Average, variability, and extremes: A framework to quantify microclimate temperature modulation

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Open research statement

All code and simulated data used in this study are deposited in a public Zenodo repository

(https://doi.org/10.5281/zenodo.19189205). The field temperature data used in our analyses are

part of the Microclimate Database (MDB) and will be made accessible through a BExIS data

portal (https://database.soilbon.org/). Accession links and DOIs for all resources will be provided

in the final published version of the manuscript.

Key words

climate analysis, climate change, microclimate ecology, microclimate indices, microclimate

modulation, forest microclimate, temperature buffering, temperature offsets

ABSTRACT

Microclimate, the climatic conditions experienced by organisms, can differ substantially from the macroclimate measured by weather stations. Microclimate modulation is the modification of the microclimate by environmental conditions. Despite its ecological importance, there is currently no standardized method for quantifying microclimate modulation, which limits comparability across studies. Commonly used indices can be categorized as targeting microclimate temperature average, variability, or extremes (maxima and minima). The average describes the central tendency of the temperature, variability quantifies its dispersion or fluctuations, and extremes capture rare but potentially important high and low values. Here, we compiled and compared 12 types of indices used in the literature to quantify microclimate temperature modulation in ecology. Using forest microclimate temperature measurements from 47 sites in Italy, we calculated the microclimate indices and showed in a Principal Component Analysis that they clustered in the categories of average, variability, maxima and minima. In a simulation framework, we modified microclimate average, variability, and extremes, and introduced error. We calculated the microclimate indices on the simulated data, and compared the indices' responses to the simulated modulation. We found that both mean and median offset (difference between microclimate and macroclimate) reliably represented average modulation and were robust to simulated error. The offset of amplitudes between the 5th and 95th percentiles best represented variability modulation. For maxima and minima, respectively, the 97.5th and 2.5th percentile best balanced error-proneness and distance from the absolute maximum or minimum. The proposed indices provide a comprehensive and widely applicable approach to quantifying microclimate temperature modulation in ecology. Since average, variability, and extremes are

52 relevant proxies for how temperature affects ecological processes, we suggest using them in

53 conjunction to characterize microclimate modulation. Widespread application of this framework

54 will enhance comparability between microclimate studies and offer new insights into how

55 microclimate modulation interacts with environmental parameters and ecosystem processes.
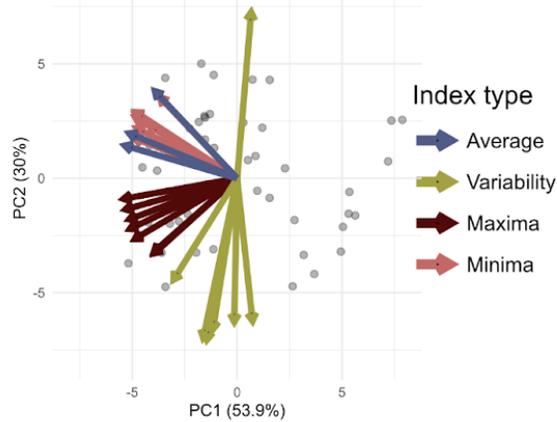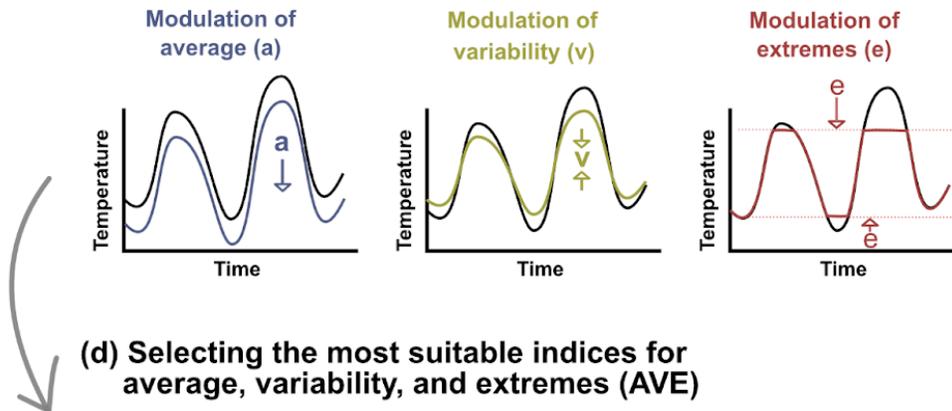
(a) Collecting and categorizing microclimate indices

Most microclimate indices target:

☐ Modulation of temperature average (A)
☐ Modulation of temperature variability (V)
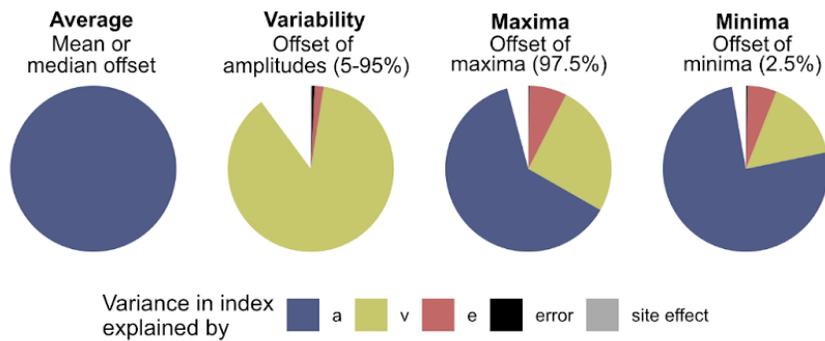☐ Modulation of temperature extremes (E)

(b) Correlating microclimate indices

Index type
→ Average
→ Variability
→ Maxima
→ Minima

PC2 (30%)
PC1 (53.9%)

(c) Simulating microclimates

Modulation of average (a)

Modulation of variability (v)

Modulation of extremes (e)

(d) Selecting the most suitable indices for average, variability, and extremes (AVE)

Average
Mean or median offset

Variability
Offset of amplitudes (5-95%)

Maxima
Offset of maxima (97.5%)

Minima
Offset of minima (2.5%)

Variance in index explained by ☐ a ☐ v ☐ e ■ error ■ site effect

Figure 1. Overview of the study. The capitalized categories A, V, and E (E_{max} and E_{min}) refer to index types, while the lowercase letters a, v, and e refer to simulation parameters. (a) We compiled indices commonly used to describe microclimate temperature in ecology and categorized them as targeting average, variability, minimum or maximum modulation. (b) We calculated these indices on forest microclimate data from Italy and found that they were generally most highly correlated with each other in the categories as we had assigned them (see Fig. 2). (c) We simulated microclimates by modifying average, variability, and extremes (maxima and minima). (d) We calculated the microclimate indices on the simulated microclimates and used variance partitioning to investigate how much variation in the indices was explained by the simulation parameters (see Fig. 3). Based on these results, we identified the indices best suited for describing modulation of average, variability, maxima, and minima in microclimate temperatures.

INTRODUCTION

Microclimate refers to climate conditions in the vicinity of organisms or ecosystems (De Frenne et al. 2024; Kemppinen et al. 2024). The term "microclimate modulation" describes the modification of the microclimate by environmental conditions, e.g., by topography and vegetation (Beugnon et al. 2024; Bramer et al. 2018; De Frenne et al. 2021). As a result of microclimate modulation, the conditions that organisms experience in ecosystems can differ substantially from the macroclimate recorded under standardized conditions, e.g., by weather stations (Kemppinen et al. 2024; Bramer et al. 2018; Lembrechts 2023). Since microclimates can buffer extreme climatic conditions (Scheffers et al. 2014; Finocchiaro et al. 2023) and reduce local extinction risks for species threatened by global warming (Suggitt et al. 2018), microclimate modulation is a crucial process in climate change adaptation and mitigation.

Although there is a wealth of ecological studies on how environments modify the microclimate, these studies apply different metrics and are therefore hard to compare. The difference between macroclimate and microclimate temperature is typically modelled as the offset of those values – e.g., the mean or median of differences between microclimate and macroclimate temperature (Aalto et al. 2022; De Frenne et al. 2019; Haesen et al. 2021; Schnabel et al. 2025; Zellweger et al. 2019); differences in temperature amplitudes (Finocchiaro et al. 2023; Ehbrecht et al. 2017), standard deviation (Frey et al. 2016), coefficient of variation (Allen 2016); or the offsets of maxima and minima (Finocchiaro et al. 2023; Zellweger et al. 2019; 2020). An approach not using offsets has been introduced by Gril et al. (2023), who suggest quantifying microclimate air temperature using the equilibrium temperature and the slope of the linear relationship between microclimate and macroclimate temperatures. However, while this framework offers an elegant alternative, it does not explicitly incorporate extreme temperatures, which are known to drive

92 mortality and limit species distributions. Overall, the lack of a unified conceptual framework for

93 the quantification of microclimate modulations means that inconsistent methods are applied

94 across microclimate ecology studies. As a result, meta-analyses and cross-site comparisons

95 remain difficult, and the ecological meaning of different indices is often unclear.

96 Here, we propose quantifying microclimate temperature modulation with micro–macroclimate

97 offsets across the complementary facets of average, variability, and extremes (maxima and

98 minima). The average describes the central tendency of the temperature, while variability shows

99 its dispersion or fluctuations. Extreme values, the limits of the distribution (maxima and

100 minima), highlight rare but potentially important events.

101 The majority of microclimate indices in the literature fall into these categories, since these

102 climate characteristics are relevant proxies for how temperature affects organisms. Average

103 temperature, perhaps the most common metric in ecological microclimate studies (Aalto et al.

104 2022; De Frenne et al. 2019; Haesen et al. 2021; Suggitt et al. 2018; Zellweger et al. 2019),

105 influences metabolic and growth rates (Brown et al. 2004). However, the average alone is not

106 sufficient for describing the impacts of temperature on ecosystems or organisms (Körner and

107 Hiltbrunner 2018). Variability determines how much organisms and ecosystems have to adjust to

108 the stress posed by fluctuations in temperature (Vasseur et al. 2014). Generally, ecosystems and

109 their functions are sensitive to climate variability (Seddon et al. 2016; Oliveira et al. 2022), and

110 increased temperature variability, as caused by climate change, has been found to decrease

111 species richness and community stability (Zhang et al. 2018). Finally, extreme values (i.e.,

112 maximum and minimum temperatures) are an important determinant of survival, since both heat

113 and cold immediately affect mortality. The upper and lower boundaries of temperature therefore

114 shape the species assembly by determining which species can survive (Körner and Hiltbrunner

115 2018; Parmesan et al. 2000). Taken together, considering the modulation of these different

116 aspects of the temperature regime of a site, namely average, variability, and extremes, is needed

117 to provide a detailed picture of the microclimate temperature experienced by the organisms

118 living in that site. While most microclimate ecology studies already use metrics targeting one of

119 these parameters, rarely are all three consciously employed.

120 In this study (Fig. 1), we aimed to identify a set of comprehensive but non-overlapping indices to

121 describe the modulating effect of the environment on microclimate temperature. We addressed

122 three main research objectives: (i) which microclimate indices are commonly used in the

123 ecological literature, (ii) to what extent these indices are collinear, and what minimum set of

124 complementary indices could be retained, and (iii) which specific aspects of microclimate

125 modulation are captured by the different indices.

METHODS

All following modeling and analyses were performed in R, version 4.4.2 (R Core Team 2024).

Figures were created using the R package "ggplot2" (Wickham 2016) and the graphic design

program Affinity Designer (Serif (Europe) Ltd. 2025). Prior to analyses, all temperatures were

converted to Kelvin.

List of microclimate indices

We compiled indices used to describe microclimate modulation in ecology, focusing on

important and recent microclimate ecology papers. Papers were retrieved based on the expertise

of the authors. We supplemented these with a search in Web of Science for

"microclimate+modulation+ecology", but discontinued the search when no new indices were

identified after scanning 50 results. The resulting list of indices was implemented in R functions

(Appendix S1). We excluded indices based on thermal sums (degree hours or degree days, i.e.

number of hours or days above or below a certain temperature threshold) (Körner and

Hiltbrunner 2018), because these can be calculated for every possible temperature threshold,

exceeding the scope of our study.

Empirical forest microclimate data

To compare the indices, we used *in situ* microclimate air temperature data and corresponding

macroclimate temperature measurements. Hourly microclimate air temperatures were recorded

with TOMST TMS-4 (Standard) dataloggers (Wild et al. 2019; TOMST 2019) in Italian forests

between June 2024 and May 2025, at 57 sites located in two regions (Appendix S2). The region

in eastern Trentino contained only sites dominated by evergreen needleleaf species (n = 23), and

the region in eastern Tuscany contained sites dominated (>65%) by evergreen needleleaf species

148 (n = 8), deciduous broadleaf species (n = 10), and mixed sites (n = 6). Microclimate temperatures

149 were measured 15 cm above the ground. Macroclimate temperatures for each site were extracted

150 from the dataset "ERA5-Land" (Copernicus Climate Change Service 2019). For every site, we

151 calculated the list of microclimate modulation indices we had compiled. To quantify

152 relationships between the indices, we calculated correlations between the indices and performed

153 a Principal Component Analysis (PCA) using the base R function "prcomp" with the indices as

154 variables and the site values as observations.

Microclimate simulation

156 While the PCA illustrates relationships between microclimate indices based on empirical data, it

157 does not identify which indices best capture changes in specific temperature facets. Therefore,

158 we compared the microclimate indices using a simulation that modified temperature average,

159 variability, and extremes directly, since we had identified these as the targets of most

160 microclimate modulation indices. We chose to use a non-mechanistic simulation where we

161 directly controlled the mathematical features of interest instead of simulating mechanistically

162 realistic microclimates, because this allowed for direct tracking of the indices' responses to the

163 target facets.

164 As a basis for the simulation, we imported Integrated Surface Hourly (ISH) temperature

165 measurements from the National Oceanic and Atmospheric Association (NOAA) using the R

166 package "climate" (Czernecki et al. 2020). We filtered for stations that were active and recorded

167 hourly temperatures in the year 2020. From these, we selected 20 stations evenly distributed

168 across those available locations (Appendix S3), using the R package "spsurvey" (Dumelle et al.

169 2023), and downloaded the data from January to December 2020.

170 We created functions to modify temperature average, variance, maxima (values above the 95th

171 percentile), and minima (values below the 5th percentile). To simulate a microclimate with a

172 different average than the macroclimate, an offset is added to all values in the macroclimate (Eq.

173 1). The input parameter is the average offset a, with a = 1 increasing the average by 1 unit (here

174 °K).

175
$$T_{micro} = T_{macro} + a \qquad \text{(Eq. 1)}$$

176 To simulate a microclimate with a different variability than the macroclimate, the variance is

177 modified by changing the dispersion of points around the mean (Eq. 2). The input parameter is v,

178 with v = 0.01 increasing the variance by 1 percent. Based on a date input, the function groups the

179 data and calculates the mean separately for each month to modify variance on a monthly basis

180 rather than across the entire data series.

181
$$T_{micro} = (T_{macro} - mean(T_{macro})) * (1 + v) + mean(T_{macro}) \qquad \text{(Eq. 2)}$$

182 In the function that simulates extreme modulation, "extremes" are defined as values above the

183 95th percentile (p95) and below the 5th percentile (p5) of the macroclimate data across the year.

184 These values are modified by the simulation function (Eq. 3). Between the 5th and 95th

185 percentile, the simulated microclimate value equals the input macroclimate value. The function

186 modifies extreme values linearly with the parameter e (emax for maxima, emin for minima),

187 with e = 0 being equivalent to the macroclimate, e > 0 decreasing extremes, e = 1 achieving

188 complete stabilization, and e < 0 increasing extremes.

189
$$if\ T_{macro} > p_{95}: \qquad T_{micro} = T_{macro} - (T_{macro} - p_{95}) * e_{max} \qquad \text{(Eq. 3)}$$

190
$$if\ p_5 < T_{macro} < p_{95}: \quad T_{micro} = T_{macro}$$

191
$$if\ T_{macro} < p_5: \qquad T_{micro} = T_{macro} + (p_5 - T_{macro}) * e_{min}$$

192 The extreme modulation function represents microclimate buffering mechanisms that

193 specifically affect very high and very low temperatures, such as buffering of cold extremes by

194 snow (Wilson et al. 2020) and buffering of heat by increased evapotranspiration (Yang et al.

195 2023). While averages and variance can be modified independently, maximum and minimum

196 temperatures are affected by both average and variability, so that the final maximum and

197 minimum values of a simulated temperature will depend on all three functions. Additionally, we

198 included an autocorrelated random error function with a variable error standard deviation (error

199 SD) to test the indices' sensitivity to measurement inaccuracies (Appendix S4).

200 To simulate microclimates with modifiable parameters, we applied the functions modifying

201 average, variance, extremes, and adding a random error to the downloaded macroclimate data (in

202 this order). The ranges of the input parameters were chosen to reflect a large scope of possible

203 microclimate modulation conditions. Average offsets ranged from -5 °K to +5 °K in steps of 2

204 °K. Variability modulation ranged from -10% to +10% in steps of 2%. Values for heat and cold

205 extreme modulation ranged from -1 (more extreme temperatures than the macroclimate) to 1

206 (complete stabilization) in steps of 0.4. The error function was applied with error SDs ranging

207 from 0 (no error added) to 1 in steps of 0.2. For each macroclimate data series, we simulated a

208 microclimate for every possible parameter value combination, resulting in 1,296 simulations for

209 each of the 20 sites (25,920 simulations total).

210 **Responses of indices to microclimate simulations**

211 We calculated the microclimate indices for the simulated microclimates and analyzed index

212 values in response to the simulation input parameters (i.e., modification of the average, variance

213 and extremes). We determined the specificity of the indices for the target facets by partitioning

214 the variance proportions explained by average (a), variability (v), and extreme (e) modification,

215 error, and site effect. For this purpose, we fit a linear model for each index with the input

216 modulation parameters as fixed effects and site as random effect. Prior to fitting the models, all

217 variables were z-standardized. The models were calculated using the function "lmer" from the R

218 package "lmerTest" (Kuznetsova et al. 2017). The linear response of indices to the parameters

219 was determined by extracting the marginal R^2 of the model, using Nakagawa's R^2 (Nakagawa et

220 al. 2022) as implemented in the function "r2_nakagawa" from the R package "performance"

221 (Lüdecke et al. 2021). To quantify the strength of the response to the individual parameters (i.e.,

222 a, v, e, and error), the marginal R^2 of each fixed effect was extracted by refitting the model only

223 including the parameter of interest as a predictor and site as a random effect. Site effect was

224 calculated by subtracting the marginal R^2 of the model from the conditional R^2 of the model.

225 Some of the microclimate indices were commonly used at different quantiles, such as the 95th

226 percentile or the absolute maximum. For these indices (offset of maxima, offset of minima, offset

227 of amplitudes), we additionally calculated the index values for a larger range of quantiles (92.5^{th}

228 to 100th for maxima and 7.5^{th} to 0th for minima, in steps of 1.25) to test how the quantile choice

229 affected the index performance.

RESULTS

List of microclimate modulation indices

We compiled a list of 12 indices that have been used to quantify microclimate modulation in ecology and categorized them according to our framework as average, variability, or extreme (maxima or mimina) indices (Table 1). We identified two main average modulation indices: the mean offset and the median offset. For variability modulation, we identified three types of indices that could be implemented in different variations: the offset of standard deviations (variation: mean daily offset of SDs); the offset of amplitudes (which also can be calculated as mean daily offset of amplitudes, as well as with different boundaries for the amplitudes, e.g., the difference between absolute minimum and maximum or between 5th percentile and 95th percentile); and the offset of the coefficient of variation (CV). For extreme modulation, most studies use the offsets of maxima and minima, but there was variation in which percentiles were defined as the maximum and minimum (e.g., absolute maximum and minimum or 95th percentile and 5th percentile). The offsets of maxima and minima can also be calculated as daily averages. Additionally, one study (Kašpar et al. 2021) used the 95th percentile of daily offsets of maxima.

Although distinct from the other approaches, we also included slope and equilibrium (Gril et al. 2023), where slope describes the linear relationship between macroclimate and macroclimate temperature and equilibrium is the temperature at which macroclimate and microclimate are equivalent. We categorized slope as a variability index and equilibrium as an average index.

Table 1. List of microclimate modulation indices. The indices are categorized according to whether they target the modulation of average (A), variability (V), maxima (E $_{max}$), or minima (E$_{min}$).
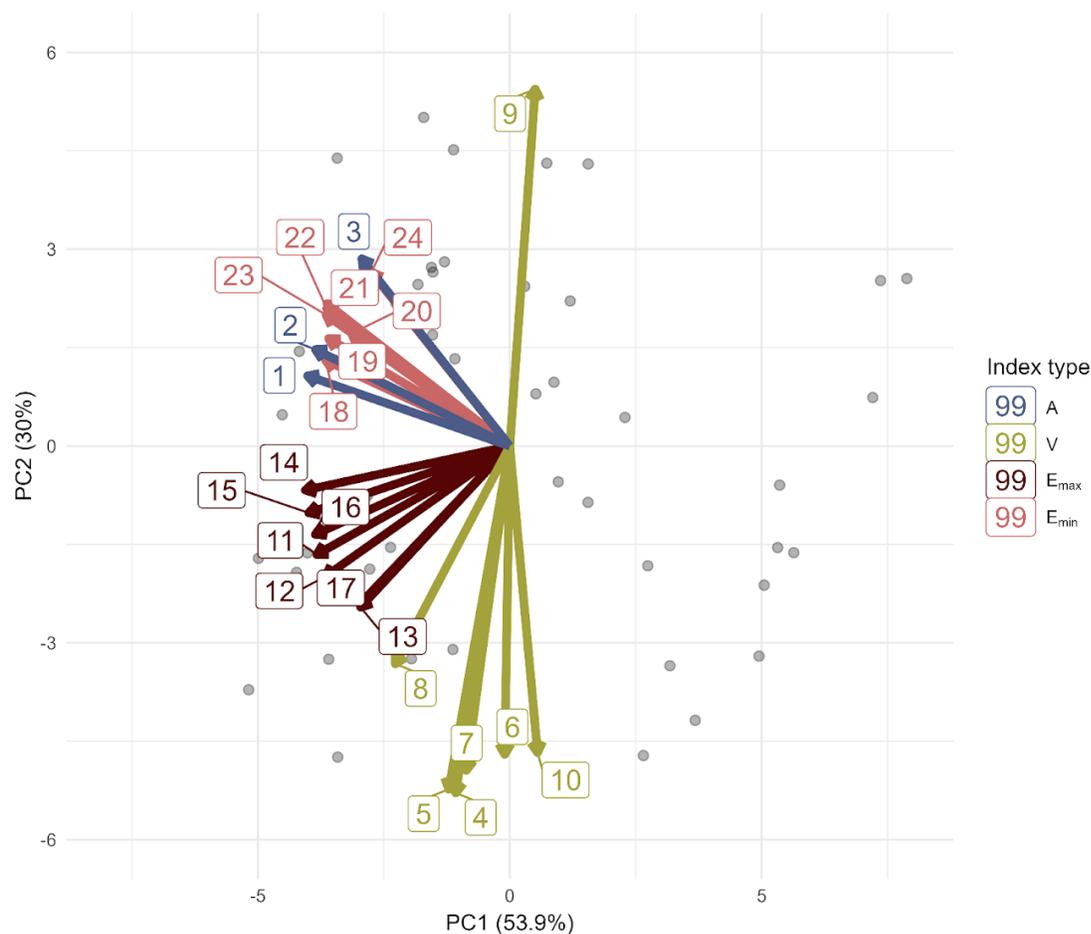
Index	Explanation	Category
Mean offset	Arithmetic mean of differences between microclimate and macroclimate (e.g. De Frenne et al. 2019; Haesen et al. 2021; Zellweger et al. 2019)	A
Median offset	Median of differences between microclimate and macroclimate (Schnabel et al. 2025)	A
Offset of SDs	Difference between standard deviations (SD) of microclimate and macroclimate (Frey et al. 2016) *Alternative version*: mean daily offset of SDs (Richter et al. 2022)	V
Offset of amplitudes	Difference between amplitudes (ranges) of microclimate and macroclimate (Ehbrecht et al. 2017; Finocchiaro et al. 2023) *Varies by quantile*: the amplitude can be defined as the difference between absolute maximum and minimum, 95th percentile and 5th percentile, or other quantiles *Alternative version*: mean daily offset of amplitude	V
Offset of CVs	Difference between coefficients of variation (CV; the ratio of the standard deviation to the mean) of microclimate and macroclimate (Allen 2016)	V
Offset of maxima	Difference between maximum temperature in microclimate and macroclimate *Quantile versions*: maximum has been defined as 1) 95th percentile (Finocchiaro et al. 2023; Aalto et al. 2022; Finocchiaro et al. 2024), 2) 97.5th percentile (Schnabel et al. 2025), 3) Absolute maximum (Zellweger et al. 2019; 2020; Ray et al. 2023) *Alternative version*: mean daily offset of maxima (Körner and Hiltbrunner 2018)	E$_{max}$
p95 of maximum offsets	95th percentile of daily offsets of maxima (Kašpar et al. 2021)	E$_{max}$
Offset of minima	Difference between minimum temperature in microclimate and macroclimate *Quantile versions*: minimum has been defined as 1) 5th percentile (Finocchiaro et al. 2023; 2024), 2) 97.5th percentile (Schnabel et al. 2025), 3) Absolute minimum (Zellweger et al. 2019; Ray et al. 2023) *Alternative version*: mean daily offset of minima (Körner and Hiltbrunner 2018)	E$_{min}$

p5 of minimum offsets	5th percentile of daily offsets of minima (analogous to maxima in Kašpar et al., 2021)	E_{min}
Slope	Slope of the linear relationship between microclimate and macroclimate (Gril et al. 2023)	V
Equilibrium	Temperature at which microclimate and macroclimate are equivalent, calculated as intercept / (1 - slope) of the linear relationship between microclimate and macroclimate (Gril et al. 2023)	A
Thermal sums	Number of hours or days above or below a certain temperature threshold (Körner and Hiltbrunner 2018)	not included

Collinearity of indices based on field data

We calculated all listed indices on forest microclimate data and performed a Principal

Component Analysis. The first and second principal components explained 54% and 30% of the

variation in the forest sites (Fig. 2). Generally, indices within the categories average, variability,

maxima, and minima were highly correlated with each other. We also found collinearity between

indices in the average and minima categories. The correlations between indices confirm that

commonly used microclimate metrics within the categories are functionally similar, targeting

distinct components of microclimate modulation.

Both average and minima indices loaded negatively on PC1 and positively on PC2, while

maxima indices loaded negatively on both. Variability indices had negative loadings on PC2

(except for the offset of CVs) and low or no loadings on PC1. The offset of CVs was correlated

negatively with the other variability indices, but only weakly correlated with the other indices

(for the correlation table see Appendix S5). This discrepancy is likely because CV normalizes by

mean temperature, conflating shifts in average and variability. It is also based on a ratio (standard

deviation divided by mean) instead of a difference like the other indices, leading to non-linear

behavior.

1: Mean offset
2: Median offset
3: Equilibrium
4: Offset of SDs
5: Mean daily offset of SDs
6: Amplitude offset (5%)
7: Amplitude offset (2.5%)
8: Mean daily amplitude offset
9: Offset of CV
10: Slope
11: Offset of maxima (95%)
12: Offset of maxima (97.5%)

13: Offset of maxima (100%)
14: Mean daily offset of maxima (95%)
15: Mean daily offset of maxima (97.5%)
16: Mean daily offset of maxima (100%)
17: p95 of daily offsets of maxima
18: Offset of minima (5%)
19: Offset of minima (2.5%)
20: Offset of minima (0%)
21: Offset of minima (5%)
22: Mean daily offset of minima (2.5%)
23: Mean daily offset of minima (0%)
24: p5 of daily offsets of minima

269

Figure 2. Ordination plot of microclimate indices calculated on 48 microclimate data from forests in Italy. The points represent the sites' scores on the first two principal components, while the arrows represent the variables' (i.e. the microclimate indices') loadings on the principal components. A small angle between arrows indicates a high correlation between variables. Index

274 *types are categorized according to whether they target the modulation of average (A; blue),*

275 *variability (V; yellow), maxima (E_{max}; dark red), or minima (E_{min}; light red).*

Indices' responses to simulated microclimate modulation

277 In a simulation that modified temperature average, variability, and extremes directly, we

278 compared the response of the indices to different aspects of microclimate temperature

279 modulation. Using variance partitioning, we identified which simulation parameters primarily
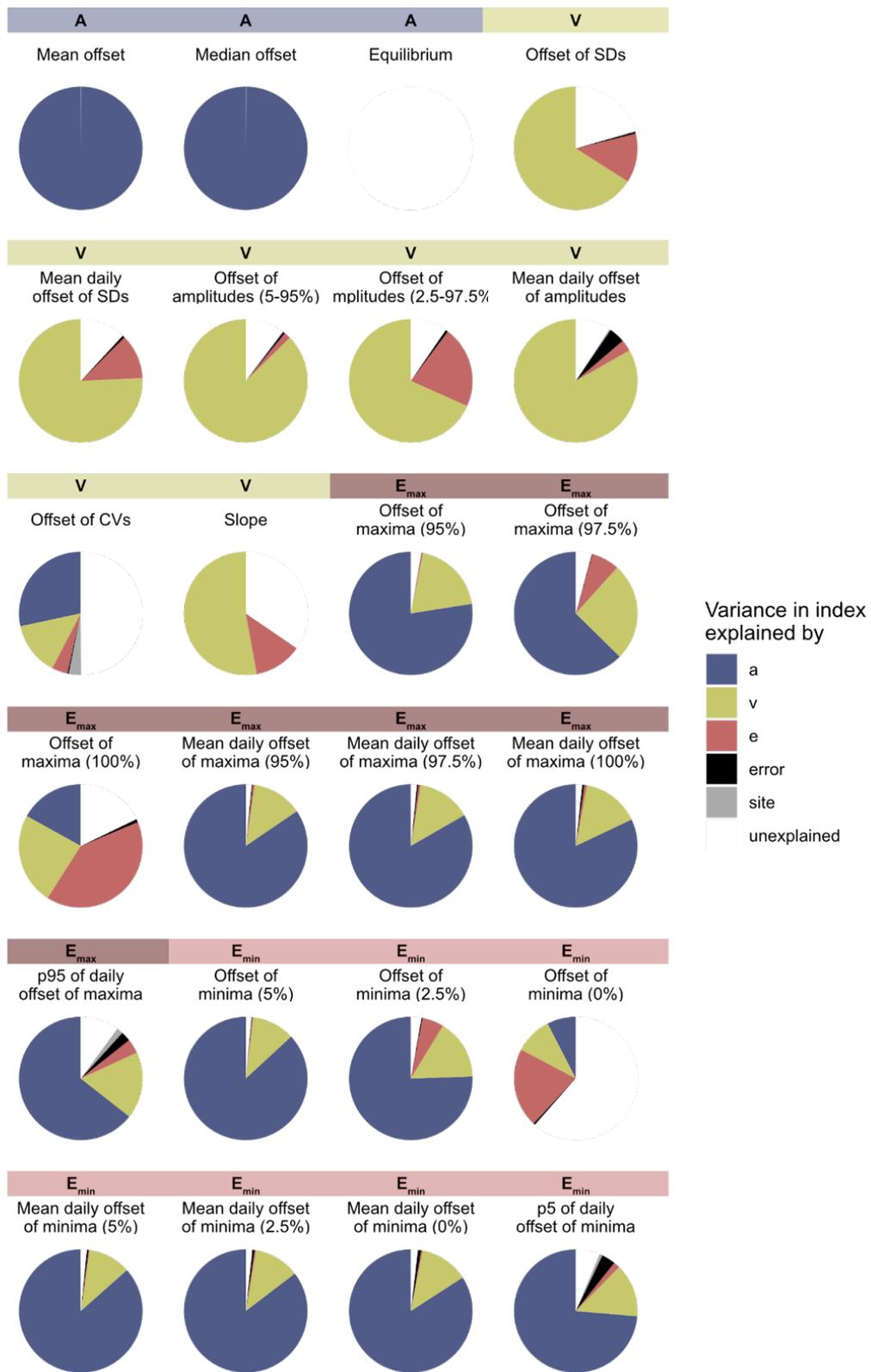
280 influenced the values of the indices (Fig. 3).

281 For the average modulation indices mean offset and median offset, 100% of the variance in the

282 index was predicted by average modulation ($R^2(a) = 1$; Fig. 3). Equilibrium, unlike other indices,

283 represents an absolute temperature (the point at which macroclimate and microclimate are equal)

284 and therefore does not respond directly to shifts in mean, variability, or extremes. None of the

285 indices grouped under average modulation showed an error effect or site effect ($R^2(site) = 0$ for

286 all).

287 Most of the variance in the indices belonging to the variability category was explained by

288 variability modulation, again except for the offset of CVs, but the proportion of explained

289 variance differed (Fig. 3). Offset of SDs and mean daily offset of SDs had similar variance

290 distributions, with $R^2(v) = 0.66$ and 0.76, $R^2(e) = 0.13$ and 0.12, and $R^2(error) = 0.005$ and 0.006,

291 respectively. The offset of amplitudes between the 5th and 95th percentiles had $R^2(v) = 0.87$ and

292 $R^2(e) = 0.02$, while the offset of amplitudes between the 2.5th and 97.5th percentiles had a larger

293 contribution of extreme modulation ($R^2(v) = 0.68$ and $R^2(e) = 0.21$). Both had $R^2(error) = 0.006$.

294 For mean daily amplitude offset, the contribution of error was increased ($R^2(error) = 0.04$), while

295 $R^2(v) = 0. 83$ and $R^2(e) = 0.03$. The index slope had $R^2(v) = 0. 53$ and $R^2(e) = 0.13$.

296 For most of the indices targeting extreme modulation, the majority of variance was explained by

297 average modulation (Fig. 3). The quantile versions of offset of maxima differed (see also Fig. 4).

298 Overall, absolute maxima and minima were highly sensitive to random noise, leading to large

299 proportions of unexplained variance, while percentile-based indices were more robust. However,

300 the further from the absolute maximum/minimum the percentile was, the less it tracked the

301 occurrence of extreme temperatures. With the 95th percentile defined as maximum, extreme

302 modulation did not contribute ($R^2(a) = 0.78$, $R^2(v) = 0.19$, $R^2(e) = 0$). This was expected, since

303 the 95th percentile threshold removed the values influenced by our extreme modulation function.

304 At the 97.5th percentile, extreme modulation, variability modulation, and average modulation all

305 explained a proportion of the variance ($R^2(a) = 0.63$, $R^2(v) = 0.26$, $R^2(e) = 0.07$). At the absolute

306 maximum, the majority of variance was explained by extreme modulation ($R^2(e) = 0.40$), but had

307 an 18% proportion of unexplained variance (i.e., variance not explained by the input parameters

308 a, v, e, and error), compared to <5% for the other quantiles. Mean daily offset of maxima had a

309 similar distribution of explained variance, regardless of quantile used ($R^2(a) \approx 0.82$, $R^2(v) \approx 0.14$,

310 $R^2(e) \approx 0$).

311 The quantile versions of the offset of minima exhibited a similar pattern as the versions of the

312 offset of maxima. Again, due to the threshold of our extreme modulation function, the 5th

313 percentile was only influenced by average and variability modulation ($R^2(a) = 0.88$, $R^2(v) = 0.11$,

314 $R^2(e) = 0$). The 2.5th percentile was influenced by average, variability, and extreme modulation

315 ($R^2(a) = 0.76$, $R^2(v) = 0.16$, $R^2(e) = 0.06$). The absolute minimum mostly represented extreme

316 modulation ($R^2(e) = 0.21$), but also had a much larger proportion of unexplained variance (61%

317 compared to <5%). Mean daily offset of minima had similar proportions of explained variance,

318 regardless of quantile used ($R^2(a) \approx 0.85$, $R^2(v) \approx 0.12$, $R^2(e) \approx 0$). Error and site effect did not

319 substantially contribute to any extreme indices ($R^2 < 0.01$) except for the 95th percentile of daily

320 offset of maxima (R^2(error) $= 0.03$, R^2(site) $= 0.02$) and the 5th percentile of daily offsets of

321 minima (R^2(error) $= 0.04$, R^2(site) $= 0.01$).

A	**A**	**A**	**V**
Mean offset	Median offset	Equilibrium	Offset of SDs

V	**V**	**V**	**V**
Mean daily offset of SDs	Offset of amplitudes (5-95%)	Offset of mplitudes (2.5-97.5%)	Mean daily offset of amplitudes

V	**V**	**E**$_{max}$	**E**$_{max}$
Offset of CVs	Slope	Offset of maxima (95%)	Offset of maxima (97.5%)

E$_{max}$	**E**$_{max}$	**E**$_{max}$	**E**$_{max}$
Offset of maxima (100%)	Mean daily offset of maxima (95%)	Mean daily offset of maxima (97.5%)	Mean daily offset of maxima (100%)

E$_{max}$	**E**$_{min}$	**E**$_{min}$	**E**$_{min}$
p95 of daily offset of maxima	Offset of minima (5%)	Offset of minima (2.5%)	Offset of minima (0%)

E$_{min}$	**E**$_{min}$	**E**$_{min}$	**E**$_{min}$
Mean daily offset of minima (5%)	Mean daily offset of minima (2.5%)	Mean daily offset of minima (0%)	p5 of daily offset of minima

Variance in index explained by

- a
- v
- e
- error
- site
- unexplained

Figure 3. Variance partitioning results of indices calculated on simulated microclimates, showing what proportion of variance in each index is explained by which input parameters (average modulation (a), variability modulation (v), extreme modulation (e), error) and by site effect. The capitalized categories A, V, E_{max}, and E_{min} refer to index types, while the lowercase letters a, v, and e refer to simulation parameters.

Effect of quantile levels

For all three indices that are based on quantiles, there was a sharply increased amount of unexplained variance at the absolute maximum and minimum, highlighting the instability of these values (18% unexplained variance for offset of maxima, 61% for offset of minima, and 34% for offset of amplitudes; Fig. 4). The contribution of extreme modulation increased towards the absolute maximum and minimum, where our simulated extreme modulation had the strongest effect, while those of average and variability modulation decreased. The contribution of error increased slightly towards the absolute maximum and minimum.
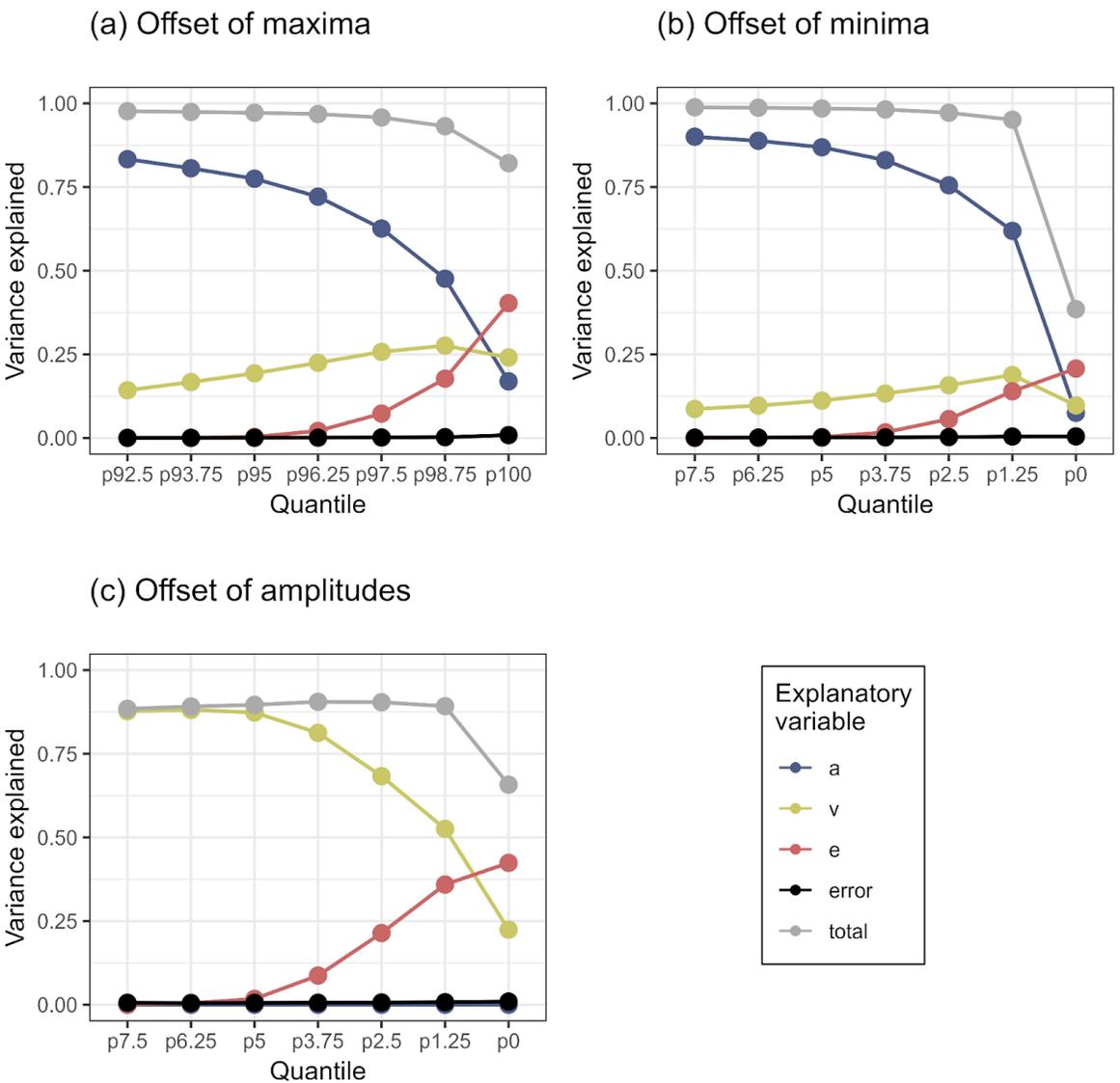
Figure 4. Proportion of variance explained by the input parameters (average modulation (a),

variability modulation (v), extreme modulation (e), error, and total variance explained by all

parameters), ranked by quantile.

DISCUSSION

Our study compiles methods to quantify microclimate modulation and proposes a unifying framework of average, variability, and extremes (AVE). We found that although across the ecological microclimate literature a large number of microclimate indices are used, they are largely collinear and quantify the modulation of either average, variability, maxima, or minima. Using temperature simulations, we showed that the different indices depict different facets of microclimate modulation. By summarizing microclimate modulation in these three facets, the AVE framework is capable of translating complex temperature dynamics into parameters that represent how temperature is shaped by its environment.

Our study provides a first attempt to unify the different metrics used across microclimate ecology in a framework tested with empirical and simulated data. An earlier effort to provide a unifying approach to quantifying microclimate was the slope & equilibrium framework (Gril et al. 2023). The authors suggested representing the microclimate-macroclimate relationship with the two titular parameters. While this model is innovative and useful for certain applications, it does not explicitly incorporate thermal extremes, which strongly and most immediately influence organismal survival and species distribution limits (Körner and Hiltbrunner 2018; Parmesan et al. 2000). By contrast, the AVE framework builds directly on established and widely used microclimate indices. This approach preserves continuity with existing research and ensures that key facets of microclimate modulation are represented.

Empirical analysis of forest microclimate data supported the grouping of indices in the categories of average, variability, and extremes. Interestingly, in our data, the average modulation indices (mean and median offset, equilibrium) overlapped with the minima indices. This implies that the values in those categories were driven by the same processes, e.g., that in our data microclimate

minima were largely affected by overall buffering and not driven by additional mechanisms. It is likely that this is a feature of our specific data situated in Southern Europe, where cold extremes are less pronounced than heat extremes (Beck et al. 2018). We retain modulation of minima as a distinct facet, since cold extremes can strongly affect mortality independently of average temperatures (Williams et al. 2015).

Practical recommendations

For average modulation, both mean and median offset are suitable indices. Studies usually use the mean offset (Aalto et al. 2022; De Frenne et al. 2019; Haesen et al. 2021; Zellweger et al. 2019) and more rarely the median offset (Schnabel et al. 2025). When choosing between mean and median offset, it should be taken into account that they can return different results if the distribution of offsets is skewed (e.g., higher temperatures could be reduced by the microclimate to a greater degree than lower temperatures are increased). The median is less influenced by skewedness than the mean, which may be desirable or not, depending on the research question. The mean offset, on the other hand, has the advantage of having been used in the majority of microclimate ecology studies and therefore enhancing comparability.

For variability modulation, we recommend the offset of amplitudes between the 5th and 95th percentiles. Among all variability indices, this one was the most robust and had the highest percentage of variation explained by variability modulation. Calculating the amplitude on a yearly basis instead of a mean daily basis captures the range of conditions that the ecosystem can experience, while the 5 and 95 percent thresholds exclude extreme values.

For extreme modulation, we suggest using the 2.5th percentile for minima and the 97.5th percentile for maxima. These values balance the trade-off between absolute maxima/minima,

which are unstable and error-prone, and lower percentiles (such as the commonly used 5th and 95th), which fail to adequately capture actual extreme temperatures.

Temporal scale plays a role in interpreting microclimate studies since microclimate modulation can vary over time. The indices can be applied to any study time frame (a season, a year, multiple years, etc.), but care must be taken when extrapolating from the results since microclimate modulation is strongly influenced by seasonal and inter-annual variation. To describe a specific microclimate in a statistically representative way, measurements over the span of multiple years would be necessary. To compare microclimates between different conditions, measurements should be taken at the same time for all conditions.

Limitations and future research directions

Although our analyses provide evidence for the utility of the AVE framework, some limitations should be acknowledged. First, the microclimate data available to us were limited to two forest regions in Italy. The patterns observed here may differ from those in other regions or ecosystems such as alpine tundra, grasslands, or shrublands. The data also only covered one year, and microclimate modulation can vary substantially across years due to interannual variation in snow cover, canopy phenology, and extreme weather. Broader validation across larger datasets will therefore be necessary to confirm the generality of the relationships between indices we observed. Second, in our simulation experiment we manipulated average, variability, and extreme temperatures independently in order to isolate index responses. However, these components frequently covary in real microclimates due to shared physical drivers. While this construction of the simulation was necessary to track index responses, it does not fully capture natural mechanistic constraints. Incorporating multi-year and multi-biome datasets as well as more mechanistic simulations would help test the robustness of the AVE framework.

Future research could explore the impact of average, variability, maxima and minima on ecological processes and specific species. Since characteristics such as heat or cold tolerance vary, the facets likely have different impacts on the survival and functioning of different species. Extending the framework to other microclimate variables than temperature, such as vapor pressure deficit, humidity, and wind speed (Bramer et al. 2018), may enhance its utility for assessing microclimate modulation holistically; however, the different mathematical principles that these climate variables follow need to be taken into account to develop appropriate methods.

Conclusions

By compiling existing microclimate modulation indices and evaluating their empirical and simulated behavior, we provide a unified and ecologically grounded framework for quantifying microclimate temperature modulation. The AVE framework summarizes the complexity of microclimate dynamics in the three biologically meaningful facets - average, variability, and extremes - and identifies robust indices for each. Using these indices will improve understanding of how different aspects of microclimate vary under different environmental conditions, as well as how microclimate dynamics impact ecosystems and species survival. Because it builds on established metrics, this framework is easy to adopt for microclimate researchers and enhances comparability across studies. As the importance of microclimate for the preservation of species and ecosystem functions grows in the context of global climate change and biodiversity loss, the AVE framework offers a practical foundation for its integration in ecological research.

Author contributions

EMG: Conceptualization (supporting), Methodology (lead), Software (lead), Visualization (equal), Writing – original draft (lead), Writing – review and editing (equal)

NE: Conceptualization (supporting), Supervision (equal), Writing – review and editing (equal)

GJAH: Investigation (equal), Data curation (equal), Writing – review and editing (equal)

FMS: Investigation (equal), Data curation (equal), Writing – review and editing (equal)

YH: Data curation (equal), Writing – review and editing (equal)

JQ: Investigation (equal), Writing – review and editing (equal)

MW: Supervision (equal), Writing – review and editing (equal)

RB: Conceptualization (lead), Methodology (supporting), Software (supporting), Visualization (equal), Writing – original draft (supporting), Writing – review and editing (equal)

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Conflict of interest statement

The authors declare that they have no conflicts of interest.

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588 **APPENDIX**

589 **Appendix S1. Functions to calculate microclimate indices**

```
590 library(lubridate)
591 library(dplyr)
592
593 # mean offset
594 mean_offset <- function(macroclimate, microclimate) {
595   offset <- microclimate - macroclimate
596   mean_offset <- mean(offset, na.rm = TRUE)
597   return(mean_offset)
598 }
599
600 # median offset
601 median_offset <- function(macroclimate, microclimate) {
602   offset <- microclimate - macroclimate
603   median_offset <- median(offset, na.rm = TRUE)
604   return(median_offset)
605 }
606
607 # offset of SDs
608 sd_offset <- function(macroclimate, microclimate) {
609   sd_micro <- sd(microclimate, na.rm = TRUE)
610   sd_macro <- sd(macroclimate, na.rm = TRUE)
611   return(sd_micro - sd_macro)
612 }
613
614 # mean offset of SD of daily mean
615 sd_offset_mean_daily <- function(time.index, macroclimate, microclimate) {
616   df <- data.frame(time.index = time.index, macroclimate = macroclimate,
617 microclimate = microclimate)
618
619   df <- df %>%
620     dplyr::group_by(day = lubridate::day(time.index)) %>%
621     dplyr::summarize(
622       sd_macro = sd(macroclimate, na.rm = TRUE),
623       sd_micro = sd(microclimate, na.rm = TRUE)
624     )
625
626   df$sd_offset <- df$sd_micro - df$sd_macro
627   return(mean(df$sd_offset, na.rm = TRUE))
628 }
629
630 # offset of amplitudes
631 amplitude_offset <- function(macroclimate, microclimate, percentile_min = .05,
632 percentile_max = .95) {
```

```
633   macro_max <- quantile(macroclimate, percentile_max, na.rm = TRUE)
634   micro_max <- quantile(microclimate, percentile_max, na.rm = TRUE)
635   macro_min <- quantile(macroclimate, percentile_min, na.rm = TRUE)
636   micro_min <- quantile(microclimate, percentile_min, na.rm = TRUE)
637
638   amplitude_macro <- macro_max - macro_min
639   amplitude_micro <- micro_max - micro_min
640   amplitude_offset <- amplitude_micro - amplitude_macro
641   return(unname(amplitude_offset))
642 }
643
644 # mean daily offset of amplitudes
645 amplitude_offset_mean_daily <- function(time.index, macroclimate,
646 microclimate) {
647   df <- data.frame(time.index = time.index, macroclimate = macroclimate,
648 microclimate = microclimate)
649
650   df <- df %>%
651     dplyr::group_by(day = lubridate::yday(time.index)) %>%
652     dplyr::summarize(
653       max_macro = max(macroclimate, na.rm = TRUE), min_macro =
654 min(macroclimate, na.rm = TRUE),
655       max_micro = max(microclimate, na.rm = TRUE), min_micro =
656 min(microclimate, na.rm = TRUE)
657     )
658
659   df$daily_amplitude_macro <- df$max_macro - df$min_macro
660   df$daily_amplitude_micro <- df$max_micro - df$min_micro
661   df$amplitude_offset <- df$daily_amplitude_micro - df$daily_amplitude_macro
662
663   return(mean(df$amplitude_offset, na.rm = TRUE))
664 }
665
666 # offset of CVs
667 CV_offset <- function(macroclimate, microclimate) {
668   cv_macro <- mean(macroclimate, na.rm = TRUE) / sd(macroclimate, na.rm =
669 TRUE)
670   cv_micro <- mean(microclimate, na.rm = TRUE) / sd(microclimate, na.rm =
671 TRUE)
672
673   return(cv_micro - cv_macro)
674 }
675
676 # offset of maxima
677 offset_of_maxima <- function(macroclimate, microclimate, percentile = .95) {
678   macro_max <- unname(quantile(macroclimate, percentile, na.rm = TRUE)) #
679 unname removes name (quantile) from value
680   micro_max <- unname(quantile(microclimate, percentile, na.rm = TRUE))
681   offset_of_maxima <- micro_max - macro_max
```

```
682   return(offset_of_maxima)
683 }
684
685 # mean offset of daily maxima
686 offset_of_maxima_mean_daily <- function(time.index, macroclimate,
687 microclimate, percentile = 1.00) {
688   df <- data.frame(time.index = time.index, macroclimate = macroclimate,
689 microclimate = microclimate)
690
691   df <- df %>%
692     dplyr::group_by(day = lubridate::yday(time.index)) %>%
693     dplyr::summarize(
694       max_macro = unname(quantile(macroclimate, percentile, na.rm = TRUE)),
695       max_micro = unname(quantile(microclimate, percentile, na.rm = TRUE))
696     )
697
698   df$daily_max_offset <- df$max_micro - df$max_macro
699   return(mean(df$daily_max_offset, na.rm = TRUE))
700 }
701
702 # 95th percentile of daily differences between the maxima of the microclimate
703 and the macroclimate
704 p95_daily_maxima_offset <- function(time.index, macroclimate, microclimate) {
705   df <- data.frame(time.index = time.index, macroclimate = macroclimate,
706 microclimate = microclimate)
707
708   df <- df %>%
709     dplyr::group_by(day = lubridate::yday(time.index)) %>%
710     dplyr::summarize(
711       max_macro = max(macroclimate, na.rm = TRUE),
712       max_micro = max(microclimate, na.rm = TRUE)
713     )
714
715   df$daily_max_offset <- df$max_micro - df$max_macro
716   max_offset_p95 <- unname(quantile(df$daily_max_offset, 0.95, na.rm = TRUE))
717   return(max_offset_p95)
718 }
719
720 # offset of minima
721 offset_of_minima <- function(macroclimate, microclimate, percentile = .05) {
722   macro_min <- unname(quantile(macroclimate, percentile, na.rm = TRUE))
723   micro_min <- unname(quantile(microclimate, percentile, na.rm = TRUE))
724   offset_of_minima <- micro_min - macro_min
725   return(offset_of_minima)
726 }
727
728 # mean offset of daily minima
729 offset_of_minima_mean_daily <- function(time.index, macroclimate,
730 microclimate, percentile = .05) {
```

```
731   df <- data.frame(time.index = time.index, macroclimate = macroclimate,
732 microclimate = microclimate)
733
734   df <- df %>%
735     dplyr::group_by(day = lubridate::yday(time.index)) %>%
736     dplyr::summarize(
737       min_macro = unname(quantile(macroclimate, percentile, na.rm = TRUE)),
738       min_micro = unname(quantile(microclimate, percentile, na.rm = TRUE))
739     )
740
741   df$daily_min_offset <- df$min_micro - df$min_macro
742   return(mean(df$daily_min_offset, na.rm = TRUE))
743 }
744
745 # 5th percentile of daily differences between the minima of the microclimate
746 and the macroclimate
747 p5_daily_minima_offset <- function(time.index, macroclimate, microclimate) {
748   df <- data.frame(time.index = time.index, macroclimate = macroclimate,
749 microclimate = microclimate)
750
751   df <- df %>%
752     dplyr::group_by(day = lubridate::yday(time.index)) %>%
753     dplyr::summarize(
754       min_macro = min(macroclimate, na.rm = TRUE),
755       min_micro = min(microclimate, na.rm = TRUE)
756     )
757
758   df$daily_min_offset <- df$min_micro - df$min_macro
759   min_offset_p5 <- unname(quantile(df$daily_min_offset, 0.05, na.rm = TRUE))
760   return(min_offset_p5)
761 }
762
763 # slope (following Gril et al. 2023)
764 slope <- function(macroclimate, microclimate) {
765   mod <- lm(microclimate ~ macroclimate, na.action = na.omit) # create linear
766 model
767   cf <- coef(mod) # get coefficients
768   slope <- unname(cf[2])
769
770   return(slope)
771 }
772
773
774 # equilibrium (following Gril et al. 2023)
775 equilibrium <- function(macroclimate, microclimate) {
776   mod <- lm(microclimate ~ macroclimate, na.action = na.omit) # create linear
777 model
778   cf <- coef(mod) # get coefficients
779   intercept <- unname(cf[1])
```

```
780   slope <- unname(cf[2])
781
782   equilibrium <- intercept / (1 - slope)
783   return(equilibrium)
784 }
```

Appendix S2. Map of forest microclimate locations
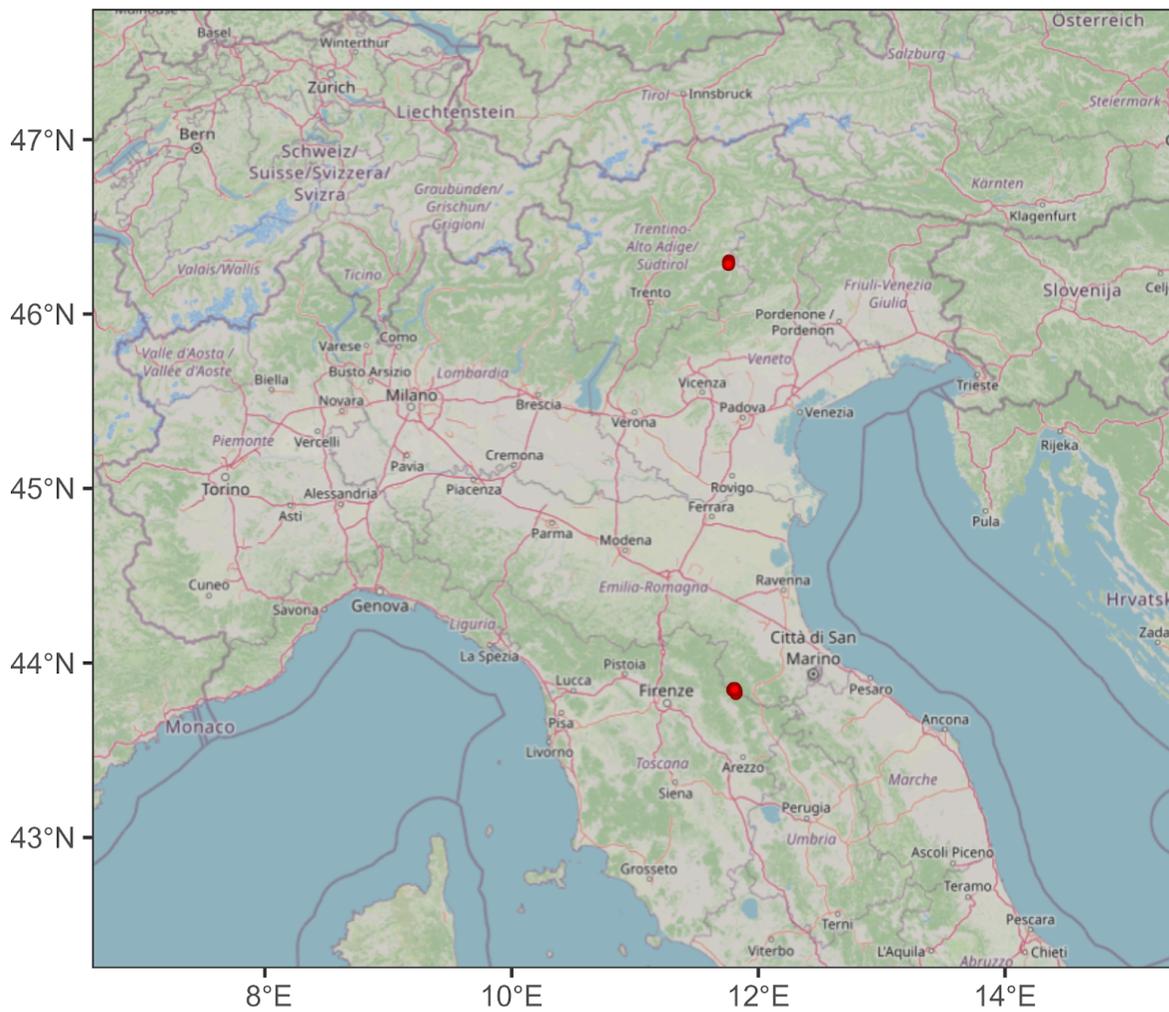
Figure S1. Approximate locations of the forest sites in Italy where microclimates were measured.

Appendix S3. Map of selected NOAA locations

Figure S2. Locations of National Oceanic and Atmospheric Administration (NOAA) weather stations from which data were extracted.

Appendix S4. Functions to simulate microclimate

```r
library(tidyverse)
library(lubridate)


# function to change average
change_average <- function(climate.variable, average.offset) {

  # create new variable that will contain simulated microclimate
  microclimate <- numeric(length(climate.variable))

  # microclimate = input climate + input offset
  microclimate <- climate.variable + average.offset

  # return vector of simulated microclimate values
  return(microclimate)
}


# function to change the variance of the data
change_variance <- function(climate.variable, time.variable,
variance.increase) {

  # convert input to dataframe (necessary for grouping by month)
  df <- data.frame(time.variable = time.variable, climate.variable =
climate.variable)
  df <- df %>%

    # group by month
    group_by(month = lubridate::month(time.variable)) %>%
    mutate(
      microclimate =

      # calculate microclimat as ( Tmacro - mean(Tmacro) ) * (1 + v) +
mean(Tmacro)
        (climate.variable - mean(climate.variable, na.rm = TRUE)) * (1
+ {{ variance.increase }})
          + mean(climate.variable, na.rm = TRUE)
    )

  # return vector of simulated microclimate values
  return(df$microclimate)
}
```

```r
836
837 # function to change extremes
838 change_extremes <- function(climate.variable, heat.stabilisation = 0,
839 cold.stabilisation = 0) {
840
841   # get 5th and 95th percentile (limits for extremes)
842   perc.05 <- quantile(climate.variable, 0.05, na.rm = TRUE)
843   perc.95 <- quantile(climate.variable, 0.95, na.rm = TRUE)
844
845   microclimate <- numeric(length(climate.variable))
846
847   for (i in seq_along(climate.variable)) {
848     if (is.na(climate.variable[i]) == TRUE) {
849
850       # NA handling
851       microclimate[i] <- NA
852     } else if (climate.variable[i] > perc.95) {
853
854       # values above 95th percentile are modified
855       microclimate[i] <- climate.variable[i] - (climate.variable[i] -
856 perc.95) * {{ heat.stabilisation }}
857     } else if (climate.variable[i] < perc.05) {
858
859       # values below 5th percentile are modified
860       microclimate[i] <- climate.variable[i] + (perc.05 -
861 climate.variable[i]) * {{ cold.stabilisation }}
862     } else {
863
864       # other values stay the same
865       microclimate[i] <- climate.variable[i]
866     }
867   }
868   # return vector of simulated microclimate values
869   return(microclimate)
870 }
871
872
873 # function to add error
874 add_error <- function(climate.variable, error.sd = 0, error.autocor =
875 0.8) {
876
877   # generate autocorrelated error series:
878
879   # create random normally distributed (with sd = input error SD)
880 number series
```

```
881   # with the same length as the temperature column
882   e <- w <- rnorm(length(climate.variable), sd = error.sd)
883   # simulate autocorrelation:
884   # entry in autocorrelated series = autocorrelation factor * previous
885 entry + current entry
886   for (t in 2:length(climate.variable)) e[t] <- error.autocor*e[t-1] +
887 w[t]
888
889   # add resulting error to the temperature
890   microclimate <- climate.variable + e
891
892   # return vector of simulated microclimate values
893   return(microclimate)
894 }
```

Appendix S5. Correlations between the microclimate indices
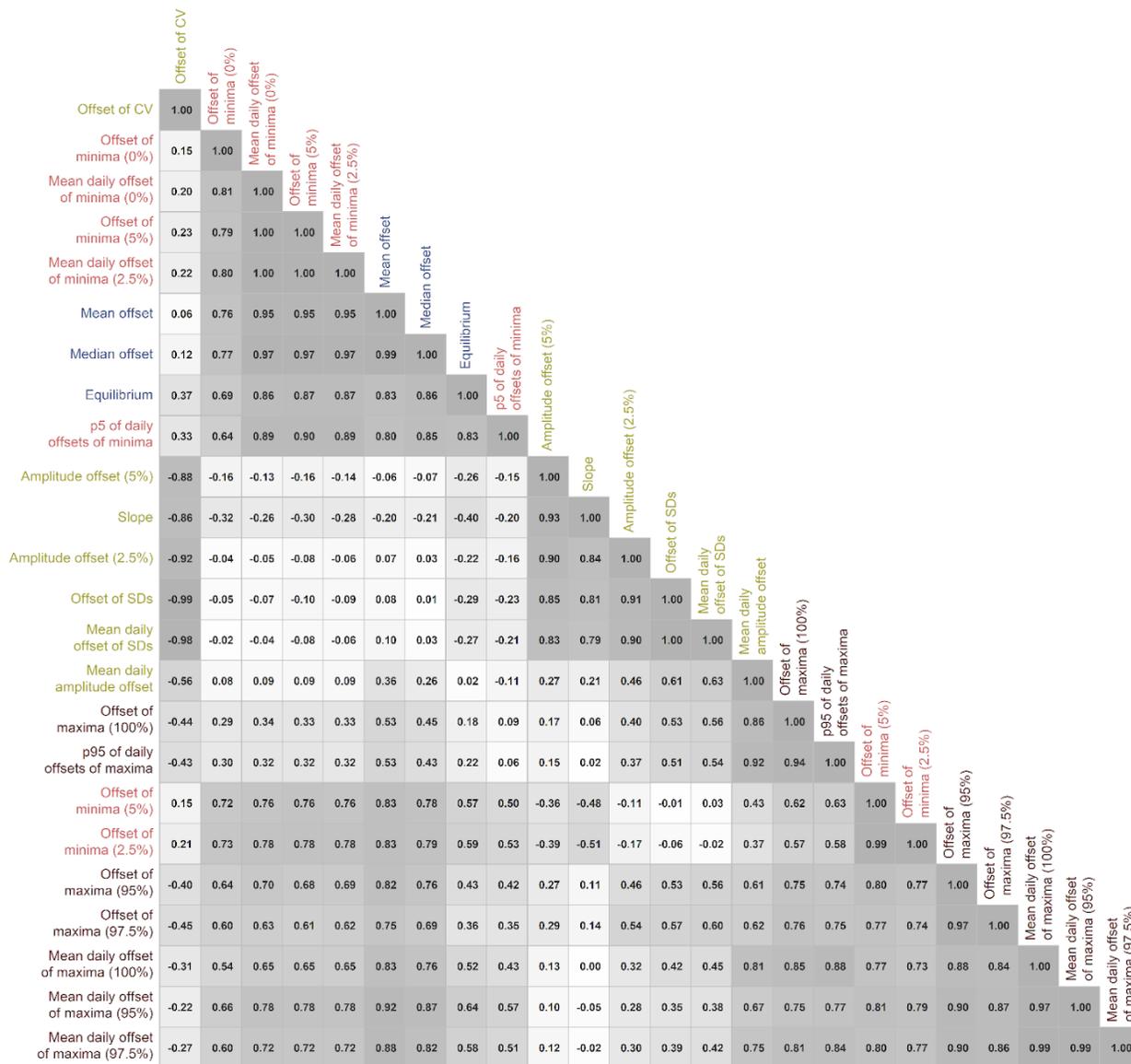
Figure S3. Correlation plot of the microclimate indices as calculated on forest microclimate data, ordered by hierarchical clustering.