



Soil thermal buffering across environmental gradients is not uniform

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Abstract. Large-scale ecological studies typically rely on gridded air temperature, although this may poorly represent the thermal conditions experienced by belowground organisms. Recent soil-temperature products make it possible to examine soil–air temperature differences over broad spatial scales, but it remains unclear whether soils buffer atmospheric heat and cold in the same way, and how these patterns vary among environments. We quantified soil–air thermal buffering across a continental soil-biodiversity network using ERA5-Land, treating warm and cold extremes separately. We compared these patterns with a SoilTemp–CHELSA representation and tested whether regional differences were related to broad climate, measured topsoil properties, and landscape composition. Cold extremes were buffered in 165 of 168 ERA5-Land cells (98.2 %), with a median soil–air offset of +2.14 °C. In contrast, only 41.1 % of cells buffered warm extremes, while 58.9 % showed heat amplification, with a median offset of −0.26 °C. Heat buffering also varied strongly among pedoclimatic regions. Mediterranean South (MDS) cells showed the greatest amplification, with a mean Heat offset of −4.41 °C and no positive buffering among the 16 cells. This regional contrast persisted after accounting for broad thermal climate and landscape composition. Measured topsoil properties showed little robust association with ERA5-Land buffering after correction for multiple testing. Cross-product agreement was much stronger for Cold than for Heat. The stronger edaphic associations obtained with SoilTemp–CHELSA were also retained after aggregation to ERA5-Land spatial support, indicating that the contrast between products was not explained by spatial resolution alone. Overall, soil thermal buffering was strongly asymmetric: soils generally moderated atmospheric cold, but not necessarily heat, and in some regions amplified warm extremes. Air temperature alone may therefore mischaracterize the thermal conditions experienced belowground.

1 Introduction

Large-scale ecological studies commonly characterize the thermal conditions using gridded air temperature derived from meteorological observations or climate models (Fick and Hijmans, 2017; Karger et al., 2017). These data generally represent the conditions at approximately 2 m above the ground and in relatively open environments. However, many terrestrial organisms and ecosystem processes occur close to or below the soil surface, where those local influences are precisely what shape the thermal environment (Bramer et al., 2018). At this level, the temperature is modified by vegetation, radiation, soil moisture, snow cover, topography, and substrate properties, and can differ substantially from the free-air conditions (Bramer et al., 2018; De Frenne et al., 2021; Kemppinen et al., 2024). The growing availability of near-surface observations has made this difference increasingly apparent. For example, the SoilTemp initiative has shown pronounced and geographically structured differences between the soil and conventional air-temperature estimates across biomes and climatic regions (Lembrechts et al., 2020, 2022).

This distinction matters because the temperature directly affects the belowground organisms and many of the processes they regulate. Microbial activity, organic-matter decomposition, and soil carbon cycling are all temperature-sensitive, while local thermal conditions can also alters the ecological responses to regional climate change (Davidson and Janssens, 2006; De Frenne et al., 2019; Zellweger et al., 2020). Yet, the difference between air and soil temperature is unlikely to be constant across the thermal range. A soil that moderates the atmospheric cold does not necessarily provide the same degree of protection from the atmospheric heat (Lembrechts et al., 2022).



Treating the soil thermal buffering as a single property may therefore obscure the differences between the processes operating during warm and cold conditions.

There are physical reasons to expect such an asymmetry. During cold periods, the soil thermal inertia and insulation by vegetation, litter, and particularly snow can limit the transmission of atmospheric temperature minima into the soil (Zhang, 2005). During warm periods, the soil temperature is more strongly influenced by radiation, shading, evapotranspiration, and water availability. Vegetation can markedly reduce daytime and summer temperature maxima, while drying can reduce the evaporative cooling and alter the partitioning of energy at the land surface (De Frenne et al., 2019, 2021; Seneviratne et al., 2010). These controls vary across the climatic regions and landscapes, and are also affected by the soil physical properties. Consequently, the magnitude and even the direction of the soil–air thermal differences may change geographically. Global soil-temperature products already show a strong spatial structure in the soil–air offsets (Lembrechts et al., 2022), but it remains less clear how consistently warm and cold extremes are buffered across a continental network. It is also unclear if these patterns are robust to the choice of the gridded temperature product, and how much of their spatial variation can be related to broad climate, landscape composition, and measured soil properties.

In this study, we used the spatially distributed SOB4ES network to examine the soil–air thermal buffering across contrasting European and Mediterranean environments. Rather than considering the soil–air differences as a single annual offset, we treated warm and cold extremes separately. Specifically, we aimed to: (1) quantify the prevalence and magnitude of the soil–air thermal buffering across the SOB4ES network; (2) assess the consistency of Heat and Cold buffering across complementary gridded temperature products; and (3) test whether the regional contrasts persisted after accounting for broad climatic, edaphic, and landscape variation. Primary cross-product comparisons were harmonized to the ERA5-Land cell support, while an additional sensitivity analysis was used to evaluate whether edaphic associations changed when SoilTemp–CHELSA was retained at its finer thermal-pixel support. This framework allowed us to distinguish effects of spatial support from differences between thermal products.

2 Methods

2.1 Study network and analytical scale

We obtained soil sampling data from the SOB4ES European network, covering different pedoclimatic gradients across Europe and Israel. The dataset contained 427 site identifiers, corresponding to 387 unique sampling locations.

We used 427 SOB4ES site identifiers corresponding to 387 unique sampling locations across Europe and Israel. Soil properties were extracted from raster products derived from the LUCAS topsoil database (Tóth et al., 2013).

Since the ERA5-Land thermal responses are defined at the grid-cell scale several SOB4ES sites that fall within the same cell share the same thermal response. To avoid spatial pseudoreplication we combined site-level environmental information to the ERA5-Land cell scale. This allowed us to obtain 168 unique ERA5-Land cells with valid Heat and Cold buffering estimates.

We conducted pedoclimatic-region and climate analyses on 167 cells that had complete regional and climatic information. For the measured soil properties, we restricted the analysis to 161 cells with complete data for clay, silt, bulk density, soil pH, and pedoclimatic region. For the SoilTemp/CHELSA cross-product comparison, we extracted values at the original SOB4ES locations and then aggregated them to the same ERA5-Land cells used in the primary analysis. This allowed us to compare the two gridded representations on a common spatial support. We quantified thermal buffering using two gridded representations: ERA5-Land (as the primary framework) and a SoilTemp–CHELSA combination (as an alternative representation of near-surface thermal extremes).



2.2 Thermal data sources and soil–air buffering metrics

We characterized air and soil thermal extremes using two gridded climate representations. Primary analyses were based on ERA5-Land, the land component of the ERA5 reanalysis produced by ECMWF, which provides spatially and temporally consistent land-surface variables at approximately 9 km resolution (Muñoz-Sabater et al., 2021).

75 We used 2-m air temperature and soil temperature from the first ERA5-Land soil layer (0–7 cm) for the period 2011–2020. For each calendar month and year, we averaged daily maximum and minimum temperatures separately to obtain the monthly means of daily maxima and minima. These monthly values were then averaged across the ten-year period to obtain 12 long-term monthly means for each variable.

We defined annual thermal extremes independently for air and soil. The warm extreme was defined as the maximum of the 12 long-term monthly means of daily maximum temperature, whereas the cold extreme was defined as the minimum of the corresponding long-term monthly means of daily minimum temperature. We calculated Heat buffering as

$$\text{Heat} = T_{\text{air, max}} - T_{\text{soil, max}} \quad (1)$$

whereas Cold buffering was calculated as

$$\text{Cold} = T_{\text{soil, min}} - T_{\text{air, min}} \quad (2)$$

85 Positive values therefore indicate attenuation of the atmospheric thermal extreme by the soil, whereas negative values indicate amplification.

To assess the consistency of buffering estimates across gridded climate products, we compared ERA5-Land results with a SoilTemp–CHELSA representation. SoilTemp provides global gridded estimates of near-surface soil temperature derived from a large database of in situ soil-temperature observations and spatial models of soil–air temperature offsets (Lembrechts et al., 2020, 2022). We used SBIO5 (maximum temperature of the warmest month) and SBIO6 (minimum temperature of the coldest month) for the 0–5 cm soil layer. Corresponding atmospheric temperatures were obtained from CHELSA v1.2 monthly climatologies of maximum and minimum near-surface air temperature for 1979–2013 at approximately 1 km resolution (Karger et al., 2017). The CHELSA atmospheric warm and cold envelopes were defined as the maximum monthly Tmax and minimum monthly Tmin climatologies, respectively. We calculated the corresponding SoilTemp–CHELSA buffering metrics as

$$95 \quad \text{Heat} = T_{\text{air, max, CHELSA}} - T_{\text{soil, max, SoilTemp}} \quad (3)$$

and

$$\text{Cold} = T_{\text{soil, min, SoilTemp}} - T_{\text{air, min, CHELSA}} \quad (4)$$

using the same sign convention as for ERA5-Land.

We extracted SoilTemp–CHELSA values at the original SOB4ES locations and subsequently aggregated them to the ERA5-Land grid cells used in the primary analysis, thereby ensuring a common analytical support. The SoilTemp bioclimatic layers combine spatially modelled soil–air temperature offsets, derived from in situ observations predominantly representing 2000–2020, with CHELSA climatologies for 1979–2013 (Lembrechts et al., 2022). We therefore used the SoilTemp–CHELSA representation as a complementary cross-product comparison rather than as an independent validation of ERA5-Land.

2.3 Regional and climatic predictors

105 The regional and climatic context was described using the pedoclimatic region assigned to each SOB4ES locality and three climatic variables derived from CHELSA v2.1 for the 1981–2010 climate period. Specifically, we considered mean annual temperature (MAT; BIO1), temperature seasonality (BIO4), and the minimum climatic moisture index (CMImin), selected to represent the mean thermal regime, annual temperature variability, and the driest climatic conditions, respectively (Brun et al., 2022). These predictors were selected to represent complementary dimensions of the broad climatic environment potentially relevant to soil thermal buffering.



110 Because soil temperature and land–atmosphere thermal coupling are influenced by both thermal conditions and water availability (Seneviratne et al., 2006, 2010; Fischer et al., 2007; Lembrechts et al., 2022), these variables provide a parsimonious representation of broad climatic controls on soil–air thermal decoupling. Pedoclimatic region was included as a broader integrative environmental descriptor, allowing us to test whether regional contrasts persisted after accounting for continuous climatic gradients.

The climatic variables were extracted at the original SOB4ES localities and subsequently averaged within ERA5-Land grid cells to
 115 match the spatial scale of the thermal response variables.

Cells with incomplete regional or climatic information were excluded, resulting in a final sample of 167 cells for the analyses. Prior to modelling, continuous climatic predictors were standardized to a mean of zero and a standard deviation of one.

2.4 Measured topsoil properties

To assess whether the variation in soil thermal buffering was also associated with local soil characteristics, we considered edaphic
 120 properties measured within the SOB4ES sites that were sufficiently well-documented across the network. Specifically, clay content, silt content, bulk density, and soil pH were used. Sand content was excluded from the models because, together with clay and silt, it forms a compositional set where the components sum to approximately 100 %. The soil properties, originally measured at the site scale, were first aggregated by location and subsequently averaged within each ERA5-Land cell to ensure consistency with the spatial scale of the response variables. Edaphic analyses were conducted on cells containing complete data for all variables and the pedoclimatic region,
 125 resulting in a final sample of 161 cells. Prior to modelling, clay content, silt content, bulk density, and soil pH were standardized to a mean of zero and a standard deviation of one.

2.5 Landscape composition

Landscape composition was characterized at a spatial scale consistent with the ERA5-Land response variables using the Copernicus Global Land Cover 100 m product for 2019 (Buchhorn et al., 2020). Original land-cover classes were aggregated into four terrestrial
 130 components: agriculture, forest, urban and open natural land. For each ERA5-Land cell, the proportional cover of these components was calculated relative to the terrestrial area of the cell; non-terrestrial classes were excluded from the denominator. Because the four components represent a composition, agriculture was used as the reference component in subsequent models. Coefficients for forest, urban and open natural land therefore represent the expected change in thermal buffering associated with replacing 10 percentage points of agricultural cover with the corresponding land-cover component, while holding the remaining model covariates constant. These
 135 variables describe broad landscape composition at the ERA5-Land cell scale and should not be interpreted as measures of land-use intensity or local management.

2.6 Statistical analyses

We ran all statistical analyses in R (R Core Team, 2025). To deal with spatial dependence among ERA5-Land cells, we used spatial error models (SEM; Anselin, 1988) to analyse the relationships between Heat and Cold buffering and the environmental predictors. We
 140 fit these models using the *errorsarlm()* function in the *spatialreg* package (Bivand et al., 2021).

Before defining the spatial neighbourhoods, we projected the ERA5-Land cell centroids to ETRS89-LAEA (EPSG:3035). We based neighbour relationships on k-nearest neighbours using the *spdep* package, which we then symmetrised before constructing row-standardised spatial weights (Bivand and Wong, 2018). We set $k = 6$ for the regional and climatic analyses, and $k = 4$ for the models using measured soil properties.

145 For both Heat and Cold, we compared several models: pedoclimatic region alone, thermal climate (mean annual temperature and temperature seasonality), region plus thermal climate, and the corresponding models adding the minimum climatic moisture index



(CMImin). To see which models had the most support, we used the Akaike Information Criterion (AIC; Akaike, 1974). We tested the additional contribution of CMImin using likelihood-ratio tests between nested models. To make sure the comparison was fair, these nested models were fitted on the exact same observations and spatial-weight structure. We also checked if the Mediterranean South (MDS) contrast persisted after accounting for broad thermal climate, simply by comparing its coefficient between the region-only model and the region-plus-thermal model. We used Alpine South (ALS) as the reference level for the pedoclimatic region, so all regional coefficients represent contrasts relative to ALS.

We looked at the associations with measured topsoil properties in separate SEMs, including pedoclimatic regions alongside clay, silt, bulk density, and soil pH. Since we tested four edaphic predictors for both Heat and Cold, we adjusted the resulting p -values for multiple testing using the Benjamini–Hochberg false discovery rate and Bonferroni procedures (Benjamini and Hochberg, 1995).

As a secondary analysis for Heat buffering, we also evaluated landscape composition. We took the region-plus-thermal model and extended it by adding forest, urban, and open-natural cover. For this primary landscape model, we kept the same $k = 6$ spatial neighbourhood used in the regional analyses. We checked for residual spatial autocorrelation using Moran’s I (*moran.test()* in *spdep*; Moran, 1950; Bivand and Wong, 2018).

2.7 Sensitivity to spatial support and thermal data products

To assess whether the differences in edaphic associations between ERA5-Land and SoilTemp–CHELSA could be explained by spatial support, we ran an additional sensitivity analysis. We used the same measured soil properties and the same spatial-error modelling framework. For the finer support, we aggregated sampling locations that fell inside the same SoilTemp–CHELSA pixel. This gave us 276 unique thermal pixels from 357 complete sampling locations. After that, we aggregated both the SoilTemp–CHELSA thermal responses and the measured soil properties to the 161 ERA5-Land cells used in the primary analysis, and refitted the models at this coarser scale.

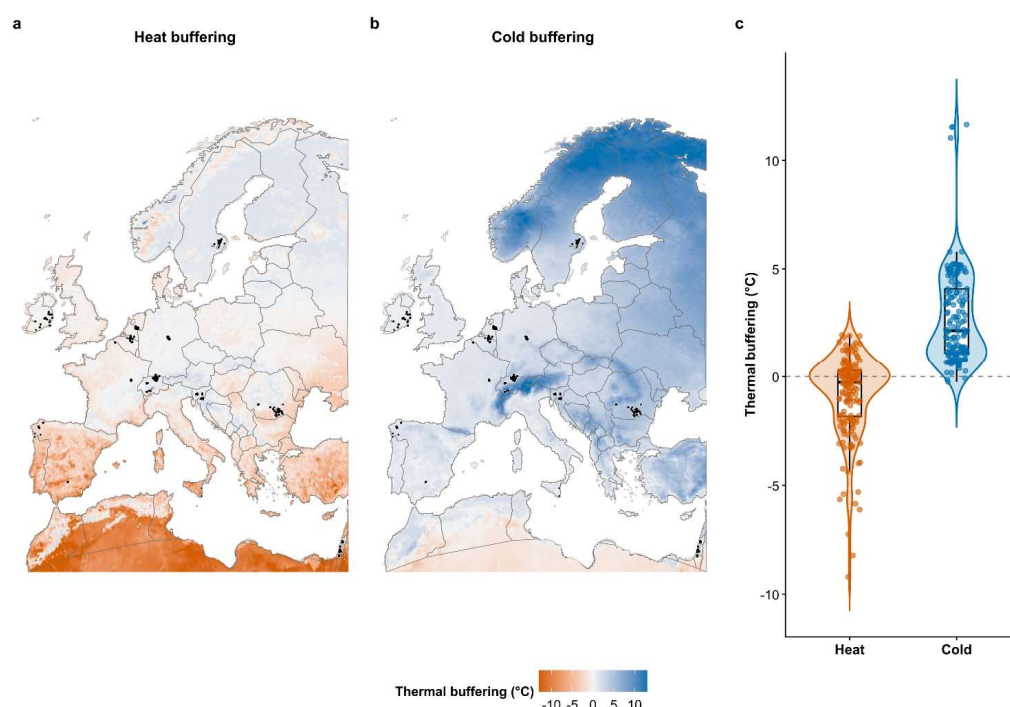
We standardized the soil predictors using a common reference scaling so we could directly compare the coefficient magnitudes across the different supports. The models included the pedoclimatic region and used symmetrised, row-standardised k -nearest-neighbour spatial weights (with $k = 4$ as the primary specification). Robustness to the definition of the spatial neighbourhood was assessed by repeating the analyses with $k = 4, 6, 8$, and 10. Because spatial aggregation also reduces sample size, we separated these two effects by repeating the fine-support analysis on 300 random subsamples, each containing 161 unique thermal pixels. To isolate differences caused by the thermal product itself, we compared ERA5-Land and SoilTemp–CHELSA edaphic coefficients on the exact same 161 cells, using identical scaling and model structure. We treated SoilTemp–CHELSA as a complementary sensitivity analysis, not an independent validation. This is because SoilTemp is a modelled product that already incorporates environmental information into its predictions.

Multiple-testing correction for the edaphic coefficients was performed using the Benjamini–Hochberg false discovery rate and Bonferroni procedures for the main spatial-support and thermal-product comparisons. For the sensitivity analyses, Benjamini–Hochberg correction was applied within each model set.

3 Results

3.1 Asymmetric buffering of thermal extremes

Heat and Cold buffering showed a strong asymmetry across the SOB4ES network. We found Cold buffering in 165 of 168 ERA5-Land cells (98.2 %), with a median Cold offset of +2.14 °C. On the contrary, only 69 cells (41.1 %) buffered heat, while 99 cells (58.9 %) showed heat amplification, with a median Heat offset of −0.26 °C (Table A1). So, Cold buffering was almost ubiquitous across the network, but the Heat responses ranged from positive buffering to negative amplification (Fig. 1).



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Figure 1. Spatial distribution and magnitude of soil–air thermal buffering across the SOB4ES network derived from ERA5-Land. (a) Heat buffering, calculated as the difference between the annual warm extremes of climatological air and soil temperature; (b) Cold buffering, calculated as the difference between the annual cold extremes of climatological soil and air temperature; and (c) distributions of Heat and Cold buffering across the 168 independent ERA5-Land cells represented in the SOB4ES network. Positive values indicate attenuation of the atmospheric thermal extreme by the soil, whereas negative values indicate amplification. Points in panels (a–b) show SOB4ES sampling locations.

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These patterns remained essentially unchanged when we evaluated the soil temperature in the calendar month of the corresponding atmospheric extreme. The agreement with the primary envelope-based metric was very high for both Heat (Spearman's $\rho = 0.995$; sign agreement = 97.6 %) and Cold ($\rho = 0.999$; sign agreement = 100 %; Table A2).

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The complementary SoilTemp–CHELSA representation showed higher cross-product consistency for Cold than for Heat. Cold exhibited a strong rank consistency between the products (Spearman's $\rho = 0.79$), with the same buffering direction in 98.2 % of the cells. Instead, the Heat agreement was weaker ($\rho = 0.46$; sign agreement = 56.0 %). The median Heat buffering differed substantially between ERA5-Land and SoilTemp–CHELSA (−0.26 vs +1.32 °C), while the median Cold buffering was similar (+2.14 vs +2.18 °C; Fig. 2). The corresponding continuous SoilTemp–CHELSA buffering surfaces are shown in Fig. A1.

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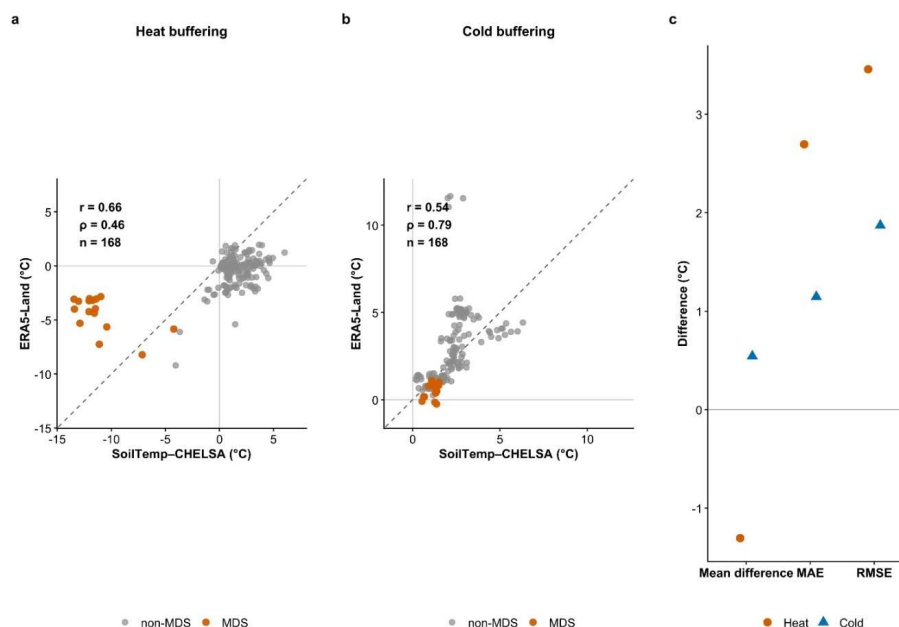


Figure 2. Cross-product consistency of soil–air thermal buffering between ERA5–Land and SoilTemp–CHELSA. Relationships between the two gridded representations are shown for (a) Heat and (b) Cold buffering across 168 ERA5–Land cells. Grey points represent non-Mediterranean South (non-MDS) cells and orange points MDS cells. Dashed lines indicate the 1:1 relationship, and horizontal and vertical reference lines indicate zero buffering. Pearson’s correlation coefficient (r) and Spearman’s rank correlation coefficient (ρ) are reported within each panel. (c) Differences in absolute agreement between products, expressed as the mean difference (ERA5–Land – SoilTemp–CHELSA), mean absolute error (MAE), and root mean squared error (RMSE) for Heat and Cold buffering. Positive values indicate attenuation of atmospheric extremes, whereas negative values indicate amplification.

3.2 Pedoclimatic variation in Heat and Cold buffering

The Heat buffering varied among the pedoclimatic regions (Fig. 3; Table A3). Mediterranean South (MDS) cells presented the most negative Heat offsets, with a mean of -4.41 °C and a median of -3.98 °C; none of the 16 MDS cells showed a positive Heat buffering. Lusitanian (LUS) cells had also consistently negative Heat offsets (mean -3.82 °C; median -3.12 °C), and no cells showed positive buffering. On the contrary, Mediterranean mountain (MDM), Continental (CON), Alpine South (ALS), and Nemoral (NEM) regions were characterized mainly by positive Heat buffering. Pannonian (PAN) cells showed mostly negative Heat offsets, with only 9.4 % of the cells showing positive buffering.

The regional variation was smaller for the Cold buffering. Cold offsets were positive in all cells outside the MDS region, while only 81.2 % of MDS cells showed a positive Cold buffering. MDS also showed the lowest Cold offsets (mean $+0.53$ °C; median $+0.73$ °C), while larger positive offsets occurred in ALS, PAN, NEM, and MDM cells (Fig. 3; Table A3).



3.3 Climatic and edaphic predictors of thermal buffering

Among the candidate spatial models, the ones combining the pedoclimatic region with mean annual temperature and temperature seasonality received the strongest support for both Heat and Cold buffering (AIC = 415.61 and 231.05, respectively; Fig. 4; Table A4). The addition of minimum climatic moisture (CMI_{min}) provided little additional model support for both the responses (Heat: Δ AIC = +2.00, likelihood-ratio p = 0.992; Cold: Δ AIC = +0.68, p = 0.250).

Within the region-plus-thermal models, MAT was negatively associated with both Heat buffering (β = -1.24 °C per SD, 95 % CI -1.88 to -0.60, p < 0.001) and Cold buffering (β = -0.61 °C per SD, 95 % CI -0.96 to -0.26, p < 0.001). Temperature seasonality showed weaker evidence of an association with Heat buffering (β = -0.53 °C per SD, 95% CI -1.12 to 0.06, p = 0.076) and no clear association with Cold buffering (β = 0.18 °C per SD, 95 % CI -0.15 to 0.50, p = 0.287; Table A5).

The Mediterranean South (MDS) contrast persisted also after accounting for the broad thermal climate. The MDS coefficient for Heat changed only slightly from -6.12 °C in the region-only model to -5.73 °C in the region-plus-thermal model (95 % CI: -8.15 to -3.30 °C). The contrast remained negative across alternative spatial neighborhood definitions (k = 4–10) and was practically unchanged after excluding the single BOR cell (Fig. A2a).

The measured topsoil properties showed little robust evidence of independent associations with the thermal buffering. No edaphic predictor was significantly associated with Heat buffering after the correction for multiple testing. Bulk density presented the strongest nominal association with Cold buffering, with higher bulk density associated with lower Cold offsets (estimate = -0.097 °C per one-standard-deviation increase, p = 0.014), but this association did not remain significant after the Benjamini–Hochberg correction (p = 0.113; Fig. 4; Table A6). The direction of this association was also retained across alternative spatial neighbourhood definitions (k = 4–10; Fig. A2b).

An additional scale-support analysis showed that the stronger edaphic associations obtained with SoilTemp–CHELSA were not substantially attenuated by spatial aggregation. Across the eight Heat and Cold soil-property coefficients, all effect directions were retained when SoilTemp–CHELSA was aggregated from 276 unique thermal pixels to the 161 ERA5-Land cells, and coefficient magnitudes were generally similar or, for some predictors, larger after aggregation. All eight aggregated coefficients fell within the 95 % distributions obtained from 300 random matched-size subsamples of 161 fine-support pixels (Fig. A3a,b; Table A7). Coefficient directions were also retained across alternative spatial-neighbourhood definitions (k = 4–10). When SoilTemp–CHELSA and ERA5-Land were analysed on the same 161 cells using common predictor scaling and identical model structure, SoilTemp–CHELSA showed larger-magnitude edaphic associations, particularly for Heat buffering (Fig. A3c,d). The contrast between the two thermal representations could not be attributed to spatial aggregation alone.

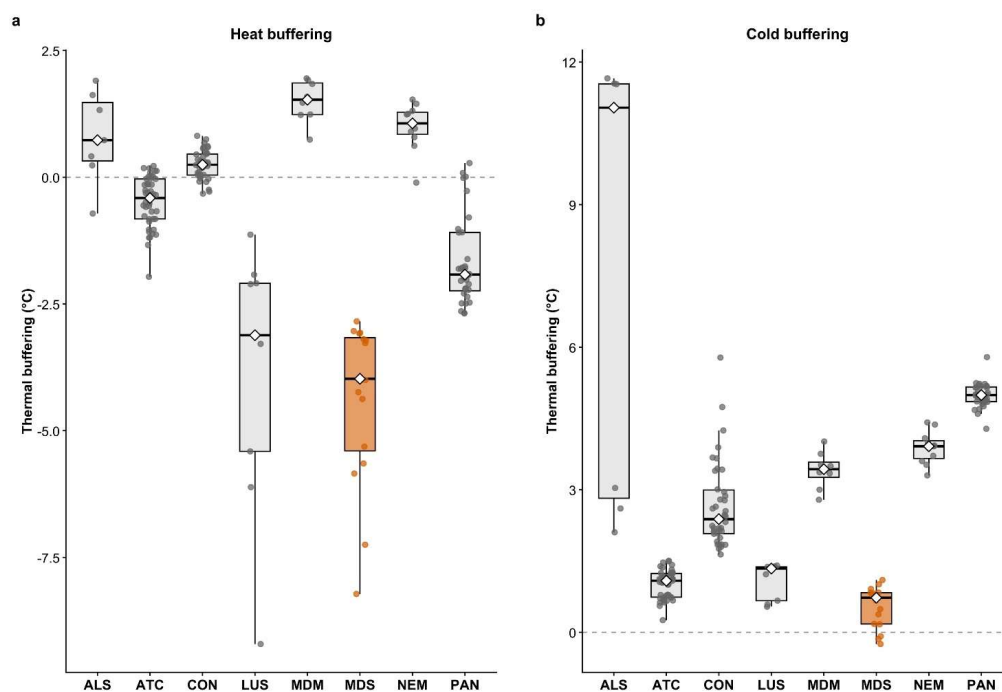


Figure 3. Regional variation in ERA5-Land soil-air thermal buffering across pedoclimatic regions. (a) Heat buffering and (b) Cold buffering across independent ERA5-Land cells. Points represent individual grid cells and boxplots summarize the distribution within each pedoclimatic region; MDS cells are highlighted. Positive values indicate buffering, whereas negative values indicate amplification. The Boreal (BOR) region was excluded from the figure because it was represented by a single cell ($n = 1$) but is reported in Table A3.

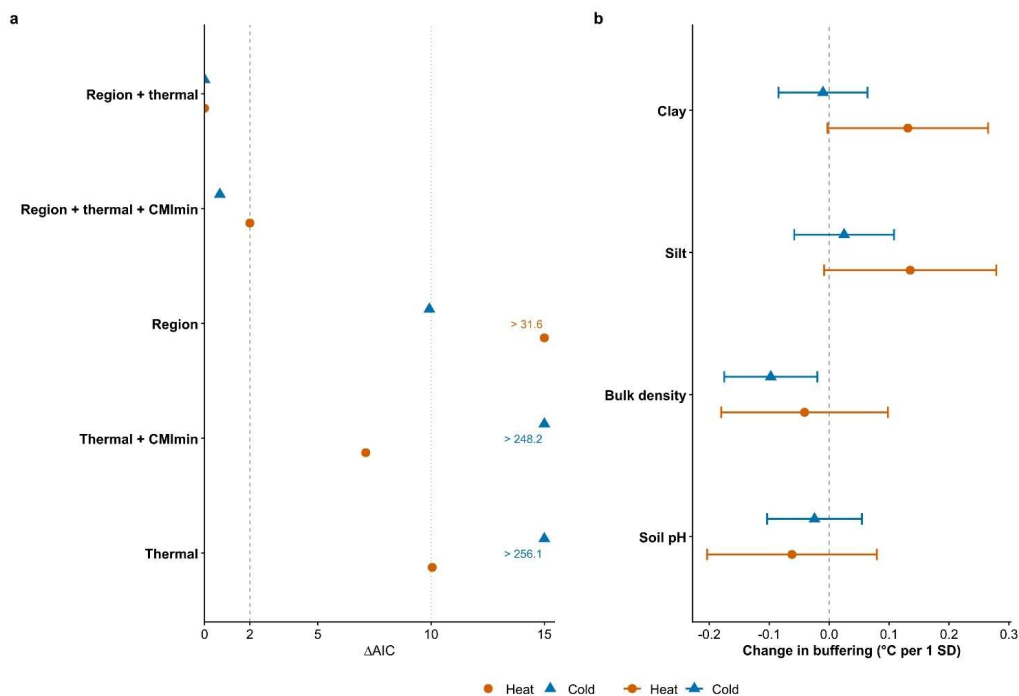
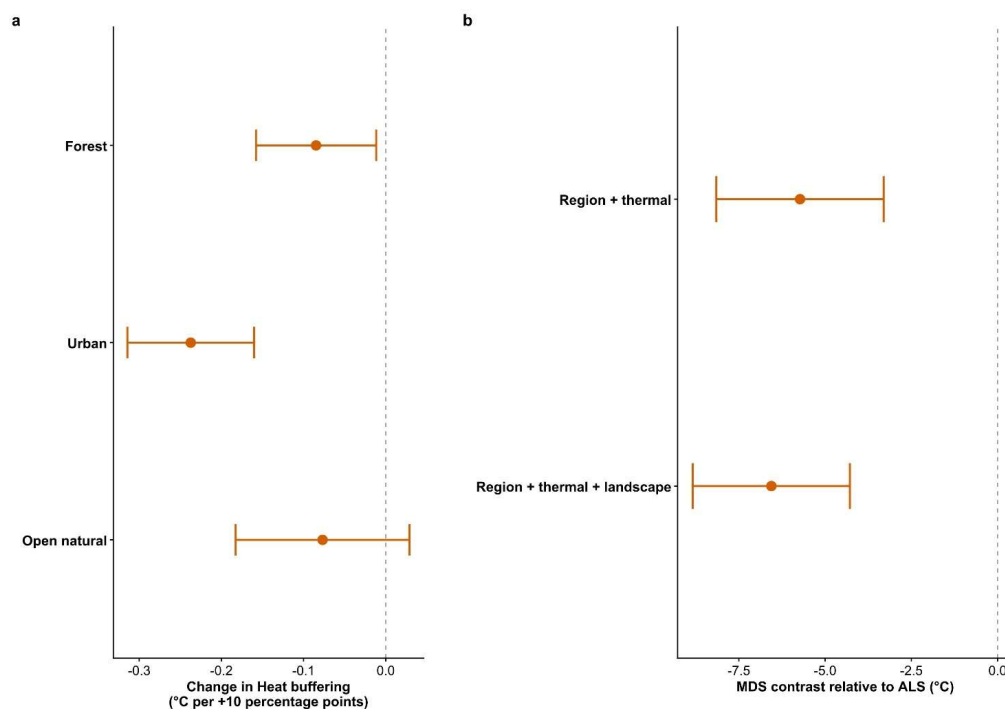


Figure 4. Climatic and edaphic associations with ERA5-Land thermal buffering. (a) Support for spatial error models of Heat and Cold buffering including pedoclimatic region, mean annual temperature, temperature seasonality and minimum climatic moisture (CMImin). ΔAIC values are shown relative to the best-supported model for each response; vertical lines mark $\Delta AIC = 2$ and 10. (b) Standardized coefficients for measured topsoil properties from the primary edaphic models. Points show estimates and horizontal lines 95 % confidence intervals. Positive coefficients indicate greater buffering and negative coefficients reduced buffering.

3.4 Landscape composition and Heat buffering

Landscape composition explained additional variation in Heat buffering after accounting for pedoclimatic region and broad thermal climate. Adding forest, urban and open-natural cover improved model support relative to the region-plus-thermal model ($AIC = 387.19$ vs 415.61 ; likelihood-ratio test: $LR = 34.42$, $p < 0.001$). A greater urban cover was associated with more negative Heat offsets (-0.24 $^{\circ}\text{C}$ per 10 percentage-point increase replacing agricultural cover; 95 % CI: -0.31 to -0.16), while the corresponding association for the forest cover was weaker (-0.08 $^{\circ}\text{C}$; 95 % CI: -0.16 to -0.01). The open-natural cover showed no clear association with the Heat buffering (-0.08 $^{\circ}\text{C}$; 95 % CI: -0.18 to 0.03 ; Fig. 5a).

Accounting for landscape composition did not reduce the MDS contrast. The MDS coefficient changed from -5.73 $^{\circ}\text{C}$ in the region-plus-thermal model to -6.56 $^{\circ}\text{C}$ after inclusion of land-cover composition (95 % CI: -8.83 to -4.28 $^{\circ}\text{C}$; Fig. 5b). The negative MDS contrast was retained across the land-cover sensitivity analyses, including alternative terrestrial-cover thresholds and spatial neighbourhood definitions.



280 **Figure 5. Landscape composition and persistence of the Mediterranean South (MDS) contrast in ERA5-Land Heat buffering. (a) Spatial-**
error-model associations between landscape composition and Heat buffering after accounting for pedoclimatic region and broad thermal
climate. Coefficients represent the change in Heat buffering associated with a 10 percentage-point increase in forest, urban or open-natural
cover replacing agricultural cover. (b) Mediterranean South (MDS) contrast relative to Alpine South (ALS) before and after inclusion of
 285 **landscape composition in the regional-thermal model. Points show coefficient estimates and horizontal lines indicate 95 % confidence**
intervals. The vertical dashed line denotes zero effect. Positive coefficients indicate greater Heat buffering, whereas negative coefficients
indicate reduced buffering or stronger heat amplification.

4 Discussion

Air temperature remains the climatic reference for many large-scale ecological analyses, largely because of the availability and spatial coverage of standardized meteorological observations (Karger et al., 2017; Lembrechts et al., 2019). However, such data can be a poor proxy for the actual thermal conditions experienced by organisms living near or below the soil surface. At these levels, temperatures can deviate substantially from 2-m air temperature because radiation, vegetation, snow cover, soil moisture, and substrate properties modify local heat exchange (Potter et al., 2013; De Frenne et al., 2019; Lembrechts et al., 2020, 2022).

Our results show that soils do not simply buffer atmospheric temperatures, and their thermal response differs markedly between warm and cold extremes. Across the SOB4ES network, cold extremes were attenuated in almost all ERA5-Land cells (98.2 %), whereas 58.9 % of cells showed amplification rather than buffering of warm extremes. Soil thermal buffering should therefore not be seen as a fixed property that acts similarly at both ends of the thermal spectrum.

The contrast between Heat and Cold is consistent with the different processes controlling soil temperature across seasons. During cold periods, soil thermal inertia and insulation by litter, vegetation, and snow, where present, can substantially decouple ground temperature from atmospheric minima (Zhang, 2005; De Frenne et al., 2019). During warm periods, soil temperature depends more strongly on



300 radiation, evapotranspiration, and soil-water availability (Seneviratne et al., 2010; Fischer et al., 2007; Miralles et al., 2012). These different controls may explain why Heat buffering was much more spatially variable than Cold buffering.

Mediterranean South (MDS) cells occupied the lower end of the heat-buffering gradient, with a mean Heat offset of -4.41°C and no positive buffering among the 16 MDS cells. This is consistent with the strong soil-moisture-temperature coupling documented in water-limited environments. As soils dry, evaporative cooling declines, and a larger fraction of the available energy is transferred through
305 sensible and ground heat fluxes. This favours stronger soil warming during periods of high atmospheric demand (Seneviratne et al., 2006, 2010; Fischer et al., 2007; Hirschi et al., 2011; Miralles et al., 2012). However, since we did not directly measure soil moisture or surface energy fluxes, this mechanism should be considered a plausible interpretation rather than a demonstrated causal explanation.

The MDS contrast remained strongly negative even after accounting for broad thermal climate, including mean annual temperature and temperature seasonality. Adding minimum climatic moisture provided little extra model support. This does not mean that water
310 limitation plays no role. A broad climatic moisture index cannot capture the timing and intensity of seasonal soil drying, or its coincidence with extreme atmospheric demand. Instead, the MDS classification likely integrates a combination of water availability, radiation, vegetation phenology, and other land-surface characteristics that are not fully represented by the continuous climatic predictors. The persistence of the MDS contrast suggests that the regional classification captures environmental controls on soil thermal behaviour that are not fully represented by the climatic, landscape, and edaphic covariates considered here.

315 Landscape composition also played a role in Heat buffering. Adding forest, urban, and open-natural cover improved model support compared with climate and pedoclimatic region alone. Specifically, replacing agricultural cover with urban cover was associated with more negative Heat offsets, indicating stronger soil warming relative to air temperature. Urbanization can substantially alter the soil thermal environment through changes in vegetation cover, surface properties, water availability, and heat storage. Higher soil temperatures have been reported in urban environments compared with rural ones, and vegetation, especially trees and shrubs, can
320 strongly reduce summer soil-temperature maxima within cities (Savva et al., 2010; Edmondson et al., 2016). This suggests that urban land cover may affect not only absolute soil temperature, but also the coupling between atmospheric and soil thermal conditions. Yet, the persistence of the MDS contrast after accounting for landscape composition indicates that land-cover differences alone do not explain the Mediterranean pattern.

Measured topsoil properties showed little robust association with ERA5-Land buffering after correction for multiple testing. This weak
325 signal was not explained by spatial support alone: aggregating SoilTemp–CHELSA to ERA5-Land cells left the direction and magnitude of the edaphic coefficients largely unchanged, and matched-size subsampling produced similar results. The stronger SoilTemp–CHELSA associations therefore appear to reflect differences between the thermal products rather than spatial aggregation alone. Because SoilTemp is a modelled product that incorporates environmental and edaphic information, however, these relationships should not be interpreted as independent evidence of causal soil-property effects (Lembrechts et al., 2022). Direct soil-temperature measurements
330 would be needed to test these relationships locally.

The product comparison also showed much greater consistency for Cold than for Heat buffering. ERA5-Land and SoilTemp–CHELSA differ in spatial resolution, reference periods, and modelling approaches, so their agreement should be interpreted as cross-product consistency rather than validation. The maps therefore represent broad spatial patterns of soil–air thermal decoupling, with greater confidence for Cold than for Heat.

335 Overall, the SOB4ES network reveals a strongly asymmetric thermal role for soils. Cold attenuation was widespread, whereas heat attenuation was inconsistent and often shifted to marked amplification in seasonally dry Mediterranean environments. Soil temperature should therefore not be treated as a simple transformation of air temperature (Suggitt et al., 2011).

For belowground organisms, the main implication is that atmospheric extremes do not translate uniformly into soil thermal exposure. Recent large-scale analyses further suggest that soil–air thermal decoupling can be ecologically relevant for different components of



340 soil fauna, including nematodes, annelids and collembolans (Nicolosi and Mulder, 2026a,b). While cold extremes appear to be strongly
 attenuated across most of the network, soils in some seasonally dry Mediterranean environments may experience thermal maxima that
 are equal to or greater than those suggested by atmospheric temperature alone. The spatial maps of thermal offsets generated here provide
 a testable framework for future studies linking thermal exposure to soil biodiversity and ecosystem functioning, without assuming that
 air temperature is an adequate proxy for belowground climate. This is particularly relevant for soil biota, as recent studies indicate that
 345 soil thermal conditions and soil–air thermal offsets can provide ecologically relevant information beyond standard macroclimatic
 temperature metrics (Lembrechts et al., 2019, 2022; Nicolosi and Mulder, 2026a,b).

5 Conclusions

In conclusion, soil–air thermal buffering across the SOB4ES network was strongly asymmetric. Cold extremes were buffered in almost
 all ERA5-Land cells, whereas Heat buffering varied widely and frequently shifted to amplification. Mediterranean South (MDS) cells
 350 showed the strongest heat amplification in ERA5-Land, and this regional contrast persisted after accounting for broad thermal climate
 and landscape composition. Edaphic relationships, however, depended on the thermal representation: they were weak in ERA5-Land
 but substantially stronger in SoilTemp–CHELSA, and this contrast was not removed by aggregating SoilTemp–CHELSA to ERA5-
 Land support. Together with the weaker cross-product agreement observed for Heat, these results show that belowground thermal
 exposure cannot be represented as a simple transformation of standard air temperature, but also caution against assuming that a single
 355 gridded soil-temperature product fully captures local thermal conditions. The spatial patterns identified here provide a basis for testing
 where air-temperature data are most likely to misrepresent the thermal environment experienced by soil biota, and for prioritizing direct
 soil-temperature observations in Mediterranean and other heat-sensitive environments.

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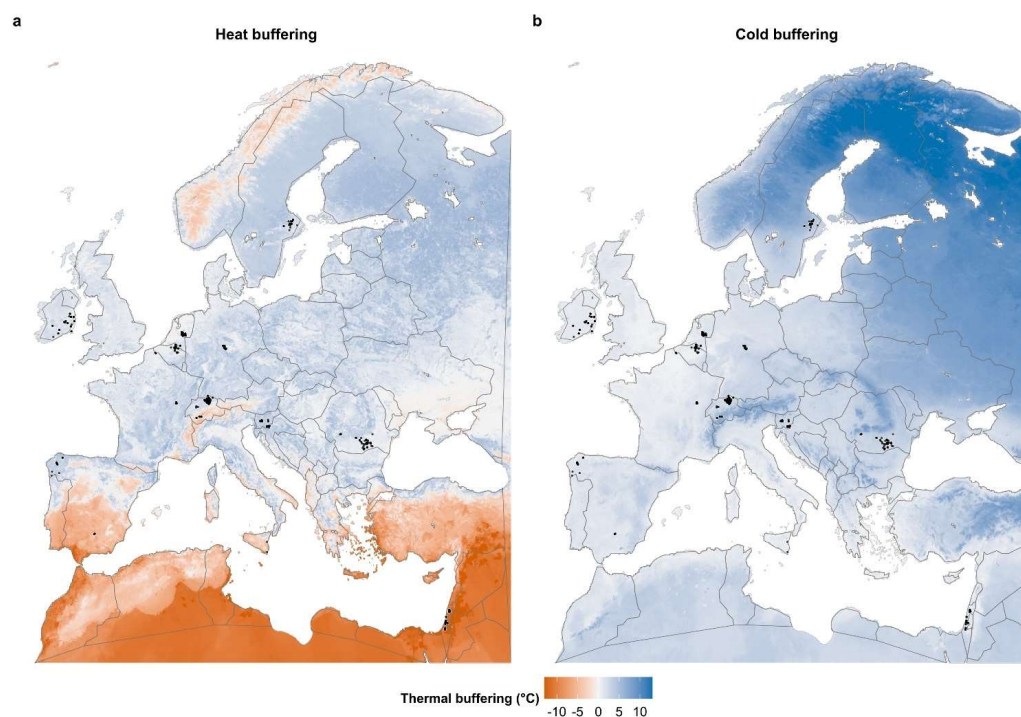
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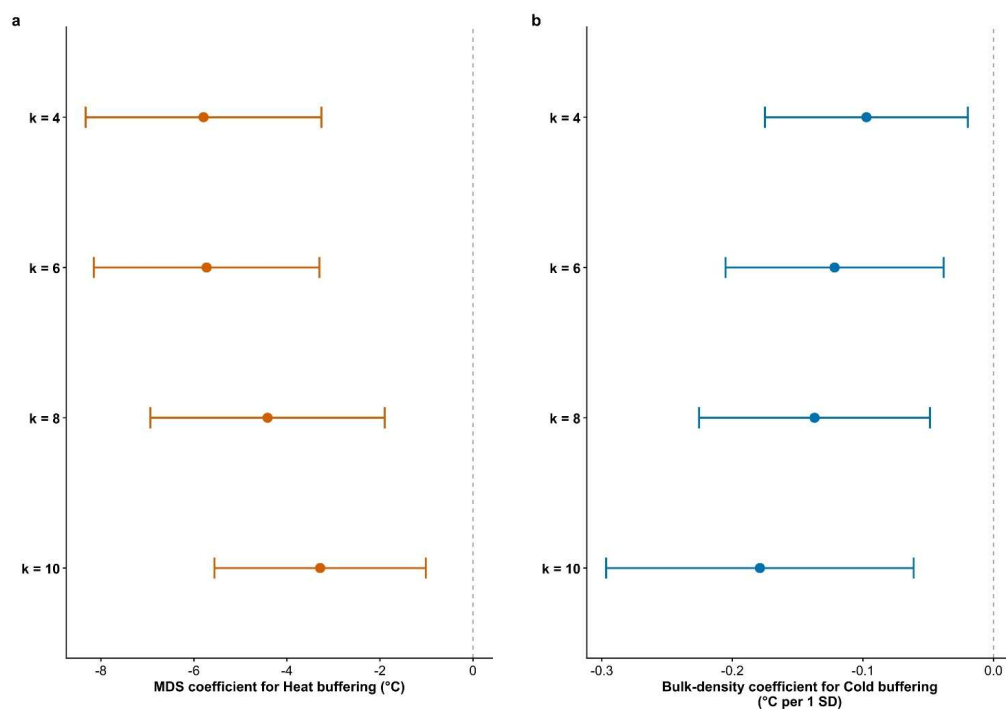
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Appendix A



380 **Figure A1. Continuous spatial representation of soil–air thermal buffering derived from SoilTemp–CHELSA. (a) Heat buffering, calculated**
 as the difference between CHELSA air maximum temperature and SoilTemp maximum soil temperature; and (b) Cold buffering, calculated
 as the difference between SoilTemp minimum soil temperature and CHELSA air minimum temperature. Positive values indicate attenuation
 of the atmospheric thermal extreme by the soil, whereas negative values indicate amplification. SoilTemp layers were projected to the CHELSA
 grid before calculating the thermal offsets. Points indicate SOB4ES sampling locations. These maps provide a complementary spatial
 385 representation of soil–air thermal decoupling and are not treated as an independent validation of the ERA5–Land estimates.



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Figure A2. Sensitivity of key spatial-error-model estimates to the definition of the spatial neighbourhood. (a) Mediterranean South (MDS) contrast in Heat buffering relative to the Alpine South (ALS) reference region, after accounting for mean annual temperature and temperature seasonality. (b) Association between bulk density and Cold buffering in the primary edaphic model. Points show coefficient estimates and horizontal lines indicate 95 % confidence intervals across alternative k-nearest-neighbour spatial weights ($k = 4, 6, 8$ and 10). The vertical dashed line denotes zero association. The direction of both effects was consistent across alternative definitions of the spatial neighbourhood.

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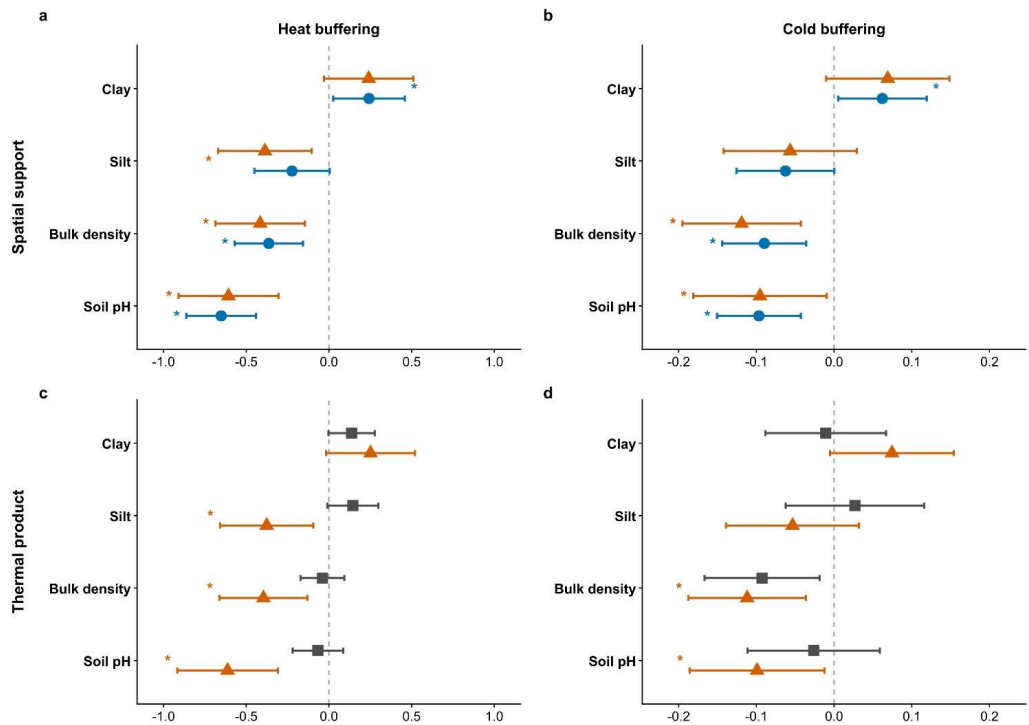


Figure A3. Sensitivity of edaphic associations to spatial support and thermal product. Standardized coefficients from spatial-error models relating measured topsoil properties to Heat and Cold buffering. Panels a–b compare SoilTemp–CHELSA (STC) coefficients estimated at unique thermal-pixel support (blue circles; $n = 276$) with coefficients obtained after aggregation to ERA5-Land cell support (orange triangles; $n = 161$), for Heat (a) and Cold (b) buffering. Panels c–d compare STC aggregated to ERA5-Land cells (orange triangles) with ERA5-Land (grey squares) on the same 161 cells, for Heat (c) and Cold (d) buffering. All models used the same measured soil predictors, common predictor scaling, pedoclimatic-region adjustment and spatial-model specification. Points represent coefficient estimates and horizontal lines 95 % confidence intervals. Coefficients indicate the change in buffering ($^{\circ}\text{C}$) associated with a one-standard-deviation increase in the corresponding soil property; positive values indicate greater buffering and negative values reduced buffering. The vertical dashed line denotes zero association. Asterisks indicate associations with Benjamini–Hochberg-adjusted $p < 0.05$.

Table A1. Descriptive statistics for ERA5-Land Heat and Cold buffering across the 168 independent SOB4ES grid cells. Positive values indicate buffering and negative values indicate amplification.

Metric	N cells	Buffering n (%)	Amplification n (%)	Mean ($^{\circ}\text{C}$)	Median ($^{\circ}\text{C}$)	SD ($^{\circ}\text{C}$)
Heat	168	69 (41.1)	99 (58.9)	-0.832	-0.265	1.901
Cold	168	165 (98.2)	3 (1.8)	2.719	2.140	2.141



425 **Table A2. Sensitivity of soil–air thermal buffering to the definition of the climatological extreme month. (A) Metric-level comparison between the primary envelope-based definition and the same-air-extreme-month definition across 168 ERA5-Land cells. (B) Comparison of the Mediterranean South (MDS) contrast from the corresponding region-plus-thermal spatial error models. CI, 95 % confidence interval.**

430 **A. Metric-level sensitivity**

Metric	N	Envelope mean	Same-air-month mean	Envelope buffering %	Same-air-month buffering %	Pearson r	Spearman ρ	Sign agreement %
Heat	168	−0.832	−0.797	41.1	43.5	0.998	0.995	97.6
Cold	168	2.719	2.752	98.2	98.2	0.999	0.999	100

B. MDS contrast under alternative thermal-envelope definitions

Response	Definition	MDS estimate	SE	95 % CI	p
Heat	Envelope	−5.727	1.237	−8.152, −3.302	<0.001
Heat	Same air-extreme month	−5.925	1.235	−8.345, −3.505	<0.001
Cold	Envelope	−1.621	0.669	−2.932, −0.310	0.015
Cold	Same air-extreme month	−1.870	0.714	−3.270, −0.469	0.009

435 **Table A3. Descriptive statistics of ERA5-Land Heat and Cold buffering across pedoclimatic regions. Heat and Cold values are expressed as soil–air thermal offsets (°C); positive values indicate buffering and negative values indicate amplification. Buffering (%) indicates the proportion of cells with a positive offset.**

Region	N cells	Heat mean (°C)	Heat median (°C)	Heat buffering (%)	Cold mean (°C)	Cold median (°C)	Cold buffering (%)
ALS (Alpine South)	7	0.788	0.731	85.7	7.65	11.0	100
ATC (Atlantic Central)	45	−0.481	−0.410	20	1.02	1.08	100
BOR (Boreal)	1	1.10	1.10	100	3.85	3.85	100
CON (Continental)	38	0.244	0.246	81.6	2.67	2.38	100
LUS (Lusitanian)	9	−3.82	−3.12	0	1.10	1.34	100



MDM (Mediterranean Mts)	8	1.50	1.53	100	3.41	3.43	100
MDS (Mediterranean South)	16	-4.41	-3.98	0	0.531	0.727	81.2
NEM (Nemoral)	11	1.00	1.06	90.9	3.88	3.91	100
PAN (Pannonian)	32	-1.66	-1.92	9.38	4.99	4.99	100

^aBOR reported for completeness but was not interpreted because it was represented by a single ERA5-Land cell.

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450 **Table A4. Comparison of spatial error models relating ERA5-Land Heat and Cold buffering to pedoclimatic region and climatic predictors. Thermal climate includes mean annual temperature (MAT) and temperature seasonality; CMImin indicates minimum climatic moisture. Moran's *I* refers to residual spatial autocorrelation.**

Response	Model	N	AIC	logLik	Lambda	Moran_I	Moran_p
Heat	Heat Region	167	447	-212.6	0.620	0.048	0.075
Heat	Heat Thermal	167	425	-207.8	0.862	-0.008	0.515
Heat	Heat Thermal + CMImin	167	422	-205.4	0.862	-0.006	0.498
Heat	Heat Region + Thermal	167	415	-194.8	0.863	0.013	0.310
Heat	Heat Region + Thermal + CMImin	167	417	-194.8	0.863	0.013	0.310
Cold	Cold Region	167	240	-109.5	0.966	0.041	0.108
Cold	Cold Thermal	167	487	-238.6	0.840	0.124	0.0002
Cold	Cold Thermal + CMImin	167	479	-233.6	0.859	0.127	0.0002
Cold	Cold Region + Thermal	167	231	-102.5	0.964	0.026	0.200
Cold	Cold Region + Thermal + CMImin	167	231	-101.9	0.965	0.018	0.263

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465 (Next page) Table A5. Complete coefficient estimates from the combined regional and climatic spatial error models of (A) Heat and (B) Cold buffering. Continuous climatic predictors were standardized to zero mean and unit variance; their coefficients therefore represent the expected change in thermal buffering (°C) associated with a one-standard-deviation increase in the predictor. ALS was the reference pedoclimatic region, and regional coefficients represent contrasts relative to ALS. BOR is reported for completeness but was represented by a single ERA5-Land cell and is not interpreted. CI, 95 % confidence interval.

A. Heat buffering

Model	Predictor	Estimate	SE	95 % CI	<i>p</i>
Region + Thermal	Intercept	0.966	0.666	−0.339, 2.271	0.147
Region + Thermal	ATC vs ALS	−1.466	0.712	−2.862, −0.070	0.04
Region + Thermal	BOR vs ALS	−1.391	1.827	−4.972, 2.190	0.446
Region + Thermal	CON vs ALS	−0.436	0.544	−1.503, 0.630	0.423
Region + Thermal	LUS vs ALS	−4.446	1.957	−8.282, −0.610	0.023
Region + Thermal	MDM vs ALS	−0.114	0.511	−1.116, 0.888	0.823
Region + Thermal	MDS vs ALS	−5.727	1.237	−8.152, −3.302	<0.001
Region + Thermal	NEM vs ALS	−1.394	1.653	−4.634, 1.846	0.399
Region + Thermal	PAN vs ALS	−1.551	1.117	−3.740, 0.637	0.165
Region + Thermal	MAT	−1.236	0.326	−1.876, −0.597	<0.001
Region + Thermal	Temperature seasonality	−0.532	0.3	−1.121, 0.057	0.076
Region + Thermal + CMImin	Intercept	0.966	0.667	−0.342, 2.275	0.148
Region + Thermal + CMImin	ATC vs ALS	−1.467	0.718	−2.875, −0.059	0.041



Region + Thermal + CMImIn	BOR vs ALS	-1.389	1.834	-4.984, 2.207	0.449
Region + Thermal + CMImIn	CON vs ALS	-0.440	0.583	-1.583, 0.703	0.451
Region + Thermal + CMImIn	LUS vs ALS	-4.443	1.992	-8.347, -0.539	0.026
Region + Thermal + CMImIn	MDM vs ALS	-0.112	0.511	-1.114, 0.889	0.826
Region + Thermal + CMImIn	MDS vs ALS	-5.720	1.332	-8.332, -3.109	<0.001
Region + Thermal + CMImIn	NEM vs ALS	-1.391	1.665	-4.656, 1.873	0.403
Region + Thermal + CMImIn	PAN vs ALS	-1.552	1.115	-3.738, 0.634	0.164
Region + Thermal + CMImIn	MAT	-1.234	0.379	-1.977, -0.490	0.001
Region + Thermal + CMImIn	Temperature seasonality	-0.531	0.325	-1.167, 0.105	0.102
Region + Thermal + CMImIn	CMImIn	0.004	0.348	-0.678, 0.685	0.991

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B. Cold buffering

Model	Predictor	Estimate	SE	95 % CI	<i>p</i>
Region + Thermal	Intercept	9.329	1.002	7.366, 11.293	<0.001
Region + Thermal	ATC vs ALS	-9.217	0.416	-10.033, -8.402	<0.001
Region + Thermal	BOR vs ALS	-6.009	3.227	-12.333, 0.316	0.063
Region + Thermal	CON vs ALS	-8.232	0.311	-8.842, -7.622	<0.001
Region + Thermal	LUS vs ALS	-7.706	3.595	-14.753, -0.659	0.032
Region + Thermal	MDM vs ALS	0.462	0.289	-0.104, 1.028	0.109
Region + Thermal	MDS vs ALS	-1.621	0.669	-2.932, -0.310	0.015
Region + Thermal	NEM vs ALS	-5.907	3.167	-12.115, 0.301	0.062



Region + Thermal	PAN vs ALS	-4.818	2.077	-8.890, -0.747	0.02
Region + Thermal	MAT	-0.611	0.18	-0.963, -0.259	<0.001
Region + Thermal	Temperature seasonality	0.177	0.167	-0.149, 0.504	0.287
Region + Thermal + CMImmin	Intercept	9.318	1.007	7.345, 11.292	<0.001
Region + Thermal + CMImmin	ATC vs ALS	-9.172	0.416	-9.988, -8.356	<0.001
Region + Thermal + CMImmin	BOR vs ALS	-5.923	3.244	-12.282, 0.436	0.068
Region + Thermal + CMImmin	CON vs ALS	-8.378	0.334	-9.034, -7.723	<0.001
Region + Thermal + CMImmin	LUS vs ALS	-7.529	3.618	-14.621, -0.437	0.037
Region + Thermal + CMImmin	MDM vs ALS	0.474	0.287	-0.089, 1.037	0.099
Region + Thermal + CMImmin	MDS vs ALS	-1.308	0.719	-2.717, 0.101	0.069
Region + Thermal + CMImmin	NEM vs ALS	-5.801	3.186	-12.046, 0.444	0.069
Region + Thermal + CMImmin	PAN vs ALS	-4.837	2.088	-8.931, -0.744	0.021
Region + Thermal + CMImmin	MAT	-0.481	0.211	-0.895, -0.068	0.023
Region + Thermal + CMImmin	Temperature seasonality	0.253	0.178	-0.097, 0.603	0.156
Region + Thermal + CMImmin	CMImmin	0.221	0.192	-0.155, 0.598	0.249

475 **Table A6. Associations between measured topsoil properties and ERA5-Land Heat and Cold buffering estimated using spatial error models. Models included pedoclimatic region together with standardized clay content, silt content, bulk density and soil pH. Estimates represent the change in thermal offset (°C) associated with a one-standard-deviation increase in each soil property. *p*-values were adjusted across the eight primary edaphic tests using Benjamini–Hochberg and Bonferroni procedures. Positive coefficients indicate greater buffering, whereas negative coefficients indicate reduced buffering.**

Response	Model	Term	Estimate	SE	Lower95	Upper95	<i>p</i> -value	BH-adjusted <i>p</i>	Bonferroni-adjusted <i>p</i>
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Heat	Primary edaphic SEM	Clay	0.131	0.068	-0.003	0.265	0.055	0.173	0.437
Heat	Primary edaphic SEM	Silt	0.135	0.073	-0.008	0.279	0.065	0.173	0.519
Heat	Primary edaphic SEM	Bulk density	-0.041	0.071	-0.180	0.098	0.563	0.643	1
Heat	Primary edaphic SEM	Soil pH	-0.062	0.072	-0.204	0.080	0.390	0.643	1
Cold	Primary edaphic SEM	Clay	-0.010	0.038	-0.084	0.064	0.787	0.787	1
Cold	Primary edaphic SEM	Silt	0.025	0.042	-0.058	0.108	0.556	0.643	1
Cold	Primary edaphic SEM	Bulk density	-0.097	0.040	-0.175	-0.020	0.014	0.113	0.113
Cold	Primary edaphic SEM	Soil pH	-0.024	0.040	-0.103	0.055	0.545	0.643	1

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Table A7. Sensitivity of edaphic associations to spatial support and sample size. Spatial-error-model coefficients are shown for SoilTemp–CHELSA (STC) at unique thermal-pixel support ($n = 276$) and after aggregation to 161 ERA5-Land cells. Matched-N values are median coefficients from 300 random subsamples of 161 STC pixels.

Response	Predictor	STC pixel, $n = 276$ Estimate [95 % CI]	p	STC on ERA5 cells, $n = 161$ Estimate [95 % CI]	p	BH-adjusted p	Matched-N median
Heat	Clay	0.243 [0.026, 0.459]	0.028	0.252 [-0.018, 0.521]	0.067	0.077	0.193
Heat	Silt	-0.223 [-0.451, 0.005]	0.055	-0.376 [-0.658, -0.094]	0.009	0.018	-0.322
Heat	Bulk density	-0.364 [-0.571, -0.157]	0.001	-0.396 [-0.662, -0.130]	0.004	0.01	-0.383



Heat	Soil pH	−0.651 [−0.862, −0.440]	<0.001	−0.613 [−0.917, −0.309]	<0.001	0.001	−0.599
Cold	Clay	0.062 [0.005, 0.119]	0.033	0.074 [−0.005, 0.154]	0.066	0.077	0.042
Cold	Silt	−0.063 [−0.125, 0.000]	0.052	−0.053 [−0.139, 0.032]	0.221	0.221	−0.112
Cold	Bulk density	−0.090 [−0.144, −0.036]	0.001	−0.112 [−0.187, −0.036]	0.004	0.01	−0.092
Cold	Soil pH	−0.097 [−0.151, −0.043]	<0.001	−0.099 [−0.186, −0.012]	0.025	0.041	−0.096

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Code and data availability

ERA5-Land temperature data are publicly available from the Copernicus Climate Data Store (CDS; DOI: 10.24381/cds.e2161bac).
 505 SoilTemp bioclimatic layers are publicly available through ZENODO (Lembrechts et al., 2022), and CHELSA climate data are available from the CHELSA database (Karger et al., 2017; Brun et al., 2022). Soil properties were obtained from raster products derived from the LUCAS topsoil database (Tóth et al., 2013), and land-cover data from the Copernicus Global Land Cover 100 m product for 2019 (Buchhorn et al., 2020). The derived soil–air thermal-buffering rasters and the R code used for data processing, statistical analyses and figure production are archived on Figshare [<https://figshare.com/s/791606d31edb7351625f>]. The underlying SOB4ES site-level data
 510 and sampling locations are not publicly available and cannot be redistributed because they are subject to the data-sharing policy of the SOB4ES consortium in the next six years.

Author contributions

GN: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing (original draft preparation). CM: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration,
 515 Resources, Supervision, Validation, Writing (review and editing).



Competing interests

The authors declare that they have no conflict of interest.

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