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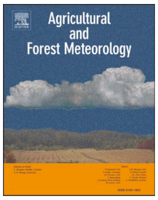

Temporal consistency of undercanopy thermal refugia in old-growth forest

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ABSTRACT

Microclimatic refugia (microrefugia) are ecologically important for the conservation of biodiversity under climate change. Year-to-year climatic consistency is an important requirement for most types of microrefugia, but refugia are often modeled using only a few years of data. Here, we used a decade-long (2009-2018) fine-scale, undercanopy microclimate temperature dataset from a landscape in the Cascades Mountains of Oregon, USA to assess the inter-annual temporal consistency of microrefugia. We used boosted regression tree microclimate models to quantify overall consistency and map locations of stable microrefugia for six biologically relevant annual temperature metrics. Microclimate temperature offsets (i.e., microclimate minus macroclimate temperatures) were remarkably stable over time, with R^2 ranging from 0.69 for minimum temperature during spring to 0.90 for mean temperature during spring. We observed a high degree of coupling; that is, broad-scale climatic variation, as reflected in free-air temperature, has a major effect on microclimate temperatures – particularly in hot years – with the potential to overwhelm thermal buffering effects. In spite of this, we identified potential microrefugia locations throughout our study area, especially with respect to spring minimum and mean temperatures. To maintain microrefugia in a rapidly changing climate, conservation of old-growth and other structurally complex forest habitat is critical, especially at sites with high elevation relative to their surroundings.

1. Introduction

While habitat loss and overexploitation are currently the dominant threats to much of Earth's biodiversity, climate change may greatly elevate extinction risk for many species (Maclean & Wilson 2011). Species distribution and bioclimatic envelope models, which link the geographic distributions of species to environmental and climatic covariates, can be used to predict the effects of climate change on species and as a basis for effective conservation planning (Elith & Leathwick 2009; Franklin 2013). However, such models can be sensitive to the spatial resolution(s) considered (Pearson & Dawson 2003; Seo et al. 2008) and often fail to account for microclimatic refugia ("microrefugia") – spatially restricted habitats with favorable microclimate conditions that support species populations in otherwise inhospitable regions (Gavin et al. 2014; De Frenne et al. 2021). Commonly used climatic datasets for species distribution modeling, especially in global studies, have low resolution (often $\geq$ 1 km) compared to the scales at which many organisms interact with their environments (Potter et al. 2013; Lenoir et al. 2017; Lembrechts et al. 2019). This mismatch motivates the analysis and modeling of microclimate at much finer scales, with grain sizes ideally approaching 1 to 10 times the length of the organisms of interest (Potter et al. 2013; De Frenne et al. 2019).

Microrefugia, which can provide small areas of habitat that would likely be overlooked when using coarse-scale climatic grids, are important to the biology and persistence of species (Ashcroft 2010). While microrefugia have been defined in multiple ways, the term was first used to reflect the possibility that some relic vegetation species could persist at favorable sites during dry periods in the Pleistocene (Rull et al. 1988). Thus, the temporal aspect of microrefugia is fundamental to their original formulation. Moreover, temporal consistency of microrefugia locations as characterized by similar seasonal temperature patterns (that match with species habitat requirements) among years is especially relevant when forecasting species' responses to climate change. Unfortunately, collecting temperature or other data suitable for

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microclimate modeling can be expensive, labor intensive, and requires careful validation. As a consequence, the temporal consistency of microrefugia locations is often treated more as an assumption of analyses, rather than as an essential component of identifying and modeling microrefugia (but see Von Arx et al. 2013). For example, a recent meta-analysis of forest microclimate temperature buffering (De Frenne et al. 2019) identified 74 relevant studies, but just one of these studies used more than 1,095 days (three years) of data (Renaud et al. 2011).

Temporal consistency of microrefugia is likely critical to the survival of species' populations, particularly for longer-lived, low-vagility species. Taxa generally fitting this profile include lichens, mosses, long-lived low dispersing herbaceous plants, tree seedlings, forest terrestrial amphibians, and many species of scorpions (Bryson Jr et al. 2013; Zellweger et al. 2020). Other species may also have restricted mobility. For example, red tree voles (*Arborimus longicaudus*) are arboreal rodents with maximum dispersal distance of ~75 meters (Swingle 2005; Linnell & Lesmeister 2019). Even species that travel long distances can be heavily reliant on microrefugia – depending on their phenology. For example, migratory birds require temporally consistent microrefugia in order for their movements to match the availability of resources in critical periods of their life cycle, with mismatches being linked to negative outcomes at the population level (Jones & Cresswell 2010; Miller-Rushing et al. 2010; Saino et al. 2010). Geographic factors may also predict species' dependence on temporally consistent microrefugia. Species restricted to mountains or islands may be more reliant on microrefugia because they have reduced potential for range shifts (Elsen & Tingley 2015; Graae et al. 2018). Where high-severity disturbances are rare, animal species may be less mobile, and consequently more reliant on stable microrefugia (Betts et al. 2019). In summary, life history traits, ecological community composition and biotic environment, and geography all interact to potentially predispose metapopulations to being dependent on temporally consistent microrefugia. Notably, species not presently dependent on microrefugia may be so in the future given climate and land-use change projections (Arneth et al. 2019).

Previous work has established that forest vegetation structure can have strong influences on microclimate conditions; specifically, old-growth forest characteristics appear to moderate temperatures during both hot and cold periods over the short term (Frey et al. 2016). However, the capacity of forests to buffer plant and animal populations from the negative effects of climate change depends on the temporal consistency of this thermal effect during periods of climatic extremes. Thus, temporal consistency of microrefugia is most important when macroclimate conditions are at the extremes of their distribution. Importantly, if forest structure itself can predict temporally reliable refugia, then conservation and management prescriptions can indirectly influence species responses to climate change (Betts et al. 2018).

Here, we conducted a spatiotemporal analysis of microclimate and microrefugia using a decade-long temperature dataset from the H. J. Andrews Experimental Forest (HJA) in the Willamette National Forest of Oregon, United States (Johnson & Frey 2019). Our objectives were (1) to quantify the temporal consistency in thermal characteristics in a mountain landscape, thereby identifying microrefugia and (2) to determine the biotic and abiotic drivers of these putative thermal microrefugia. We hypothesized that the temporal consistency of sites' thermal characteristics would depend on the extent to which they are governed by factors that are relatively stable across seasons and years (vegetation structure and topographic shading) versus the dynamics of local weather patterns and airflows, which vary on daily and seasonal as well as inter-annual time scales.

2. Materials and methods

2.1. Terminology

Here, we provide definitions of the key concepts referenced in our analysis. All definitions except the ones related to microrefugia are adapted from those presented in De Frenne et al. (2021). **Macroclimate temperatures** are free-air temperatures associated with open conditions whereas **(forest) microclimate temperatures** are undercanopy temperatures. **Temperature offsets** refer to the differences between microclimate and macroclimate temperatures (microclimate minus macroclimate), whereas **unadjusted temperatures** refer to actual microclimate temperatures (see Supplementary Methods). When considering microclimate versus macroclimate temperatures, we distinguish between three possibilities for β, the regression slope of a model in which macroclimate temperatures are used to predict microclimate temperatures: **coupling** (β=1), **decoupling** (β=0), and **buffering** ($0 < \beta < 1$) (De Frenne et al. 2021). A **microrefugium** (at a specific time) is an area with suitable temperatures and/or temperature offsets for a given organism. Finally, **temporally consistent microrefugia** are microrefugia with stable locations across time.

These definitions are intended to clarify our analysis and to align with standard usage, where appropriate (De Frenne et al. 2021). Ultimately, operationalized definitions, which may require specifying spatial and/or temporal scales (e.g., with regard to microrefugia or microclimate), are almost certainly context dependent. That is, they can vary depending on the focal organism(s) being considered, research questions being studied, processes involved, and so on. For example, microrefugia that are not temporally consistent in terms of their locations over time, but rather shift around on a landscape, may be adequate for some highly mobile organisms. While we acknowledge such organism dependence (Bütikofer et al. 2020), it is beyond the scope of our analysis (described below) to fully consider. Here, we consider microrefugia with respect to (1) unadjusted temperatures, (2) offset temperatures, and (3) their combination (our primary focus) because each may be relevant to different species.

2.2. Study area

Our study area (HJA) is a 6,400 ha experimental forest located in western Oregon, USA (44.23° N, 122.188° W). Elevation ranges from 410-1630 m, and the forest is dominated by Douglas-fir (*Pseudotsuga menziessii*) and western hemlock (*Tsuga heterophylla*) at lower elevations and Pacific silver fir (*Abies amabilis*) at higher elevations. Variation in disturbance history, including fire, landslides, wind storms, and timber harvesting, produce a mosaic of forest ages, from 30-700 years. Steep, complex topography is common. At the primary meteorological station (elevation: 426 m), mean monthly temperatures range from 0.6°C in January to 17.8°C in July and annual precipitation averages 2.30 m (Bierlmaler & McKee 1989). Precipitation is highly seasonal, leading to a dry growing season.

2.3. Data sources and processing

We obtained fine-scale, undercanopy temperature data for the HJA from Johnson & Frey (2019). Specifically, we used undercanopy daily minimum, mean, and maximum temperatures between 2009 and 2018 associated with 184 sites in the HJA (Supplementary Methods, Figure S1). As described in Frey et al. (2016), sampling locations were selected by stratifying by forest type, elevation, and distance to roads. We aggregated the data to the annual scale using six biologically relevant temperature metrics: spring minimum, mean, and maximum temperature, summer mean and maximum temperature, and winter growing degree days (GDD) (Table S1). While there are other temperature summaries that could be calculated, these six are associated with species phenology and survival (Supplementary Methods; Miller et al. 2001; Sparks et al. 2005; Yang et al. 2017).

Because fine-scale temperatures are influenced by regional weather patterns reflected in broad-scale, free-air (i.e., macroclimate) temperatures, we obtained ~4-km resolution daily minimum and maximum temperatures from the gridMET dataset (Abatzoglou 2013) to act as a region-wide baseline (Figure S2). GridMET synthesizes multiple climatic datasets (PRISM, NLDAS-2) to accurately track temperatures and other variables over time (Abatzoglou 2013). We averaged gridMET free-air temperature estimates across the entire HJA for each day. As an alternative free-air reference temperature baseline, we also considered data from the Vanilla Leaf Meteorological Station (VANMET)—one of the benchmark meteorological stations in the HJA (Supplementary Methods). These data are more accurate at the station location (since they are obtained through direct measurement), although they may not be as representative of the HJA as a whole. For comparison, we redid the main parts of our analysis (detailed below) using the VANMET data for free-air temperature (Supplementary Methods).

We used a suite of spatial predictor variables to model microclimate temperatures with temperature metrics as described above (Table S1, Figure S3). These predictors were selected to capture the important elements of our hypothesized drivers of microclimate: vegetation, macrotopography (elevation), and microtopography. These three categories were considered because of prior evidence for (1) old-growth temperature buffering effects, (2) surface temperature lapse rates, and (3) topographic shading and cold air pooling respectively (Minder et al. 2010; Curtis et al. 2014; Frey et al. 2016; Macek et al. 2019; Rupp et al. 2020). The vegetation and elevation variables are based on a 2008 lidar (light detection and ranging) survey of the HJA (Spies 2019). Thus, the vegetation variables do not reflect changes in forest structure that may have occurred after 2008, which could be significant in some areas. Lidar has been shown to accurately characterize both topography and vegetation structure in forest ecosystems (Lefsky et al. 2002; Kane et al. 2010; Zald et al. 2016). The microtopography variables – slope, aspect, topographic position index (TPI), and topographic convergence (wetness) index (TCI) – were all calculated directly from elevation.

2.4. *Statistical modeling*

Because relationships between microclimate temperature metrics and vegetation and topography predictor variables can be complex and non-linear, we used boosted regression trees (BRTs) as our primary tool for statistical modeling (Elith et al. 2008). Briefly, BRTs use a sequence of regression (decision) trees to model a response variable where each successive tree predicts the residuals from the previous tree, which helps to increase the diversity of trees in the ensemble, thus potentially improving predictive performance (Elith et al. 2008; Hastie et al. 2009). BRTs are well-suited to large datasets and may outperform other methods, including random forests, neural networks, and kriging in temperature modeling (Appelhans et al. 2015). For our analysis, we used the 'LightGBM' high performance BRT framework (Ke et al. 2017). We varied the predictor variable sets, spatial extents (for smoothing), model loss functions, and other parameters to address different research questions as described in this section.

We first modeled microclimatic conditions across years using the full suite of predictor variables summarized at multiple extents (Table S1, Figure S3, Supplementary Methods). We calculated the mean value of each predictor at radii 10 m, 20 m, …, 100 m for vegetation variables, and by resampling elevation at 25 m, 100 m, 250 m, and 500 m before calculating microtopographic variables (elevation as a predictor was not averaged). In this context, we use spatial "extent" to refer to the area associated with smoothing or coarsening (rather than the extent of the entire study area); for example, an extent of 100 m means that information within roughly 100 m of each point was used in the associated calculation (Holland et al. 2004). To assess accuracy, we used prediction-based R^2 and mean absolute error (MAE) with cross-validation based on blocking by year, which accounts for similarity within years (Roberts et al. 2017). This accuracy assessment quantifies temporal consistency across years in that high model accuracy indicates that the relationships between temperature metrics and landscape drivers are similar regardless of inter-annual climatic variation. We used the associated plots of observed versus predicted values to provide insight into the degree of microclimate-macroclimate coupling; specifically, strong coupling would be evidenced by additive shifts in microclimate temperatures from year to year, paralleling shifts in macroclimate temperatures. Additionally, we calculated MAE for each year separately to determine if temperatures in certain years were especially difficult to predict using data from the other years. We used two versions of the response variables: (1) the "unadjusted" undercanopy annual temperature summaries and (2) the associated temperature offsets (undercanopy minus free-air) annual temperature summaries (De Frenne et al. 2019). We used the latter approach to quantify the effect of adjusting for year-to-year changes in broad-scale temperatures. This approach provides insight into how both broad-scale climatic patterns and local-scale spatial variables together drive microclimate temperatures. To further assess temporal consistency, we computed Spearman's rank correlations between years. In this case, we only considered unadjusted temperatures because rank correlation is less sensitive to year-to-year variation.

Predicting temperatures in one year using data from other years does not directly address the temporal consistency aspect of microrefugia, although it is implicitly tested. We therefore used BRTs with quantile loss functions to model temperature extremes (Cade & Noon 2003). The quantile loss function, defined as $\rho_\tau(u) = u[\tau - I(u < 0)]$, has the property that, for a random variable Y and constant u, the expected value of $Y - u$ is minimized when u equals the τ-quantile of Y (Koenker 2004). This approach therefore allowed us to directly model extreme quantiles of the response variables, thereby identifying areas where the most extreme temperatures are moderated. Although extreme cold or hot temperatures can be problematic for some species, we focused on the hot upper-tail (90% quantile of the response distribution) for all of the temperature metrics. Thermal refugia are therefore the locations across the entire landscape that exhibit the most dampened temperature extremes (i.e., where the 90% quantile of the response variable is relatively low in comparison to the rest of the landscape). This reflects temporal consistency (i.e., annual temperatures can be predicted well using factors that vary little between years) in the sense that such locations are more likely to be consistently habitable by temperature-sensitive organisms (Fig. 1). In particular, when temperatures are hottest across the landscape as a whole, the relatively cold places (in unadjusted terms and/or relative to macroclimate) are most important as potential microrefugia. In contrast, directly modeling variability instead (e.g., standard deviations) could be used to identify areas with temporally consistent microclimatic conditions. However, these areas are not necessarily microrefugia since they can be, for example, too hot for organisms to persist. Modeling the upper-tails of the response variable distributions avoids this problem because they incorporate information about both the mean (which areas are cool on average?) and the standard deviation (which areas have consistent temperatures?) (Figure S4).

The focus of our analysis is on temporal consistency of microclimatic *refugia*, which we note is different from temporal consistency of microclimate. Microrefugia are organism-dependent because they are defined in terms of habitat, which is itself an organism-dependent concept (Betts et al. 2014). Thus, a small area that is consistently hot would have a temporally consistent (thermal) microclimate, but would not be a microrefugium for species requiring cooler temperatures. Conversely, sites where temperatures are low but more variable could function as microrefugia for certain organisms (Fig. 1). Because our interest is in modeling microrefugia, we used quantile regression to identify areas that are consistently cool (in both absolute terms and relative to free-air conditions) from year to year and thus likely to function as microrefugia for many species, especially in the face of climate change.

For our main quantile regression models, we used the full set of predictors (Table S1). We quantified overall model performance using the pseudo-R^2 (Koenker & Machado 1999). We mapped predictions (i.e., predicted 90% quantile values for each 5-m pixel in the HJA as a function of local vegetation and topographic characteristics) for extreme values of the temperature metrics (both unadjusted values and offsets). This provides some information about where microrefugia may be

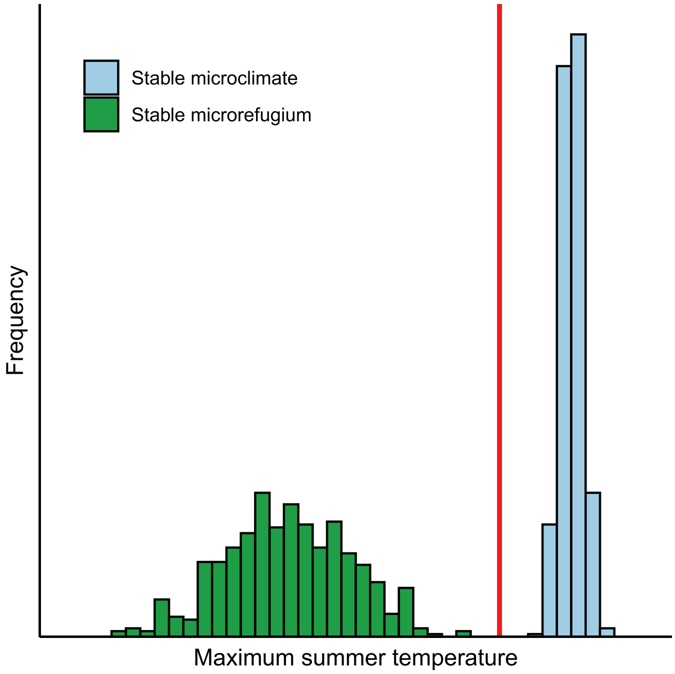

Fig. 1. Illustration of the difference between stability of microclimate versus stability of microrefugia. Hypothetical distributions of an example annual statistic at two sites are shown. The right distribution is associated with greater microclimatic stability with respect to maximum summer temperature because it has lower variability. In contrast, for a species that requires maximum summer temperatures below the vertical line, only the left distribution is characteristic of a stable microrefugium. Importantly, these definitions are both statistic and species dependent.

located spatially, which can be of use to future studies (e.g., a study of patterns of mortality rates or persistence of temperature-sensitive species). To further facilitate spatial identification of microrefugia, we calculated a "microrefugial suitability index" for each temperature metric, which we defined as:

$$M = 1 - \max\{prop_1,\ prop_2\}$$

where $prop_1$ and $prop_2$ represent the proportions of (90% quantile) predicted values with lower unadjusted temperatures and temperature offsets respectively. Thus, M takes on high values (indicating high potential suitability) when both unadjusted temperatures are low and negative offsets relative to free-air are large (in the predicted 90% quantiles; see Supplementary Methods). Although unadjusted and offset temperatures may be individually useful when identifying microrefugia, this hybrid approach combines two important criteria into a single index.

To quantify the relative importance of each temperature metric predictor (and their summaries at multiple extents; Table S1, Supplementary Methods), we used the 'gain' metric, which measures the increase in model performance associated with each variable. We summarized relative gain in two ways: (1) total gain summed across variables within groups, calculated separately for each predictor spatial extent, and (2) gain associated with each variable summed across spatial extents. Together, these summaries show which groups of variables are particularly important for each temperature metric, and how this importance varies with respect to spatial extent. To determine how gain varies with respect to quantile, we repeated the variable-specific gain calculations separately for quantiles ranging from 10% to 80% in increments of 10%, although our main results are for the 90% quantile only.

We used accumulated local effects (ALE) plots to assess relationships between each predictor and each temperature metric response (both unadjusted responses and offsets) (Apley 2018). To estimate the effect of an individual predictor, it is necessary to specify the distribution of the other covariates (because of interactions). For ALE plots, the estimated conditional distribution of the other covariates is used, which improves interpretability. To further facilitate interpretability, we used principal components analysis (PCA) on the vegetation predictor variables (Table S1) to calculate two primary principal components that adequately captured stand-structure characteristics – particularly, a gradient in forest complexity (Schulze & Lienkaemper 2015; Frey et al. 2016). As a sensitivity analysis, we used only data from the four most complete years (2012-2015), omitting sites that did not have data for all four years. This helps to mitigate issues with some sites potentially lacking data in unusual years.

3. Results

Inter-annual variation in gridMET (regional baseline) temperatures was often on the order of several degrees Celsius (Figure S2). VANMET (meteorological baseline) daily minimum and maximum temperatures were generally comparable to gridMET estimates, although VANMET daily maximum temperature estimates tended to be consistently lower than gridMET ones (Figure S2). This effect could be due to the location of VANMET at an elevation of 1,275 meters (since the HJA has a significant elevational gradient and mean elevation of roughly 1,000 meters) or possibly due to small or large scale buffering effects associated with forested land (the primary land cover type in the HJA). GridMET and VANMET temperature metrics (e.g., winter growing degree days) showed similar patterns as evidenced by associated slope parameter estimates (predicting VANMET from gridMET) being near 1 in most cases, although gridMET temperatures were consistently higher (Figure S5). Summer maximum temperature was a notable exception to this pattern, exhibiting high year-to-year variation in temperature offsets (Figure S5).

3.1. *Model performance*

Microclimate temperature offset models were highly predictive (despite substantial inter-annual variation in the response variables; Figure S6): R^2 based on cross-validation by year ranged from 0.69 for spring minimum temperature to 0.90 for spring mean temperature (Fig. 2). Performance was mixed for the unadjusted temperature models (i.e., those that did not account for year-to-year variation in free-air temperatures) (Fig. 2). R^2 and MAE by year were consistent with these overall patterns, both tending to indicate better performance when modeling temperature offsets (Figure S7). However, performance was often poor in 2009 and 2010, when relatively few sites had data loggers (Figures S1, S7). Quantile regression models for the unadjusted temperature metrics (with the full suite of predictors; Table S1) had pseudo-R^2 values ranging from 0.29 (summer maximum temperature) to 0.76 (winter GDD).

3.2. *Temporal consistency in thermal characteristics*

The cross-validated results show that temperature offsets in a given year can be effectively predicted using data from other years (Fig. 2). That is, relatively cold spots (putative refugia) tended to be in consistent locations year to year since they could be identified in one year using data from the other years (provided the data logger locations cover the entire gradient of conditions in the HJA). This provides strong evidence for temporal consistency in our microclimate temperature response variables. This was further supported by the remarkably high Spearman's (rank) correlation values between cross-validated unadjusted predictions in different years. All 450 correlations (each associated with a different variable and pair of years), were greater than 0.93 (Figure S8). The mean of the correlations was 0.99 and the median was 1.00. Among the response variables, summer maximum temperature

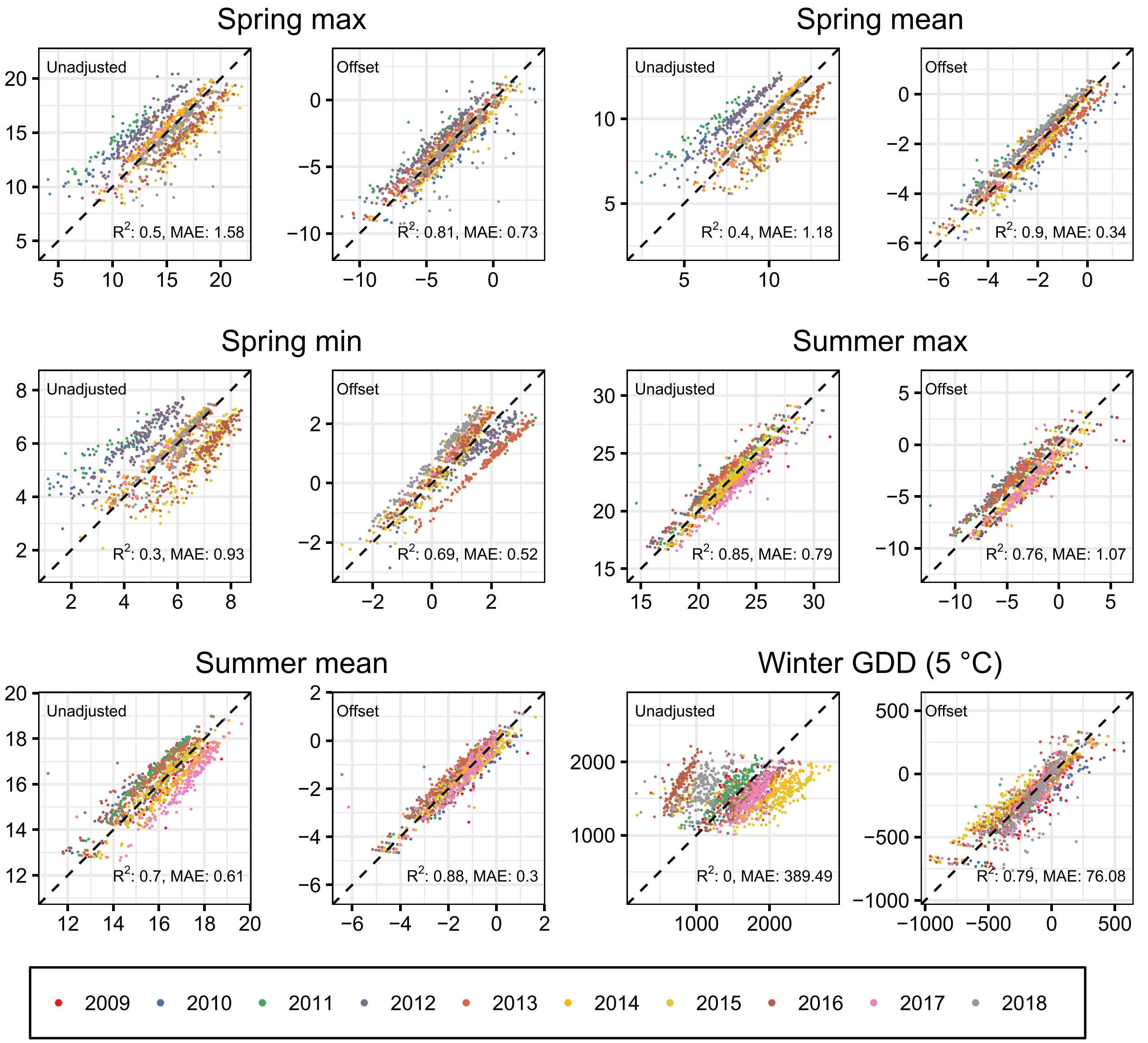

Fig. 2. Observed and predicted temperature metric values using cross-validation by year. The predicted values for each year were obtained using models fit to all other years of data (to guard against overfitting). For each temperature metric (Table S1), the left plot is based on undercanopy temperatures, while the right plot is for temperature offsets (differences between corresponding free-air and undercanopy temperature metric values). Taking the difference accounts for some years being overall hotter or colder than others (Figure S2), which improves the predictive performance of vegetation and topographic variables as indicated by mean absolute error (Figure S7).

had the highest mean correlation (1.00) and winter GDD had the lowest mean correlation (0.98).

3.3. Predictors of microclimatic extremes and potential microrefugia

The vegetation variables collectively were strongly predictive of microclimate temperature extremes, with combined relative influences ranging from 46.4% (spring minimum temperature) to 52.2% (winter GDD) (Fig. 3). Although variable relative influence estimates indicate that site-scale temperatures are dependent on elevation, microtopography, and vegetation structure, there was substantial variability in covariate contributions across temperature metrics (Fig. 3). Elevation was most predictive of spring mean temperature (11.8%) and spring minimum temperature (7.36%). Microtopography variables collectively had relatively consistent influence, ranging from 41.4% for spring mean temperature to 47.7% for summer maximum temperature (Fig. 3). In general, elevation had the greatest relative importance at intermediate quantiles, and less importance at extremes, which were the primary focus of our analysis because they highlight the coldest (or hottest) areas across time (Figure S9).

Potential microrefugia – locations with consistently low temperatures and temperature offsets (i.e., large negative offsets) occurred in many parts of the HJA, especially at higher elevations (Figs. 4, S10). Across the entire HJA, total microrefugia area, when calculated using a 0.8 threshold for M, was smallest when temperatures were summarized using summer maximum (4.85 km^2) and winter growing degree days (5.44 km^2) and highest when spring minimum (8.08 km^2) and spring mean (8.01 km^2) were used (Fig. 4). This amounts to between 7.5% (summer max) and 12.5% (spring min) of the HJA.

The vegetation variables were generally highly positively correlated with each other (Figure S11). This supported our decision to focus on the first two principal components for these variables when constructing accumulated local effects plots. Together, the first two principal components explained 69.7% of the total variance and were generally

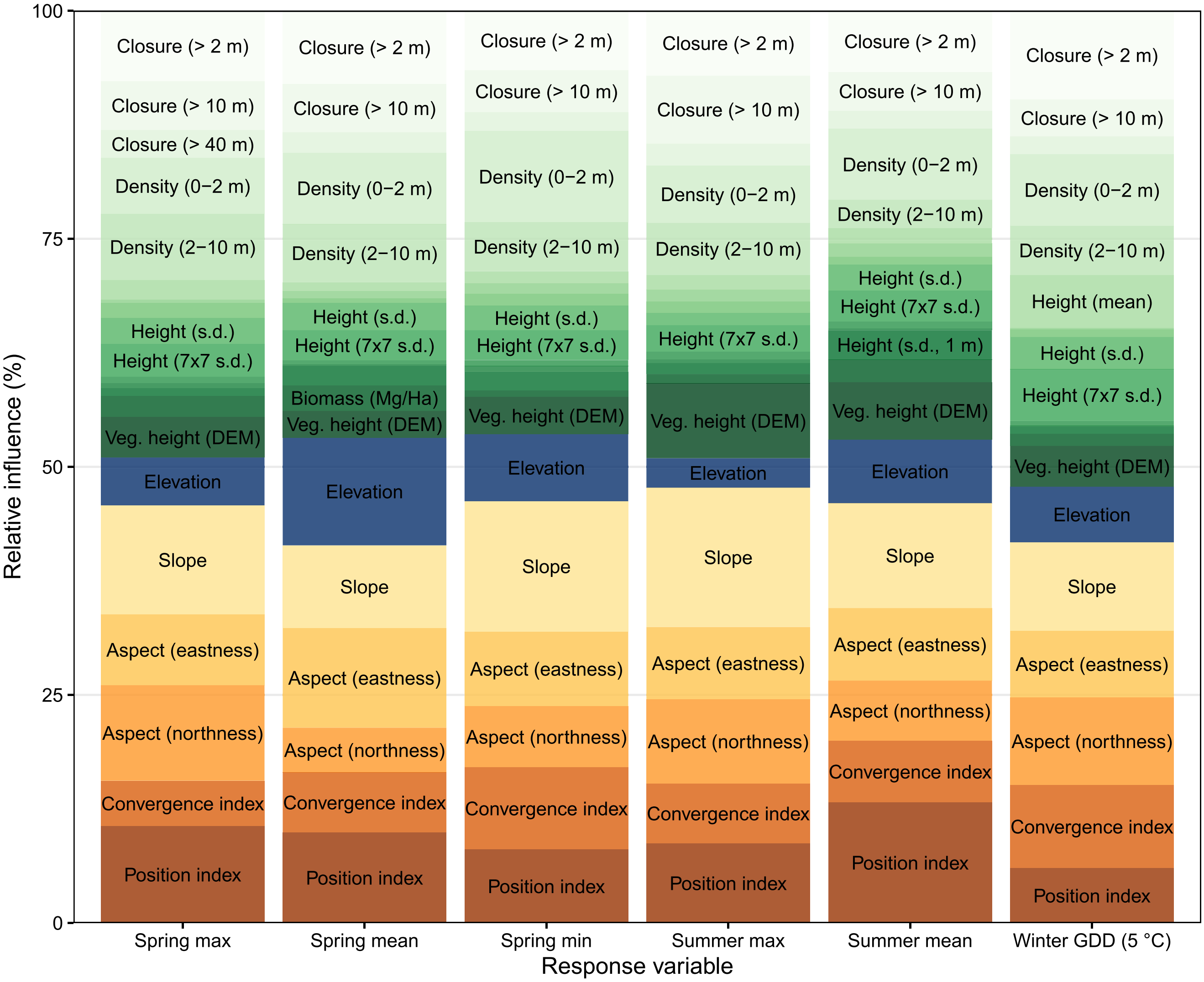

Fig. 3. Relative influence of vegetation (green) microtopography (orange), and elevation (blue) predictor variables on temperature extremes for different unadjusted annual temperature metrics (Table S1). The 90% quantile is modeled for all variables in order to focus on relationships between predictors and temperature metrics at temperature extremes (results for other quantiles are shown in Figure S9). The variable relative influences indicate that, across temperature metrics, microtopography and vegetation are important predictors of undercanopy temperatures, even after accounting for elevation.

successful in separating plantation sites from mature forest or old-growth sites (Figure S12). In particular, the first principal component was strongly associated with the plantation to mature forest or old-growth gradient, with scaled values greater than ~0.45 being associated with mature forest or old-growth (Figure S12).

The ALE plots show large variation in effect magnitudes and directions for the elevation, microtopographic, and forest structure and composition variables (Fig. 5). A shift from young plantations to older undisturbed forests (represented by the first vegetation principal component) tended to result in cooler spring and summer maximum temperatures (Fig. 5). As expected, the effect of elevation on temperatures was generally negative, even after subsetting to exclude incomplete data (Figure S13). Patterns were also generally similar, especially for elevation and the first vegetation principal component, when using the VANMET free-air temperature baseline instead of gridMET (Figure S14). In contrast, the effects of microtopographic variables were mixed—possibly a consequence of the extent considered (10 m)—although topographic convergence index frequently had a negative effect on temperatures.

3.4. *Spatial extent*

Elevation, microtopography, and vegetation all helped to explain microclimate temperatures (Figs. 4, S8). This shows that the importance of these variable groups holds over longer time scales. The robustness of these results may be partly attributable to the use of multi-extent modeling, with spatial extents of covariates ranging from 5 to 500 meters. The relative influence of these variable groups was frequently extent-dependent. Together, the vegetation-related variables declined in relative influence with increasing extent (Figure S15). In contrast, the microtopographic variables tended to maintain their relative influence across spatial extents, even out to 500 meters (Figure S15), although the associated relationships (i.e., effects on temperatures) likely depended on the extent considered.

4. Discussion

Our model R^2 and MAE results show that spatial patterns in temperatures in the HJA tend to be consistent and predictable over the long term – a critical criterion for thermal refugia (Figs. 2, S7). The fact that temperatures for a given location (i.e., data logger position) in each year

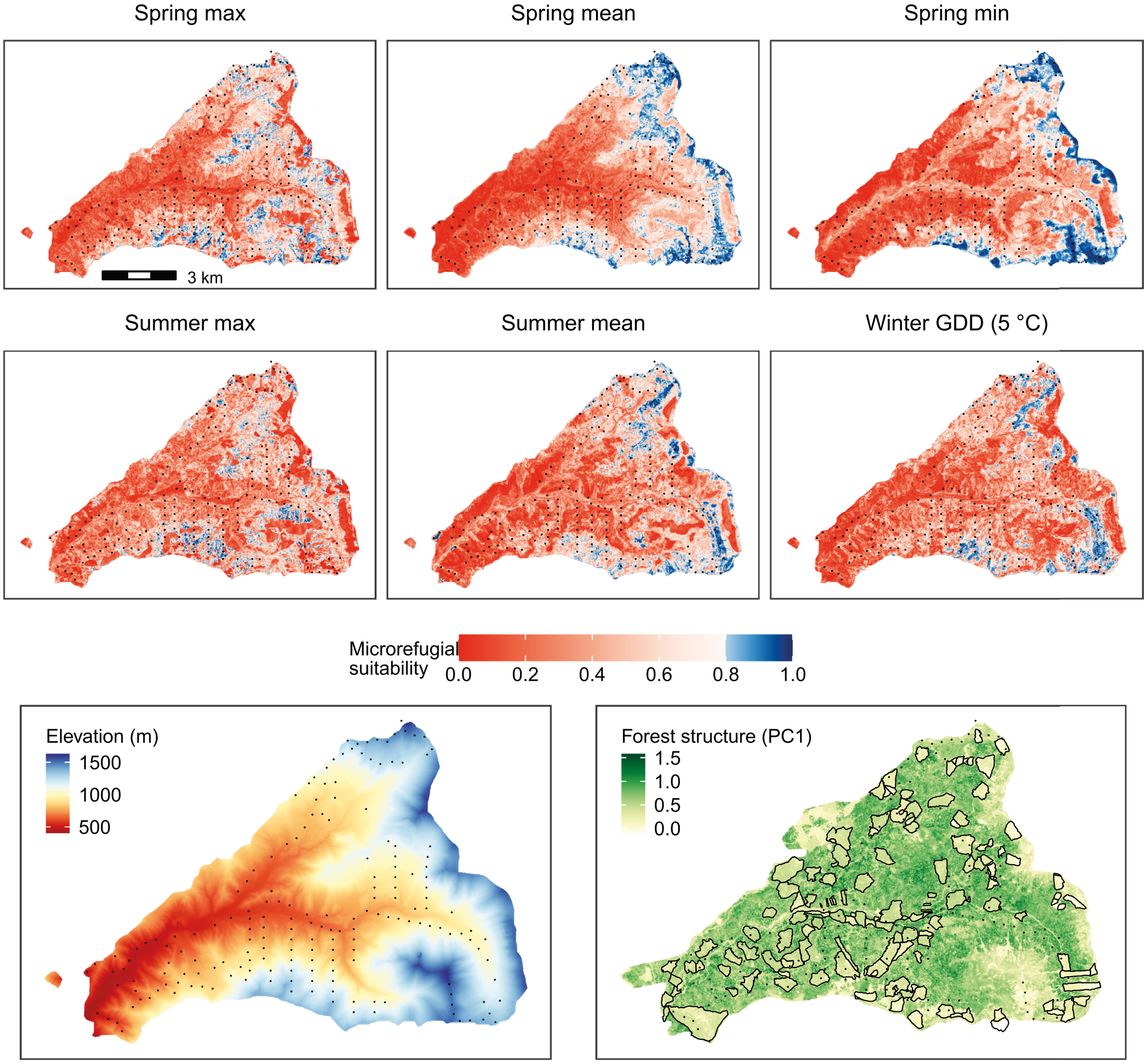

Fig. 4. Predicted microrefugia locations in the HJA for each temperature metric using data from 2009 to 2018 (Table S1). Predictions are based on a “microrefugial suitability” index which has high values when both the temperature metrics themselves (e.g., winter growing degree days) and the associated temperature offsets (relative to free-air) have low values. Blue regions (top two rows) show locations of microrefugia based on a 0.8 threshold. For context, maps of elevation and forest structure gradient are shown in the bottom row. The forest structure gradient ranges from plantations (outlined in black) to mature forest and old-growth, and is based on principal component analysis (with values linearly rescaled to range from 0 to 1 at data logger sites). Predicted temperature and temperature offset maps are also available (Fig. S10).

can be predicted well given data from the other years strongly supports this expectation. Moreover, this provides evidence for our hypothesis that the consistency of sites’ thermal characteristics is largely driven by relatively stable factors (i.e., topography and, to a lesser extent, vegetation). This is especially true when we considered temperature offsets (i.e., controlled for year-to-year changes in free-air temperature), an adjustment that had a modest impact on the locations of cool spots (Figure S10). The high predictability of microclimate temperature offsets (Figs. 2, S16) provides evidence for microclimate coupling (additive shifts in temperature), rather than decoupling (Lenoir et al. 2017; De Frenne et al. 2021). That is, the magnitude of the offset remains relatively stable over time despite the current macroclimate warming trend (2009-2018; Fig. 2), thus suggesting a strong coupling between microclimate warming and macroclimate warming (De Frenne et al. 2021). Thus, areas that are consistently cool relative to their surroundings still track free-air temperatures, and can be hot in hot years; that is, although cold areas are consistently cold, they are less so (in absolute terms) in years when macroclimate conditions are hotter. The HJA contains a diversity of forest types that are representative of much of the old-growth and older plantation area throughout the Washington and Oregon Cascades. This suggests that microrefugia are likely to be temporally consistent at broader scales as well.

The connection between old-growth and microrefugia is particularly important in unmanaged forests where the length of time between major disturbances can be 500+ years, with old-growth potentially giving species a chance to persist over the long term in the face of broad-scale climatic events (Zellweger et al. 2020). The thermal effects of forest structure can be dominated by year-to-year temperature variation – which may be greater in magnitude than thermal buffering effects. However, even when the magnitude of thermal buffering is overcome by macroclimate warming, consistently “cold” microrefugia are still more hospitable than anywhere else in the landscape, and thus might buy time for species to move or adapt. In the cases of spring and summer maximum temperatures, old-growth forest structure was associated with cooler temperatures (relative to all vegetation present) on the order of 3-5°C (Fig. 5), often exceeding inter-annual variation in free-air temperature in magnitude (Figure S2). These larger effects are comparable to the ~5°C shifts in monthly minimum and maximum temperatures

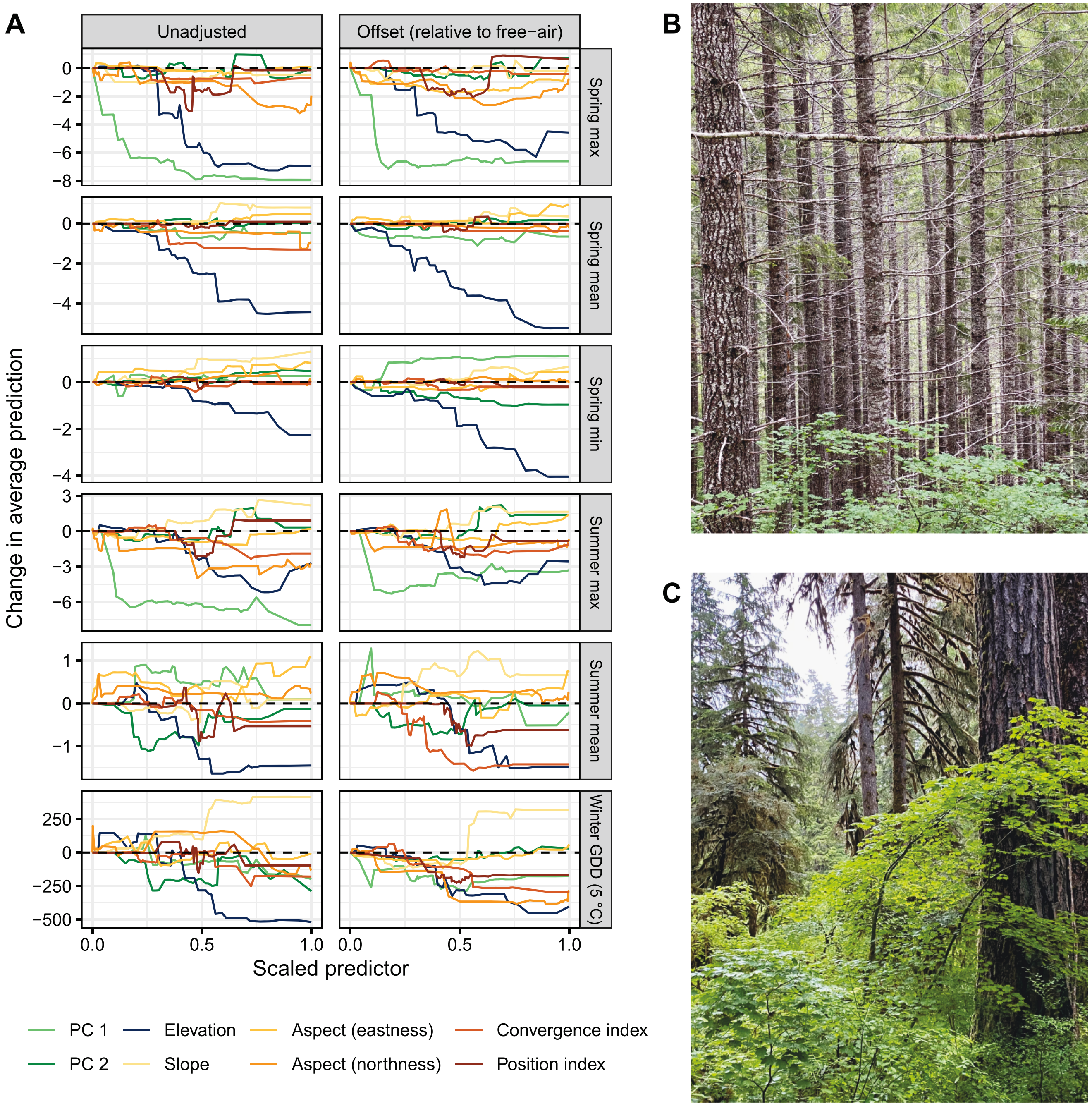

Fig. 5. Accumulated local effects (ALE) plots indicating the effects of each predictor on the extremes of different temperature metrics (90% quantile, panel A). Predictors have been scaled so they can be plotted on the same axis. Large negative effects associated with elevation are apparent. Additionally, the first principal component “PC 1” (Fig. S12), which spans the gradient from tree plantations (B) to old-growth (C), often has a negative effect, consistent with old-growth buffering of microclimate temperatures. Photo credit: Matthew Betts.

linked to habitat type (grassland, heathland, or deciduous woodland) in northern England (Suggitt et al. 2011) and to reductions in microclimate maximum temperatures of up to 3.3°C associated with forest ecosystems in Switzerland (Von Arx et al. 2013). They are also comparable to the Intergovernmental Panel on Climate Change’s projected surface temperature change of 3.7°C (likely range: 2.6°C to 4.8°C) for 2081-2100 under the RCP8.5 high emission scenario (Stocker et al. 2013). If managers wish to maintain landscapes that incorporate some less climatically stressful habitats for species of interest, conserving old-growth forests may remain a priority. Such management could prioritize sites where elevation and microtopographic characteristics also favor the occurrence of microrefugia (Figs. 3, S3). Importantly, the bulk of PC1’s negative effect was realized prior to reaching a value of 0.45, the value associated with the transition to old-growth (Figure S12). More work is needed to identify the specific forest structure characteristics shaping understory microclimate; knowledge about such characteristics could form the basis for silvicultural prescriptions aiding the development of microrefugia.

Our results indicate that vegetation, particularly forest structure, effectively reduces maximum temperatures, which can be an important driver of species distributions at the landscape scale (Macek et al. 2019), but has weaker effects on minimum and mean temperatures. This is generally consistent with the results of prior forest microclimate studies (e.g., Zellweger et al. 2019) and with the overall pattern of microclimate buffering derived using a global meta-analysis, which estimated the average forest buffering effect relative to macroclimate temperatures was 1.7°C, 4.1°C, and -1.1°C for mean, maximum, and minimum temperatures respectively (De Frenne et al. 2019). However, our results for mean temperatures were more mixed ("PC 1" in Fig. 5). This discrepancy may be due to fine-scale variation in vegetation near the data loggers or to our focus on undercanopy temperatures in general, rather than forest versus non-forest temperatures (although sites on the upper left of the PC1-PC2 plot correspond to nearly open conditions). The observed patterns in summer maximum temperatures may be important for forest wildfire behavior and management. Recent evidence that high severity fires may be less likely in some types of older forests (Zald & Dunn 2018; Meigs et al. 2020) could, in part, be explained by the capacity of these old forests to temper extreme temperatures. This implies that the prevalence of old-growth forest could help determine forest landscape resistance to high severity fire in the western Cascade Mountains.

As expected, the relative influence and effects of microtopographic variables varied greatly depending on the temperature metric considered (Figs. 3, 5). This is a consequence of the dynamic nature of the interaction between topography and local airflows (Daly et al. 2010). Among drivers of microclimate variability, some effects of topography (e.g., cold air flows and pooling) tend to be more transient than those of old-growth vegetation. Ultimately, the locations and stability of microrefugia are dependent on complex interactions between predictors that vary at daily, seasonal, annual, and likely even centennial, and millennial (for topography) temporal scales.

4.1. Future work

While our analysis shows that certain spots have been consistently cool relative to free-air temperatures and other locations within the same watershed over the last decade (Fig. 4), in the future, it will be important to understand the varying and interacting drivers of microrefugia consistency in order to accurately quantify the medium- and long-term stability of microrefugia. An important step toward improving assessments of microrefugia is to incorporate other response variables, such as measurements related to water balance, snow cover, snow depth, and snow duration (Lenoir et al. 2017; McLaughlin et al. 2017; Davis et al. 2019). Long-term temperature patterns under old-growth canopy in the HJA suggest that vegetation and topography combine to influence local air flow and understory temperature dynamics (Rupp et al. 2020) and that cold air pooling driven by local topography can lead to decoupling from free-air temperatures (Daly et al. 2010). These findings provide some potential mechanisms for buffering to climate change via combined vegetation and topographic influences, which can be helpful in refining our understanding of the strength and stability of microrefugia in forested landscapes. This understanding will ideally be based on mechanistic models – for example, simulating the flow of air across the landscape and directly modeling shading and solar radiation (Ogée et al. 2003; Bennie et al. 2008; Dobrowski et al. 2009; Maclean et al. 2019). Such mechanistic or process-based models may offer greater predictive power than purely statistical methods when generalizing to novel circumstances, including anthropogenic climate change (Cuddington et al. 2013). This is supported by the promising results shown by recently developed, global microclimate models (e.g., Kearney et al. 2020; Maclean, 2020), although these models do not incorporate the mechanistic approach of Ogée et al. (2003) and may have limited ability to predict forest microclimate (undercanopy) conditions [but see (Maclean and Klinges, 2021)]. Importantly, long-term studies, such as the one described here, offer an ideal data source for developing and validating such mechanistic models, which could then be linked to biodiversity responses (Supplementary Discussion).

4.2. Conclusion

For microrefugia to be effective in a changing climate, they must be temporally consistent. Generalizing our results over the last decade to long-term future climate conditions is difficult, but important for setting conservation priorities at the landscape-scale and broader scale. The strong elevational gradient in temperatures means that high-elevation sites are likely to be doubly important: first, they may function as microrefugia for species populations at lower elevations, and second, high-elevation sites with high temporal consistency due to factors such as topographic shading and vegetation structure are vital because species that are already dependent on high-elevation microrefugia may have little potential for further range shifts. Because vegetation is also predictive of microrefugia locations, when managing for and protecting microrefugia, old-growth in high elevation and high topographic position index areas should be conserved when possible (Morelli et al. 2016). Conversely, mid elevation old growth stands with low topographic position might be equally important in managing species responses to climate change because they have the added benefit of being some of the locations that have served as fire refugia over the last 500 years, in contrast to a lot of the higher elevation forests in the HJA. While our analysis deals with the effects of vegetation on microclimate, microclimatic conditions associated with forest can, in turn, promote tree recruitment (Badano et al. 2015). Thus, positive feedback loops wherein decreases in forest structural complexity and increases in undercanopy temperatures reinforce each other can lead to undesirable alternative stable states, providing additional motivation to conserve old-growth and mature forest (Schröder et al. 2005).

Another management consideration is that minimum, maximum, and mean temperatures may be differentially affected by both climate change and the presence of old-growth (Dobrowski 2011; De Frenne et al. 2019; Zellweger et al. 2019). Thus, a holistic approach is needed to achieve conservation and other management goals. The availability and persistence of microrefugia must be considered alongside potential benefits of old-growth forests to biodiversity, including increased habitat diversity and vegetation structure (Mladenoff et al. 1993). Such an approach could consider the effects of microclimate on species' populations more generally, accounting for inter-annual variability, including among less extreme years. For example, relatively short-term variation in climate can help or hinder tree regeneration, allowing for range expansion, maintenance, or contractions (Jackson et al. 2009). This implies that the temporal variation in microclimate is a key component for understanding historical and future species range shifts. By modeling microrefugia over a decade, our analysis represents a step toward taking a long-term view of microclimate (Lenoir et al. 2017), which will be necessary to ensure effective biodiversity conservation as climate change accelerates.

Data availability

All data are publicly available; sources are given in the methods sections. Code is available at https://github.com/wolfch2/HJA_microclimate.

Supporting Information

mmc1.docx

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2021.108520.

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