Jul T_{max} and Aug T_{min}) (Figures 4a and 4b). Statewide average July T_{max} and August T_{min} in Oregon changed at similar rates (Figures 4a and 4b). In other months (March, April), 45-year temperature changes were less than the spatial differences in air temperature between the coolest site (RS04, a cool moist site at 1,300 m in subalpine forest, Table S2 in Supporting Information S1) and the warmest site (RS20, a hot dry site at 683 m in Douglas-fir/western hemlock forest) (Figures 4c and 4d). Rates of temperature change varied, but no differences in monthly rates of change among sites were significant (Figure 3, Table S3 in Supporting Information S1). Seasonal rates of temperature change in summer (June–August) were higher at two reference stands compared to regional rates in WA and higher at one reference stand compared to regional rates in both OR and WA (Figure 3, Table S3 in Supporting Information S1). Year to year understory air temperature was highly correlated among reference stands at the Andrews Forest, with COOP sites 5–65 km away, and with Oregon and Washington statewide averages (Figure 4, Table S4 in Supporting Information S1); lower correlations for summer T_{min} and winter T_{max} and T_{min} reflect local cold air pooling processes, described below.

3.2. Vegetation Effects on Temperature

The effects of vegetation on forest understory temperature are evident from fine-resolution data in instrumented trees and a tower in the Andrews Forest. Vegetation modifies temperature between the forest canopy and the understory, and energy exchanges between the surface and boundary layer generate local daytime upslope winds and nighttime downslope winds (Figures 1d and 5). The top of the canopy typically reaches a higher T_{max} than the understory (e.g., Figure 5). Daytime heating of the canopy generates upward, upslope, and up-valley winds (dashed double ended arrows), and nighttime cooling generates downward, downslope, and down-valley winds both at the top of the canopy and in the understory (1.5 m) (Figure 5). Daytime wind speeds are much higher at the

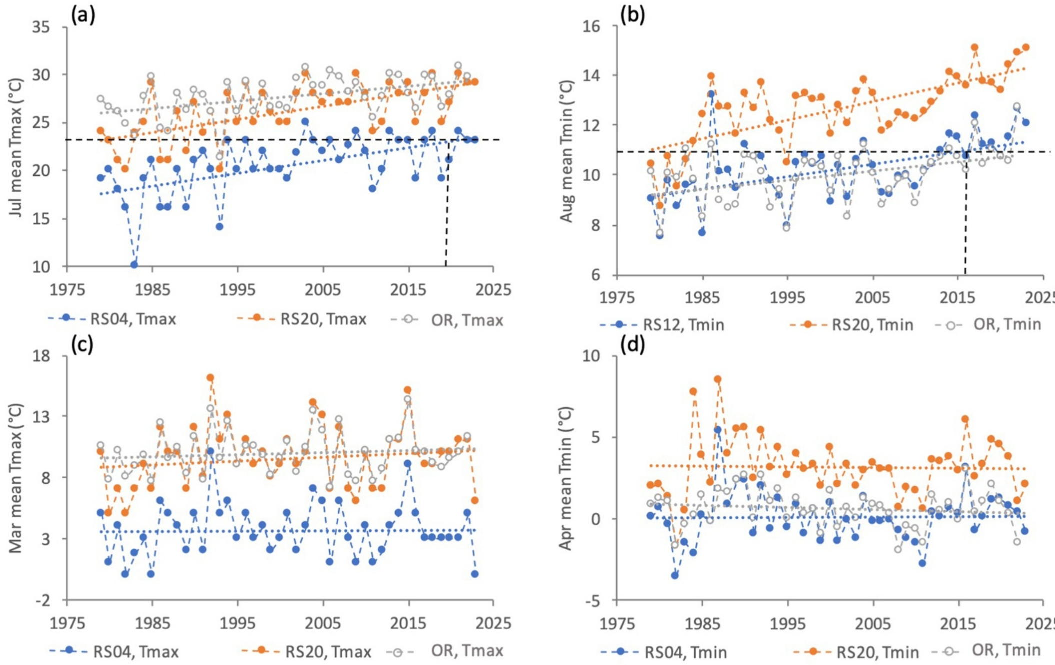

Figure 4. Comparison of temperature time series (1979–2023) in the coolest and warmest sites in the Andrews Forest and statewide average temperature for Oregon for selected months. (a, b) Examples of time series for months with the highest rates of temperature change: monthly T_{max} in July (a) and T_{min} in August (b). (c, d) Examples of time series for months with the lowest rates of temperature change: monthly T_{max} in March (c) and T_{min} in April (d). Plots also illustrate the strong correlations among time series of air temperature within the Andrews Forest and with statewide average temperature for Oregon (Table S4 in Supporting Information S1). Data sources: Daly et al. (2024), Menne et al. (2009).

top of the canopy (up to 3 m s^{-1}) than in the understory (<0.5 m s^{-1}), and downslope winds persist longer in the understory (Figure 5).

Vegetation effects also are evident from comparisons of air temperature in the forest understory versus the forest canopy or versus meteorological stations in canopy openings at the same elevation (B-B′, C-C′, Figure 1). Monthly T_{max} at 1.5 m in the understory of vertically instrumented trees was on average 2–3°C and as much as 4–5°C lower than at 36.5 m in the canopy, and monthly T_{min} in the forest understory was on average 0.1–0.3°C lower than in the canopy (B′-B, Figure 1c, Table S5 in Supporting Information S1). Monthly T_{max} in the forest understory was on average 1–3°C lower than in the canopy opening at the nearby meteorological stations, and monthly T_{min} in the forest understory was on average 0.2–0.8°C higher than in the canopy opening at nearby meteorological stations (C′-C, Figure 1c, Table S5 in Supporting Information S1). The diurnal temperature range was several degrees smaller in the forest understory compared to the canopy or openings.

3.3. Topographic and Elevation Effects on Temperature

Effects of topographic shading and elevation on forest understory temperature within the Andrews Forest are evident from 45-year T_{max}, T_{min}, and mean diel range at the seven reference stands (Figure 6, Table S6 in Supporting Information S1). Understory T_{max} and T_{min} were higher at reference stands (RS20 and RS26) on illuminated slopes versus shaded slopes (RS05, RS12) (D'-D, Figure 1). The 45-year mean T_{max} at reference stands varied with elevation by as much as 7°C in April through July, and T_{min} varied by as much as 3°C in February through May (E′-E, Figures 1 and 6, Table S6 in Supporting Information S1).

Topographic shading/illumination effects on air temperature in the forest understory also were evident in 2009–2018 mean monthly values from distributed temperature sensors at 1.5 m height in the Andrews Forest (D′-D, Figures 1 and 7). Monthly T_{max}, T_{min}, and average diel range in the understory varied by 3–5°C among slopes with varied orientation and gradients within 25-m elevation bands. Monthly T_{max} and T_{min} in the understory of reference stands generally fell within the range of the forest understory sensor network (Figures 2 and 7).

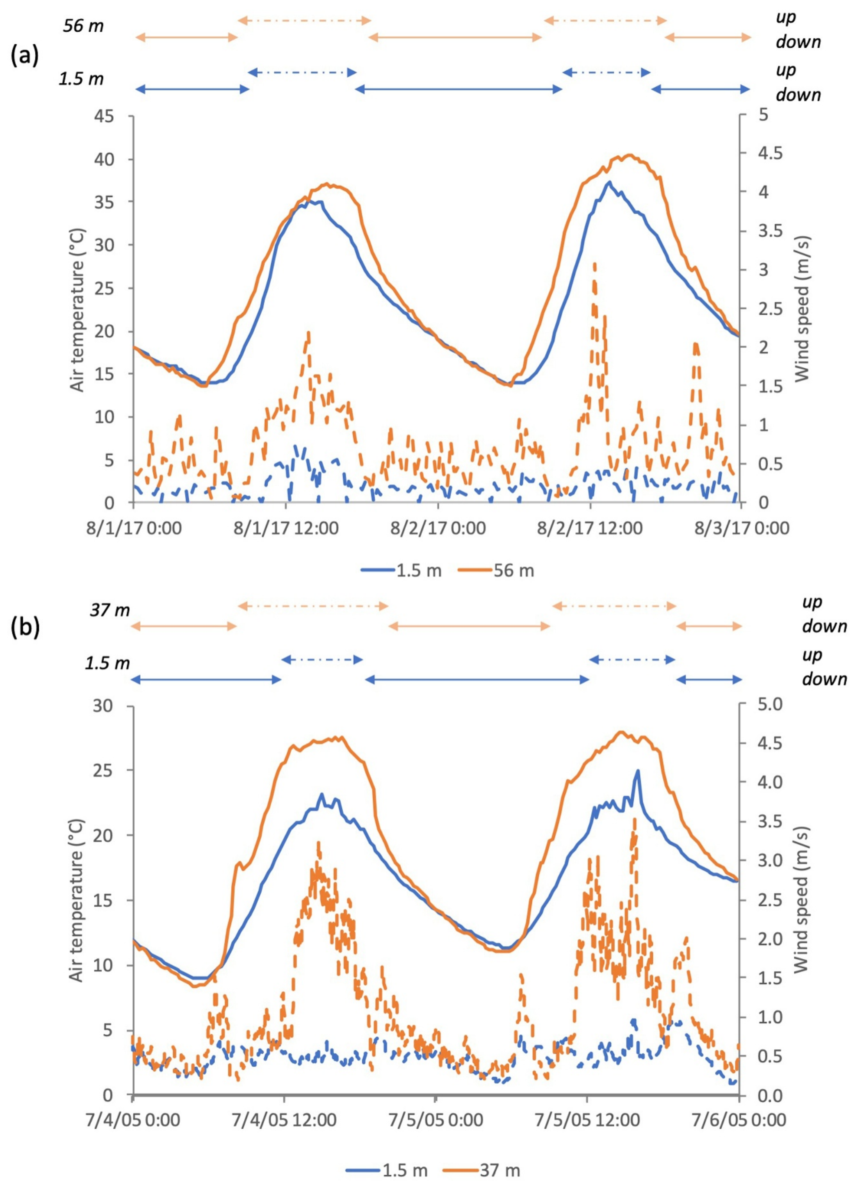

Figure 5. Air temperature and wind at the top and the base of (a) a 56-m instrumented tree and (b) a 36-m tower at the mouth of a 1 km^2 tributary on typical clear days in July and August. Data excerpted from multi-year data sets (C. J. Still et al., 2023; Thomas, 2013). Tree and tower locations are shown in Figure 2.

T_{max} and T_{min} in the forest understory also varied with elevation (450–1,600 m) (Figure 7). The elevation gradient of mean monthly T_{max} (daytime) and T_{min} (nighttime) (E′-E, Figure 1) varied from −1 to −7°C/1,000 m, depending on month and time of day. Elevation gradients were steep for mean monthly T_{max} and T_{min} in spring (Figure 7b) and T_{max} in summer (Figure 7c) but flat for T_{max} and T_{min} in winter (Figure 7a) and T_{min} in summer (Figure 7c) and fall (Figure 7d).

3.4. Air Flows, Air Temperature, and Rates of Change of Air Temperature

Elevation gradients of air temperature in the forest understory (Figure 7, Table S5 in Supporting Information S1) are influenced by vegetation effects on air temperature and air flows (Figures 5 and 8). Air flows were mostly upslope/up-valley during the day in spring and summer (April–September) in the valley (~450 m) and year-round at the near-ridge station (1,300 m) (Figure 8a). Daytime air flows were predominantly downslope in winter in the valley at both the meteorological station and the instrumented tree (Figure 8a). Nighttime air flows were

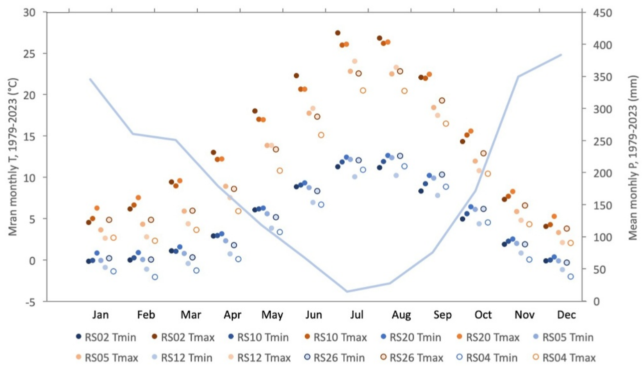

Figure 6. Mean monthly maximum (T_{max}) and minimum (T_{min}) air temperature and average diel temperature range at reference stands in the Andrews Forest, 1979–2023 (open and filled circles of different colors). For each month, reference stands are arranged from low to high elevation, left to right, dark to light shades. Elevations are: RS02—490 m, RS10—610 m, RS20—683 m, RS05—880 m, RS12—1,010 m, RS26—1040 m, RS04—1310 m (Table S2 in Supporting Information S1). Mean monthly precipitation (P, blue line), 1979–2023 at CS2 meteorological station (430 m). Data sources: Daly et al. (2019) and Daly et al. (2024).

predominantly downslope in all months, especially July to September, at both the meteorological station and the instrumented tree in the valley, and they are frequent at the near-ridge station (Figure 8b).

Elevation gradients of mean monthly T_{max} and T_{min} in the forest understory (blue lines in Figure 8, data from Figure 7) match the frequency of downslope air flows (colored bars) (Figure 8). When down-valley air flows are infrequent (e.g., spring and summer days), elevation gradients of mean monthly T_{max} and T_{min} are closest to the environmental lapse rate (−6.5°C/1,000 m). When down-valley air flows are frequent (e.g., fall and winter days, all nights), elevation gradients of mean monthly T_{max} and T_{min} are much less negative. When elevation gradients of mean monthly T_{max} and T_{min} in the forest understory are steep, predominantly upslope air flows have median wind speeds of 0.5–1.5 m s^{-1} (data not shown), indicating that air is well-mixed within the landscape and the forest canopy. When elevation gradients of understory temperature are flat, downslope air flows have median wind speeds of 0.2–0.5 m s^{-1} at the meteorological station and the instrumented tree in the valley, indicating frequent conditions in which air is less well-mixed in the forest landscape.

The seasonal timing of rates of air temperature change does not match the seasonal timing of cold air pooling (Figures 3 and 8). Both high (July) and low

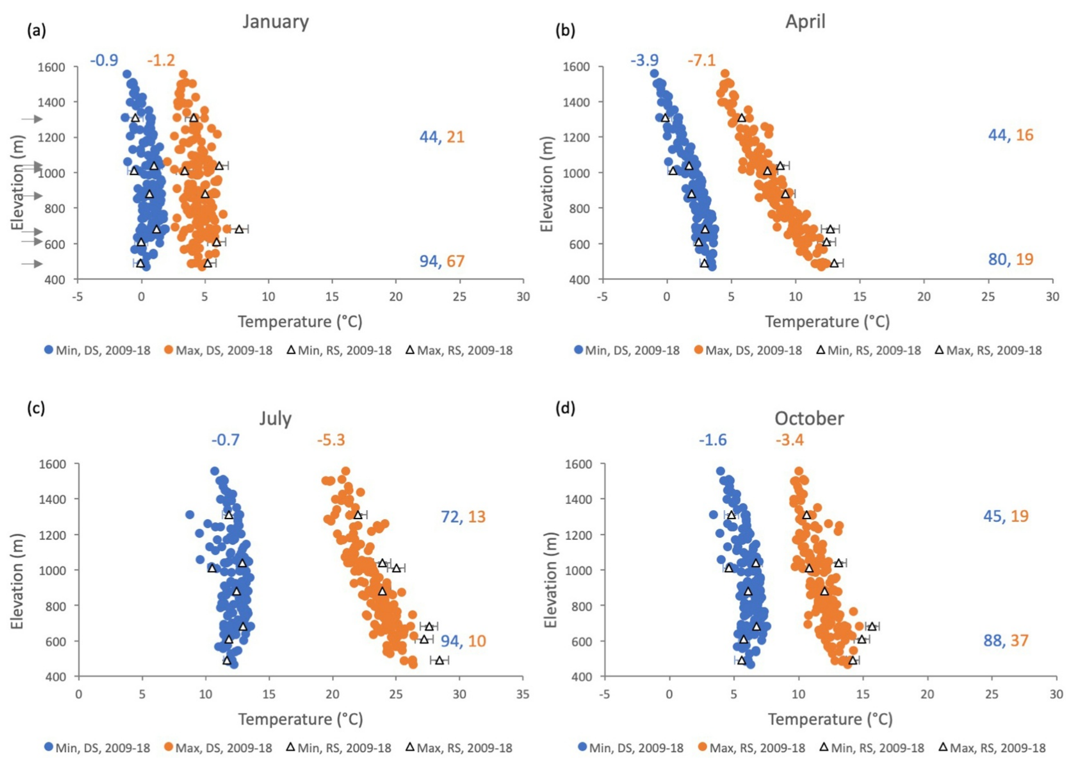

Figure 7. Average monthly T_{min} (blue) and T_{max} (orange), 2009–2018, at distributed temperature sensors (circles) and reference stands (open black triangles) in the forest understory (*X* axis) versus elevation (*Y*-axis) for (a) January, (b) April, (c) July, and (d) October. Values are mean ± SE (sensor height 1.5 m). Arrows at left in (a) indicate elevations of the seven reference stands used for long-term trend analysis (Figure 3). Numbers at top are the temperature gradient with elevation (°C/1,000 m) based on linear models fitted to the 2009–2018 means (circles). Numbers to the right are the percent of hours of down-slope, down-valley winds during the night (first number) and during the day (second number) at near ridge (VAN, 1,268 m, Figure 2) and valley bottom (PRI, 436 m, Figure 2) meteorological stations from 2015 to 2018. Data sources: Schulze et al. (2023) and Daly et al. (2024).

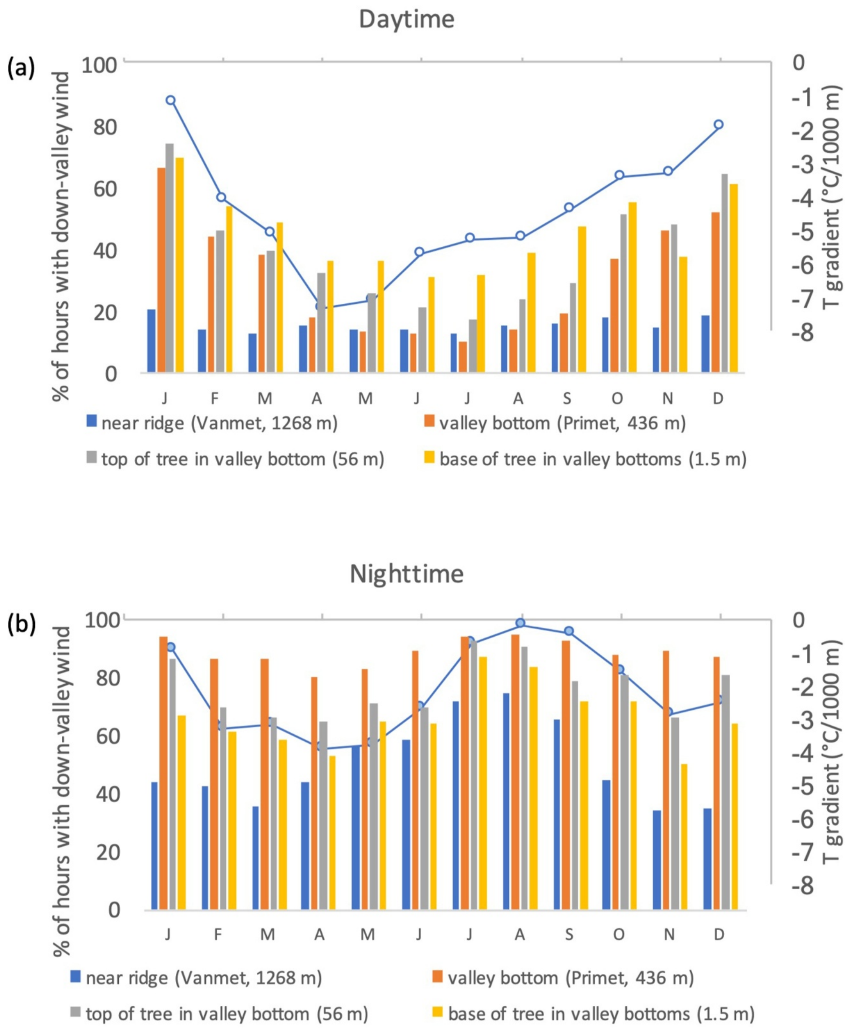

Figure 8. Effects of the forest canopy and mountain topography on the frequency of downslope winds (vertical bars) and the gradient of air temperature with elevation (open blue dots and line) during (a) daytime and (b) nighttime, by month, in a forested mountain landscape (Andrews Forest). Data are from meteorological stations near the ridge (blue bars, VAN, 1,263 m, Figure 1) and at the valley bottom (orange bars, PRI, 436 m) for the period 2014 to 2018 and at the top (gray bars) and base (yellow bars) of an instrumented tree in the valley bottom for 2017. Data sources: Daly et al. (2019), Schulze et al. (2023), and C. Still (2023).

(April) rates of warming occurred in months when steep elevation gradients of temperature (Figure 7), upslope winds (Figure 8), and high correlations of air temperature among sites (Table S4 in Supporting Information S1) indicate that air in the forest mountain landscape is well mixed with regional air masses (April days and nights, July days). Both high (January) and low (October) rates of warming also occurred in months when flat elevation gradients of temperature, downslope winds, and lower correlations of air temperature among sites indicate that air in the forest landscape is frequently isolated from regional air masses (January days and nights, October nights) (Figures 3, 7, and 8). Collectively these measurements demonstrate that air is continually in motion, moving heat within the forest canopy and between the forest and the atmosphere at time scales from hours to decades both during periods when cold air pooling is frequent and when it is rare, thereby transmitting long-term regional temperature change throughout the landscape.

3.5. Spatial Variation Versus Rates of Change in Air Temperature

Warming over time in the forest understory exceeded spatial differences in temperature in many months of the year. The 45-year increases of T_{max} (January, May through August, and October) and of T_{min} (January, May

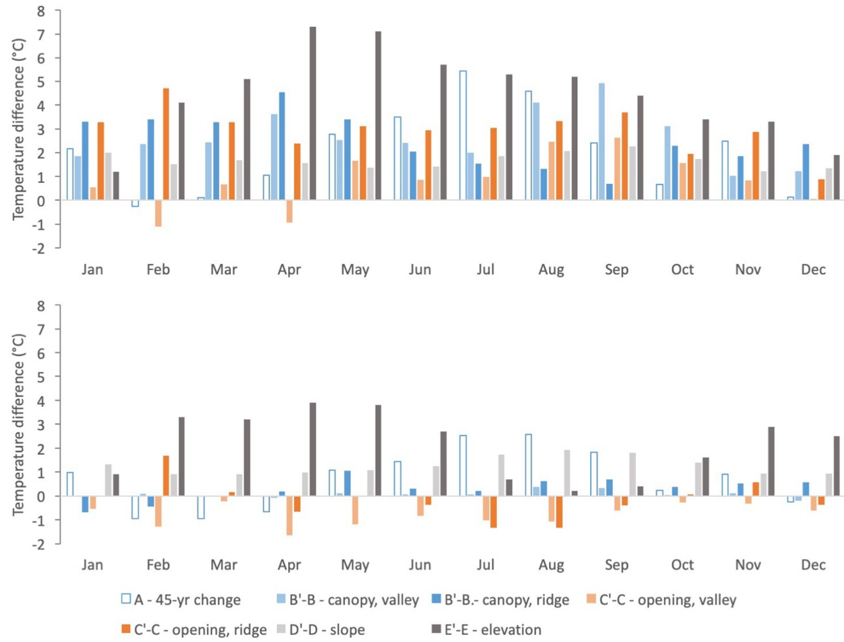

Figure 9. Long-term rates of temperature change exceed spatial temperature differences in the Andrews Forest in many months of the year. (a) Mean monthly T_{max} and (b) mean monthly T_{min}. Columns (from Figure 1) are A = 45-year total temperature change (Figure 3, Table S3N in Supporting Information S1) (°C/decade times 4.5 decades, 1979–2023); B′-B = temperature at 36.5 m height in the canopy (B′) minus at 1.5 m in the understory (B) of instrumented trees from trees in valley floor and ridge landscape positions, for 2016–2017 (Table S1 in Supporting Information S1); C′-C = temperature at 1.5 m in openings (C′) versus at 1.5 m in the understory (C) of nearby forest in valley floor and ridge landscape positions, for 2016–2017 (Table S1 in Supporting Information S1); temperature in the forest understory on equator-facing slopes (D′) versus polar-facing slopes (D) controlling for elevation (Figure 7); E′-E = temperature in the understory at low elevation (E′] minus high elevation (E] (°C/1,000 m) (Figure 7).

through September, and November) equaled or exceeded the spatial differences in forest understory temperature between the canopy (36.5 m) and the understory (1.5 m) of instrumented trees (B′-B), between canopy openings and nearby forest understory (C′-C), and with topographic shading (D′-D) (Figures 1 and 9, Tables S5 and S6 in Supporting Information S1). The 45-year increases of T_{max} (July) and of T_{min} (July through September) also equaled or exceeded the spatial variation of understory temperature from low to high elevation (E′-E) (Figure 6, Table S5 in Supporting Information S1).

4. Discussion

To walk into a forest on a warm sunny day is to be impressed by the relatively cool environment under the forest compared to openings. Such effects of the forest canopy on temperature have long been recognized. Less well understood, however, is how the processes that govern understory air temperature may influence how forests are experiencing anthropogenic climate change.

Drawing on a unique set of climate studies in the Andrews Forest over the past half century (Table S1 in Supporting Information S1), this study highlights how a forested mountain landscape influences the energy budget via impacts on radiation fluxes and latent and sensible heat exchanges (Figure 1), producing diverse microclimates (Figure 6) associated with distinct plant communities identified in the 1970s (Dyrness et al., 1974; Zobel et al., 1976).

Nevertheless, rates and seasonal patterns of air temperature change did not differ among microclimates in the forest, or between the forest understory and standard (USHCN) meteorological stations in Oregon and Washington, which encompass rainforests to deserts (Figure 3, Table S3 in Supporting Information S1). Forty-five-year time series of air temperature change were consistent with the concept of buffering (different intercepts, similar slopes, sensu Lenoir et al., 2017), but not decoupling (different slopes). Stations in our analysis differed in shading, moisture, and cold air pooling, producing differences in mean T_{max} and T_{min} among sites (buffering) (Figure 6). Long-term changes in forest shading, moisture, or cold air pooling could potentially produce different rates of temperature change among stations (decoupling), but we did not find any evidence that these factors led to lower rates of long-term warming in the understory of stable forests. On the contrary, seasonal (summer) rates of temperature change were higher in three sites in the forest understory compared to average rates in the region.

An energy budget perspective (Geiger et al., 2009; Oke, 2002) reveals how microclimates result from the interaction of solar and thermal radiation with vegetation and topography and their effects on heating and cooling, local winds, and cold air pooling (Figures 1, 5–9), as demonstrated by many studies in the Andrews Forest (Drake et al., 2022; Dyrness et al., 1974; Rosentrater, 1997; Rupp et al., 2020; Sibley et al., 2022; Smith, 2002; Zobel et al., 1976) and elsewhere (e.g., De Frenne et al., 2021; Dobrowski, 2011; Minder et al., 2010; Nadeau et al., 2022; Pastore et al., 2022; Vitasse et al., 2017; Zellweger et al., 2020). However, the processes that create microclimate are distinct from, and do not counteract increased downward longwave radiation from increased greenhouse gases in the atmosphere.

These findings are globally relevant because they demonstrate how vegetation, topography and elevation combine with local winds to produce microclimates, while also mixing heat and moisture within forested mountain landscapes—a new finding relative to prior studies (e.g., Davis et al., 2019; De Frenne et al., 2021; de Lombaerde et al., 2022; Dobrowski, 2011; Drake et al., 2022; Finocchiaro et al., 2023; Frey et al., 2016; Lenoir et al., 2013; MacLean et al., 2021; Patsiou et al., 2017; Rupp et al., 2020; Sibley et al., 2022; Wolf et al., 2021; Zellweger et al., 2020).

These findings also are broadly relevant because they indicate that spatial patterns of temperature (microclimates) provide only a transient refuge from climate change, even in stable forests in a mountain landscape. When buffering prevails, ecosystem response depends on how rapidly temperatures favorable to ecological processes disappear from a landscape. In multiple months, the 45-year warming equaled or exceeded the spatial differences in temperature among microclimates in the landscape (Figures 1, 4, 6, and 9).

Warming may surpass season-specific temperature cues or thresholds for ecological processes. For example, in the Andrews Forest, summer temperatures in the sub-alpine forest zone (>1,000 m) now resemble those of the Douglas-fir/western hemlock forest zone (<1,000 m). Warmer summers with more frequent heat waves may exceed thresholds for leaf metabolism (e.g., C. J. Still et al., 2023) and impede forest growth (Ford et al., 2017) and regeneration after disturbance. Warmer summers may alter temperature cues for pollinator activity (Jones et al., 2018; Vickers, 2022) and neotropical migratory bird species (Betts et al., 2018; Kim et al., 2022). In contrast, the lack of warming in late winter/early spring is consistent with smaller than expected declines in seasonal snowpack since 1980 (Nolin & Daly, 2006; Siler et al., 2019). Season-specific changes in temperature are likely to produce complex patterns of change in phenology (e.g., Cleland et al., 2007; Ward et al., 2018), decomposition (e.g., Harmon, 2021; Harmon et al., 2020), and nutrient export (e.g., Argerich et al., 2016; Lajtha & Jones, 2018). High rates of warming in July and August (Figure 3) likely have contributed to increased forest fire intensity and spread in the region (e.g., Abatzoglou & Williams, 2016; Jain et el., 2024; Williams et al., 2019), and indeed, 70% of the Andrews Forest burned in 2023, which will further alter microclimates. Such complex, season-specific changes in ecological processes have been observed at long-term ecological research sites in many types of ecosystems (Campbell et al., 2022; Ducklow et al., 2022; Hudson et al., 2022; Jones & Driscoll, 2022; Reed et al., 2022).

As noted in the introduction, in order for a location to be decoupled in the context of long-term climate change, it must experience some change in a component of the energy budget that counteracts the warming from increased downward longwave radiation. For example, Daly et al. (2009) hypothesized that an increase in the frequency of synoptic circulation patterns associated with cold air pooling events could counteract warming trends in topographic depressions. However, Pepin et al. (2011) found no difference in the rate of temperature change 1948–2006 at 460 Global Historical Climatology Network sites in locations where the free atmosphere controls temperature versus locations prone to cold air pooling, and the frequency of synoptic circulation patterns associated with cold air pooling did not change appreciably over that period.

5. Conclusion

This study tested how the processes that produce diverse microclimates within ecosystems contribute to climate refugia. Rates of temperature change in the understory of stable old forests in a 64 km^2 mountain landscape were similar to those across the states of Oregon and Washington (>500,000 km^2), indicating that forest understories are buffered, but not decoupled, from regional temperature trends. As expected from an energy balance perspective, rates of temperature change were independent of vegetation, topographic shading, or the presence of cold air pooling, and no long-term compensatory changes were detected that would produce decoupling. In the most rapidly warming times of year (July and August) areas of relatively cool temperatures four decades ago have apparently been eliminated over the >1,000-m elevation range of this landscape.

The findings of this study are of global importance because these unusual records demonstrate that forest understories are buffered but not decoupled from climate change. The findings illustrate a general principle: that from an energy balance perspective, microclimate refugia are not decoupled from broader climate warming trends driven by increased downwelling longwave radiation, unless some concurrent change in the energy balance compensates for this heating. More work is needed to examine microclimate refugia from an energy balance perspective, and to relate season-specific rates of change to ecological thresholds.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

Many data sets that support the findings of this study are openly available from the Andrews Forest Program website, https://andrewsforest.oregonstate.edu. All data sets are documented by citations in the text and included in the reference section. Andrews Forest data sets are available from DOIs in Bond (2012), Daly et al. (2019, 2024), Franklin et al. (2024), Frey and Jones (2020), Schulze et al. (2023), C. Still (2023), Thomas (2013, 2017). USHCN and COOP station data are available from Menne et al. (2009, 2012), https://climate.washington.edu/climate-data/trendanalysisapp/.

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References

Abatzoglou, J. T., & Williams, A. P. (2016). Impact of anthropogenic climate change on wildfire across western US forests. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(42), 11770–11775. https://doi.org/10.1073/pnas.1607171113

Acker, S. A., Boetsch, J. R., Fallon, B., & Denn, M. (2023). Stable background tree mortality in mature and old-growth forests in western Washington (NW USA). *Forest Ecology and Management*, *532*, 120817. https://doi.org/10.1016/j.foreco.2023.120817

Acker, S. A., Halpern, C. B., Harmon, M. E., & Dyrness, C. T. (2002). Trends in bole biomass accumulation, net primary production and tree mortality in *Pseudotsuga menziesii* forests of contrasting age. *Tree Physiology*, *22*(2–3), 213–217. https://doi.org/10.1093/treephys/22.2-3.213

Acker, S. A., McKee, W. A., Harmon, M. E., & Franklin, J. F. (1998). Long-term research on forest dynamics in the Pacific Northwest: A network of permanent forest plots. In F. Dallmeier & J. A. Comiskey (Eds.), *Forest biodiversity in North, Central, and South America and the Caribbean: Research and Monitoring; 1995 May 23–25* (Vol. 21). The Parthenon Publishing Group, Inc. 93-106. [Jeffers, J. N. R., ed; Man and the Biosphere Series.

Anders, J. M. (1882). Forests-Their influence upon climate and rainfall. *The American Naturalist*, *16*(1), 19–30. https://doi.org/10.1086/272992

Argerich, A., Haggerty, R., Johnson, S. L., Wondzell, S. M., Dosch, N., Corson-Rikert, H., et al. (2016). Comprehensive multiyear carbon budget of a temperate headwater stream. *Journal of Geophysical Research: Biogeosciences*, *121*(5), 1306–1315. https://doi.org/10.1002/2015jg003050

Betts, M. G., Phalan, B., Frey, S. J. K., Rousseau, J. S., & Yang, Z. (2018). Old-growth forests buffer climate-sensitive bird populations from warming. *Diversity and Distributions*, *24*(4), 439–447. https://doi.org/10.1111/ddi.12688

Bond, B. (2012). Airshed tower data in Watershed 1 in the Andrews Experimental Forest from streaming data, 2005–2010 [Database]. *Long-Term Ecological Research. Forest Science Data Bank, Corvallis, OR*. http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=MV001

Campbell, J. L., Driscoll, C. T., Jones, J. A., Boose, E. R., Dugan, H. A., Groffman, P. M., et al. (2022). Forest and freshwater ecosystem responses to climate change and variability at US LTER sites. *BioScience*, *72*(9), 851–870. https://doi.org/10.1093/biosci/biab124

Cleland, E. E., Chuine, I., Menzel, A., Mooney, H. A., & Schwartz, M. D. (2007). Shifting plant phenology in response to global change. *Trends in Ecology & Evolution*, *22*(7), 357–365. https://doi.org/10.1016/j.tree.2007.04.003

Daly, C., Conklin, D. R., & Unsworth, M. H. (2009). Short Communication Local atmospheric decoupling in complex topography alters climate change impacts. *International Journal of Climatology*, 10.

Daly, C., McKee, W., Schulze, M., Remillard, S., Cohn, G., Kennedy, A., & Schmidt, S. (2024). Air and soil temperature data from the Reference Stand network at the Andrews Experimental Forest, 1971 to present [Database]. *Long-Term Ecological Research. Forest Science Data Bank, Corvallis, OR*. https://doi.org/10.6073/pasta/374667d4bdcb0cecad04bcf84708f044

Daly, C., Schulze, M., & McKee, W. (2019). Meteorological data from benchmark stations at the HJ Andrews Experimental Forest, 1957 to present [Database]. *Long-Term Ecological Research. Forest Science Data Bank, Corvallis, OR*. https://doi.org/10.6073/pasta/c021a2ebf1f91adf0ba3b5e53189c84f

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), 1–11. https://doi.org/10.1111/ecog.03836

De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B. R., Zellweger, F., Aalto, J., et al. (2021). Forest microclimates and climate change: Importance, drivers and future research agenda. *Global Change Biology*, *27*(11), 2279–2297. https://doi.org/10.1111/gcb.15569

DellaSala, D. A., Mackey, B., Norman, P., Campbell, C., Comer, P. J., Kormos, C. F., et al. (2022). Mature and old-growth forests contribute to large-scale conservation targets in the conterminous United States. *Frontiers in Forests and Global Change*, *5*, 979528. https://doi.org/10.3389/ffgc.2022.979528

De Lombaerde, E., Vangansbeke, P., Lenoir, J., Van Meerbeek, K., Lembrechts, J., Rodríguez-Sánchez, F., et al. (2022). Maintaining forest cover to enhance temperature buffering under future climate change. *Science of the Total Environment*, *810*, 151338. https://doi.org/10.1016/j.scitotenv.2021.151338

Dobrowski, S. Z. (2011). A climatic basis for microrefugia: The influence of terrain on climate. *Global Change Biology*, *17*(2), 1022–1035. https://doi.org/10.1111/j.1365-2486.2010.02263.x

Drake, S. A., Rupp, D. E., Thomas, C. K., Oldroyd, H. J., Schulze, M., & Jones, J. A. (2022). Increasing daytime stability enhances downslope moisture transport in the subcanopy of an even-aged conifer forest in Western Oregon, USA. *Journal of Geophysical Research: Atmospheres*, *127*(9). https://doi.org/10.1029/2021JD036042

Ducklow, H., Cimino, M., Dunton, K. H., Fraser, W. R., Hopcroft, R. R., Ji, R., et al. (2022). Marine pelagic ecosystem responses to climate variability and change. *BioScience*, *72*(9), 827–850. https://doi.org/10.1093/biosci/biac050

Dyrness, C. T., Franklin, J. F., & Moir, W. H. (1974). A preliminary classification of forest communities in the central portion of the western Cascades in Oregon. In *Coniferous Forest Biome Bull. 4* (p. 123). University of Washington.

Ernakovich, J. G., Hopping, K. A., Berdanier, A. B., Simpson, R. T., Kachergis, E. J., Steltzer, H., & Wallenstein, M. D. (2014). Predicted responses of arctic and alpine ecosystems to altered seasonality under climate change. *Global Change Biology*, *20*(10), 3256–3269. https://doi.org/10.1111/gcb.12568

Finocchiaro, M., Médail, F., Saatkamp, A., Diadema, K., Pavon, D., & Meineri, E. (2023). Bridging the gap between microclimate and microrefugia: A bottom-up approach reveals strong climatic and biological offsets. *Global Change Biology*, *29*(4), 1024–1036. https://doi.org/10.1111/gcb.16526

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. *Global Change Biology*, *23*(8), 3348–3362. https://doi.org/10.1111/gcb.13690

Franklin, J., Bell, D., Remillard, S., Pabst, R., Bluhm, A., & Powers, M. (2024). Long-term growth, mortality and regeneration of trees in permanent vegetation plots in the Pacific Northwest, 1910 to present. Long-Term Ecological Research [Database]. *Forest Science Data Bank, Corvallis, OR*. https://doi.org/10.6073/pasta/5835a1fadb7fd65842f90256edae999c

Franklin, J. F., Cromack, K., Denison, W., McKee, A., Maser, C., Sedell, J., et al. (1981). *Ecological characteristics of old-growth Douglas-fir forests* Gen. Tech. Rep. PNW-118 (p. 48). U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station.

Franklin, J. F., & Dyrness, C. T. (1973). *Natural vegetation of Oregon and Washington* (Vol. 8). US Government Printing Office.

Frey, S., & Jones, J. (2020). Vertical tree air temperature measurements within the canopy of the HJ Andrews Experimental Forest, 2011-2019 [Database]. *Long-Term Ecological Research. Forest Science Data Bank, Corvallis, OR*. https://doi.org/10.6073/pasta/50c497d3d87de2d623d9d88c8c486cf1

Frey, S. J., 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*, *2*(4), e1501392. https://doi.org/10.1126/sciadv.1501392

Geiger, R., Aron, R. H., & Todhunter, P. (2009). *The climate near the ground*. Rowman & Littlefield.

Goodman, A. C., Segura, C., Jones, J. A., & Swanson, F. J. (2022). Seventy years of watershed response to floods and changing forestry practices in western Oregon, USA. *Earth Surface Processes and Landforms*, *48*(6), 1–16. https://doi.org/10.1002/esp.5537

Harmon, M. E. (2021). The role of woody detritus in biogeochemical cycles: Past, present, and future. *Biogeochemistry*, *154*(2), 349–369. https://doi.org/10.1007/s10533-020-00751-x

Harmon, M. E., Fasth, B. G., Yatskov, M., Kastendick, D., Rock, J., & Woodall, C. W. (2020). Release of coarse woody detritus-related carbon: A synthesis across forest biomes. *Carbon Balance and Management*, *15*(1), 1–21. https://doi.org/10.1186/s13021-019-0136-6

Hawk, G. M., Franklin, J. F., McKee, W. A., & Brown, R. B. (1978). H.J. Andrews Experimental Forest reference stand system: Establishment and use history. In *Coniferous Forest Biome Bull. 12* (p. 79). University of Washington.

Hudson, A. R., Peters, D. P., Blair, J. M., Childers, D. L., Doran, P. T., Geil, K., et al. (2022). Cross-site comparisons of dryland ecosystem response to climate change in the US Long-Term Ecological Research Network. *BioScience*, *72*(9), 889–907. https://doi.org/10.1093/biosci/biab134

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. *Communications Earth & Environment*, *5*(1), 202. https://doi.org/10.1038/s43247-024-01346-2

Jones, J. A., & Driscoll, C. T. (2022). Long-term ecological research on ecosystem responses to climate change. *BioScience*, *72*(9), 814–826. https://doi.org/10.1093/biosci/biac021

Jones, J. A., Hutchinson, R., Moldenke, A., Pfeiffer, V., Helderop, E., Thomas, E., et al. (2018). Landscape patterns and diversity of meadow plants and flower-visitors in a mountain landscape. *Landscape Ecology*, *34*(5), 997–1014. https://doi.org/10.1007/s10980-018-0740-y

Kim, H., McComb, B. C., Frey, S. J. K., Bell, D. M., & Betts, M. G. (2022). Forest microclimate and composition mediate long-term trends of breeding bird populations. *Global Change Biology*, *28*(21), 6180–6193. https://doi.org/10.1111/gcb.16353

Kittredge, J. (1948). *Forest influences: The effects of woody vegetation on climate, water, and soil, with applications to the conservation of water and the control of floods and erosion*. McGraw-Hill. Retrieved from https://digital.library.cornell.edu/catalog/chla3137328

Lajtha, K., & Jones, J. (2018). Forest harvest legacies control dissolved organic carbon export in small watersheds, western Oregon. *Biogeochemistry*, *140*(3), 299–315. https://doi.org/10.1007/s10533-018-0493-3

Lee, R. (1978). *Forest microclimatology*. Columbia University Press.

Lee, X., Goulden, M. L., Hollinger, D. Y., Barr, A., Black, T. A., Bohrer, G., et al. (2011). Observed increase in local cooling effect of deforestation at higher latitudes. *Nature*, *479*(7373), 384–387. https://doi.org/10.1038/nature10588

Lenoir, J., Graae, B. J., Aarrestad, P. A., Alsos, I. G., Armbruster, W. S., Austrheim, G., et al. (2013). Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. *Global Change Biology*, *19*(5), 1470–1481. https://doi.org/10.1111/gcb.12129

Lenoir, J., Hattab, T., & Pierre, G. (2017). Climatic microrefugia under anthropogenic climate change: Implications for species redistribution. *Ecography*, *40*(2), 253–266. https://doi.org/10.1111/ecog.02788

Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, *462*(7276), 1052–1055. https://doi.org/10.1038/nature08649

Maclean, I. M., Duffy, J. P., Haesen, S., Govaert, S., De Frenne, P., Vanneste, T., et al. (2021). On the measurement of microclimate. *Methods in Ecology and Evolution*, *12*(8), 1397–1410. https://doi.org/10.1111/2041-210x.13627

Menne, M. J., Durre, I., Vose, R. S., Gleason, B. E., & Houston, T. G. (2012). An overview of the global historical climatology network-daily database. *Journal of Atmospheric and Oceanic Technology*, *29*(7), 897–910. https://doi.org/10.1175/JTECH-D-11-00103.1

Menne, M. J., Williams Jr, C. N., & Vose, R. S. (2009). The US Historical Climatology Network monthly temperature data, version 2. *Bulletin of the American Meteorological Society*, *90*(7), 993–1008. https://doi.org/10.1175/2008bams2613.1

Minder, J. R., Mote, P. W., & Lundquist, J. D. (2010). Surface temperature lapse rates over complex terrain: Lessons from the Cascade Mountains. *Journal of Geophysical Research*, *115*(D14). https://doi.org/10.1029/2009jd013493

Morelli, T. L., Barrows, C. W., Ramirez, A. R., Cartwright, J. M., Ackerly, D. D., Eaves, T. D., et al. (2020). Climate-change refugia: Biodiversity in the slow lane. *Frontiers in Ecology and the Environment*, *18*(5), 228–234. https://doi.org/10.1002/fee.2189

Morrison, P. H., & Swanson, F. J. (1990). *Fire history and pattern in a Cascade range landscape* Gen Tech. Rep. PNW-GTR-254 (p. 77). U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Nadeau, C. P., Giacomazzo, A., & Urban, M. (2022). Cool microrefugia accumulate and conserve biodiversity under climate change. *Global Change Biology*, *28*(10), 3222–3235. https://doi.org/10.1111/gcb.16143

Nolin, A. W., & Daly, C. (2006). Mapping "at risk" snow in the Pacific Northwest. *Journal of Hydrometeorology*, *7*(5), 1164–1171. https://doi.org/10.1175/jhm543.1

Office of the Washington State Climatologist. (2024). PNW temperature, precipitation, and SWE trend analysis tool. Retrieved from https://climate.washington.edu/climate-data/trendanalysisapp/

Oke, T. R. (2002). *Boundary layer climates*. Routledge.

Pastore, M. A., Classen, A. T., D'Amato, A. W., Foster, J. R., & Adair, E. C. (2022). Cold-air pools as microrefugia for ecosystem functions in the face of climate change. *Ecology*, *103*(8), e3717. https://doi.org/10.1002/ecy.3717

Patsiou, T. S., Conti, E., Theodoridis, S., & Randin, C. F. (2017). The contribution of cold air pooling to the distribution of a rare and endemic plant of the Alps. *Plant Ecology & Diversity*, *10*(1), 29–42. https://doi.org/10.1080/17550874.2017.1302997

Pelz, K. A., Hayward, G., Gray, A. N., Berryman, E. M., Woodall, C. W., Nathanson, A., & Morgan, N. A. (2023). Quantifying old-growth forest of United States Forest Service public lands. *Forest Ecology and Management*, *549*, 121437. https://doi.org/10.1016/j.foreco.2023.121437

Pepin, N. C., Daly, C., & Lundquist, J. (2011). The influence of surface versus free-air decoupling on temperature trend patterns in the western United States. *Journal of Geophysical Research*, *116*(D10), D10109. https://doi.org/10.1029/2010jd014769

Reed, D. C., Schmitt, R. J., Burd, A. B., Burkepile, D. E., Kominoski, J. S., McGlathery, K. J., et al. (2022). Responses of coastal ecosystems to climate change: Insights from long-term ecological research. *BioScience*, *72*(9), 871–888. https://doi.org/10.1093/biosci/biac006

Rosenberg, N. J., Blad, B. L., & Verma, S. B. (1983). *Microclimate: The biological environment*. John Wiley & Sons.

Rosentrater, L. D. (1997). *The thermal climate of the H.J. Andrews Experimental Forest, Oregon* M.S. thesis (p. 133). University of Oregon.

Rupp, D. E., Shafer, S. L., Daly, C., Jones, J., & Frey, S. J. K. (2020). Temperature gradients and inversions in a forested Cascade Range basin: Synoptic-to local-scale controls. *Journal of Geophysical Research: Atmospheres*, *125*, 23. https://doi.org/10.1029/2020JD032686

Rupp, D. E., Shafer, S. L., Daly, C., Jones, J. A., & Higgins, C. W. (2021). Influence of anthropogenic greenhouse gases on the propensity for nocturnal cold-air drainage. *Theoretical and Applied Climatology*, *146*, 231–241. https://doi.org/10.1007/s00704-021-03712-y

Schulze, M., Betts, M., & Frey, S. (2023). Air temperature at core phenology sites and additional bird monitoring sites in the Andrews Experimental Forest, 2009 to present [Database]. *Long-Term Ecological Research. Forest Science Data Bank, Corvallis, OR*. https://doi.org/10.6073/pasta/cbf6e8a684a074cca95b5f422ca5f0f2

Sibley, A., Schulze, M., Jones, J., Kennedy, A., & Still, C. (2022). Canopy wetting patterns and the determinants of dry season dewfall in an old growth Douglas-fir canopy. *Agricultural and Forest Meteorology*, *323*, 109069. https://doi.org/10.1016/j.agrformet.2022.109069

Siler, N., Proistosescu, C., & Po-Chedley, S. (2019). Natural variability has slowed the decline in western US snowpack since the 1980s. *Geophysical Research Letters*, *46*(1), 346–355. https://doi.org/10.1029/2018gl081080

Smith, J. W. (2002). *Mapping the thermal climate of the H.J. Andrews Experimental forest, Oregon* M.S. thesis (p. 222). Oregon State University.

Spies, T. A., & Franklin, J. F. (1988). Old growth and forest dynamics in the Douglas-fir region of western Oregon and Washington. *Natural Areas Journal*, *8*(3), 190–201.

Still, C. (2023). Meteorological data from the Discovery Tree at the Andrews Experimental Forest, 2015 to present [Database]. *Long-Term Ecological Research. Forest Science Data Bank, Corvallis, OR*. https://doi.org/10.6073/pasta/88040f52946c09c74ac0bfc2a3167717

Still, C. J., Sibley, A., DePinte, D., Busby, P. E., Harrington, C. A., Schulze, M., et al. (2023). Causes of widespread foliar damage from the June 2021 Pacific Northwest Heat Dome: More heat than drought. *Tree Physiology*, *43*(2), 203–209. https://doi.org/10.1093/treephys/tpac143

Swanson, F. J., & James, M. E. (1975). *Geology and geomorphology of the H.J. Andrews Experimental forest, western Cascades, Oregon* Res. Pap. PNW-188 (p. 14). U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station.

Tepley, A. J., Swanson, F. J., & Spies, T. A. (2013). Fire-mediated pathways of stand development in Douglas-fir/western hemlock forests of the Pacific Northwest, USA. *Ecology*, *94*(8), 1729–1743. https://doi.org/10.1890/12-1506.1

Tepley, A. J., Swanson, F. J., & Spies, T. A. (2014). Post-fire tree establishment and early cohort development in conifer forests of the western Cascades of Oregon, USA. *Ecosphere*, *5*(7), 1–23. https://doi.org/10.1890/es14-00112.1

Thomas, C. (2013). Biomicrometeorological tower data in Watershed 1 in the Andrews Experimental Forest processed at 1 minute intervals from 1 Hz streaming data, 2012 to present [Database]. *Long-Term Ecological Research. Forest Science Data Bank, Corvallis, OR*. Retrieved from http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=MV004

Thomas, C. (2017). Advanced Resolution Canopy FLOw (ARCFLO) experiment employing the SUbcanopy Sonic Anemometer Network (SUSAN) in WS01 of the HJ Andrews Experimental Forest, July-September 2012 [Database]. *Long-Term Ecological Research. Forest Science Data Bank, Corvallis, OR*. https://doi.org/10.6073/pasta/e1dcac713961e62c3aaad2816bbf7780

USDA Forest Service. (2023a). Land management plan direction for old-growth forest conditions across the National forest system. *Federal Register*, *88*(243), 88042.

USDA Forest Service. (2023b). Mature and old-growth forests: Definition, identification, and initial Inventory on lands managed by the Forest Service and Bureau of Land Management. In *Fulfillment of Executive order 14072, Section 2(b). FS-1215a*. US Forest Service.

Vickers, M. (2022). *Climate Variability and plant-pollinator networks in the Cascade range, Oregon* M.S. thesis (p. 152). Oregon State University.

Vitasse, Y., Klein, G., Kirchner, J. W., & Rebetez, M. (2017). Intensity, frequency and spatial configuration of winter temperature inversions in the closed La Brevine valley, Switzerland. *Theoretical and Applied Climatology*, *130*(3–4), 1073–1083. https://doi.org/10.1007/s00704-016-1944-1

Ward, S. E., Schulze, M., & Roy, B. (2018). A long-term perspective on microclimate and spring plant phenology in the Western Cascades. *Ecosphere*, *9*(10), e02451. https://doi.org/10.1002/ecs2.2451

Weisberg, P. J., & Swanson, F. J. (2003). Regional synchroneity in fire regimes of western Oregon and Washington, USA. *Forest Ecology and Management*, *172*(1), 17–28. https://doi.org/10.1016/s0378-1127(01)00805-2

Williams, A. P., Abatzoglou, J. T., Gershunov, A., Guzman-Morales, J., Bishop, D. A., Balch, J. K., & Lettenmaier, D. P. (2019). Observed impacts of anthropogenic climate change on wildfire in California. *Earth's Future*, *7*(8), 892–910. https://doi.org/10.1029/2019ef001210

Winslow, L. A., Read, J. S., Hansen, G. J., Rose, K. C., & Robertson, D. M. (2017). Seasonality of change: Summer warming rates do not fully represent effects of climate change on lake temperatures. *Limnology & Oceanography*, *62*(5), 2168–2178. https://doi.org/10.1002/lno.10557

Wolf, C., Bell, D. M., Kim, H., Nelson, M. P., Schulze, M., & Betts, M. G. (2021). Temporal consistency of undercanopy thermal refugia in old-growth forest. *Agricultural and Forest Meteorology*, *307*, 108520. https://doi.org/10.1016/j.agrformet.2021.108520

Zellweger, F., De Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-Römermann, M., et al. (2020). Forest microclimate dynamics drive plant responses to warming. *Science*, *368*(6492), 772–775. https://doi.org/10.1126/science.aba6880

Zobel, D. B., McKee, A., Hawk, G. M., & Dyrness, C. T. (1976). Relationships of environment to composition, structure, and diversity of forest communities of the central western Cascades of Oregon. *Ecological Monographs*, *46*(2), 135–156. https://doi.org/10.2307/1942248