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Eco-Cultural Niche Breadth and Overlap Within the Cucuteni–Trypillia Culture Groups During the Eneolithic

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One of the most applied tools for documenting cultural variability and for tracing cultural trajectories within the environmental context is eco-cultural niche modeling and its associated methodology. The niche breadth characterization quantitatively evaluates the links between a given adaptive system and ecological constraints, which provides valuable information for archeology. For this purpose, in this study, 10 independent climatic and topographic environmental variables were interpolated, and eco-cultural niche modeling techniques were used to determine whether these differences in geographic distributions and niche breadth are consequences of differences in five Cucuteni–Trypillia groups that flourished in Eastern Europe during the Eneolithic (cal. 5,400/5,300–2,800/2,700 BCE). Our results showed that the eco-cultural niches of Cucuteni–Trypillia groups are significantly overlapping, and the expansion trend of the last two cultural groups (Late Eneolithic–cal. 4,100/4,000–2,800/2,700 BCE) into the northeastern steppe regions was not due to ecological niche differences but rather a result of other cultural factors. Furthermore, we highlighted that the first three Cucuteni–Trypillia groups (Early-to-Middle Eneolithic—cal. 5,400/5,300–4,100/4,000 BCE) had slightly more constrained ecological niches in the mid-Holocene ecosystems than the Late Eneolithic groups. The results have significant implications for understanding the geographical range dynamics and distribution of the last great Chalcolithic society of Old Europe and contribute to the characterization of ecological niches they have exploited during the cultural evolutionary process.

Keywords: eco-cultural niche modeling, Eneolithic, Cucuteni–Tripolye cultural complex, spatial distribution, ecological and bioclimatic variables, niche breadth and overlap, Old Europe

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INTRODUCTION

One of the broad goals of modern archeology is to understand and describe the behaviors of prehistoric populations by documenting cultural variability and tracing cultural trajectories within the environmental context (Banks et al., 2006; Banks et al., 2013; d'Errico and Banks, 2013; Banks, 2017). In recent decades, the development of Geographic Information System (GIS) software (Anderson and Raza, 2010), geostatistical models based on the R package for statistics (R Core Team, 2015), and the tools for estimating species distributions (Phillips et al., 2006; Phillips and Dudík, 2008; Elith et al., 2010), together with free access to archeological datasets (Harper et al., 2019), has attracted the interest of researchers in implementing new or upgraded software extensions to approach the links among 1) environmental conditions (Argyriou et al., 2017; Noviello et al., 2018;

Mihu-Pintilie and Nicu, 2019; Tapete and Cigna, 2019), 2) bioclimatic conditions (Lemmen et al., 2011; Birks et al., 2015; Krauß et al., 2017; Ivanova et al., 2018), and 3) cultural evolutionary processes of past human populations (Tallavaara et al., 2015; Pétillon et al., 2016; Harper et al., 2019; Whitford, 2019). One of these GIS-based applications, frequently used by archaeologists within interdisciplinary studies (e.g., geo-archaeological research), is eco-cultural niche modeling (ECNM) and its associated methodology (Banks et al., 2006).

Broadly, ECNM has been adopted by archeologists (Banks, 2017) to explore the interactions between cultural and natural systems and to understand how ecological dynamics influenced the adaptations and movements of prehistoric populations (Banks et al., 2008; Banks et al., 2009). Therefore, even if the concept of ecological niche modeling (ENM) is derived from and commonly used in biodiversity (Soberón and Peterson, 2005; Bobrowski et al., 2018; Gherghel et al., 2019) and geographic ecology (Peterson et al., 2011), ECNM applies the same methodology to analyses of the archaeological record and prehistoric human culture using GIS. The usefulness of ECNM for archeology is that it offers the opportunity to quantitatively evaluate the hypothesis that a given adaptive system was influenced by ecological constraints or alternatively that the characteristics and geographic distribution may have been influenced more by non-ecological processes (e.g., cultural factors) (Banks et al., 2011). At the same time, the ability to identify and characterize ECNM that prehistoric populations exploited during the different cultural periods is an important aspect of any environmental modeling effort in conjunction with cultural variability analysis, especially when significant climate change was recorded (Banks et al., 2013; Banks, 2017).

The Eneolithic (cal. ~ 5,000–3,000 BCE in Eastern Europe) has been broadly categorized as a period of transition from that of continuous spatial dynamics to relatively sedentary settlement-based agriculture (Harper et al., 2019; Mihu-Pintilie and Nicu, 2019). Prehistoric populations adapted to the environment through complex, often specialized, subsistence strategies, allowing human cultures to spread across relatively heterogeneous landscapes (Banks et al., 2006). For this reason, successive human migration and colonization of resource-rich areas with productive loess soils (e.g., Chernozem) (Argyriou et al., 2017; Noviello et al., 2018; Tapete and Cigna, 2019) and high mineral resources (e.g., salt, flint, and clay) (Lemmen et al., 2011; Krauß et al., 2017; Brigan and Weller, 2018; Ivanova et al., 2018) have been found all over Europe (Tallavaara et al., 2015; Pétillon et al., 2016; Harper et al., 2019). In this context, one of the first approaches to apply ECNM in geographical and archaeological studies was to identify the links between agricultural practices derived from large- (Banks et al., 2008) to middle-scale (Ivanova et al., 2018; Whitford, 2019) environmental and bioclimatic patterns, with the cultural evolution of the most representative prehistoric communities (Peterson et al., 2011). Despite this, only a few studies on the niche construction theory (NCT) have been developed for the same Eneolithic cultural unity in Eastern Europe (Harper et al., 2019; Whitford, 2019), even if the amount of archeological evidence meets the requirements for ECNM methodology. This is also the case in the current territories of Romania, Moldova, and Ukraine, where the entire geographic area has a high density of Eneolithic archaeological sites corresponding to Precucuteni/Cucuteni (in Romania and Moldova) and Trypillia (in Ukraine) culture or Cucuteni–Trypillia cultural unity (CTU), together known as the last great Chalcolithic society of Old Europe (cal. 5,400/5,300–2,800/2,700 BCE) (Gimbutas, 1974; Monah and Monah, 1997; Chapman et al., 2019) (**Figure 1**). However, by constructing, characterizing, and comparing the niche breadth of CTU groups, we aimed to test for ECNM applicability, contributing to a broader perspective on the ecological adaptation and spatiotemporal dynamics inside the most representative culture of Old Europe.

Consistent with this study's main goal, we tested the hypothesis that the observed differences in the geographic distribution of CTU groups reflect the exploitation of different ecological niches inside of the same Eneolithic culture. We provided the first GIS-based Eneolithic ECNM for a vast area in Eastern Europe among Eastern Carpathians to the west, the Dnieper river valley to the east and north, and the Black Sea to the south (**Figure 1**). To this end, the location of more than 2,200 Eneolithic archaeological sites belonging to the CTU complex, divided into five chronological cultural groups (cal. 5,400–2,700 BCE) (Mantu, 1998; Shukurov et al., 2015), was investigated. The correlation of archaeological data with environmental conditions was made using 10 ecological variables, of which five were terrain variables (Moore et al., 1991; Riley et al., 1999; Sørensen et al., 2006; De Reu et al., 2013; Burrough et al., 2015; Mihu-Pintilie and Nicu, 2019; Whitford, 2019) and five were bioclimatic variables selected from three different global climatic model databases corresponding to the mid-Holocene climatic conditions (Hijmans et al., 2005). This information should allow us to identify the differences in eco-cultural niche breadth among CTU groups and analyze possible links between human adaptive systems and the ecological niches exploited in the heterogeneous environment of the study area. Also, based on niche characterization, we aimed to answer the following questions: 1) Did the heterogeneous ecological and bioclimatic characteristics in Eastern Europe play a significant role in the evolutionary process of successive phases of the CTU? and 2) Were these particular traits of the successive cultural groups correlated with modifying habitation practices (e.g., subsistence agriculture and population growth) and the subsequent occupation of other territories?

Data and Methods

Figure 2 summarizes the workflow chart followed in this study describing the archeological geodatabase construction in GIS, the ecological variable-obtaining process, the key steps for ECNM modeling, and the statistical tools and metrics used for niches' interpretation. Each methodological step will be detailed in the subsections as follows.

Study Area Delineation

Spanning approximately two and a half millennia (cal. ~ 5,400–2,700 BCE), the CTU complex spreads from a small

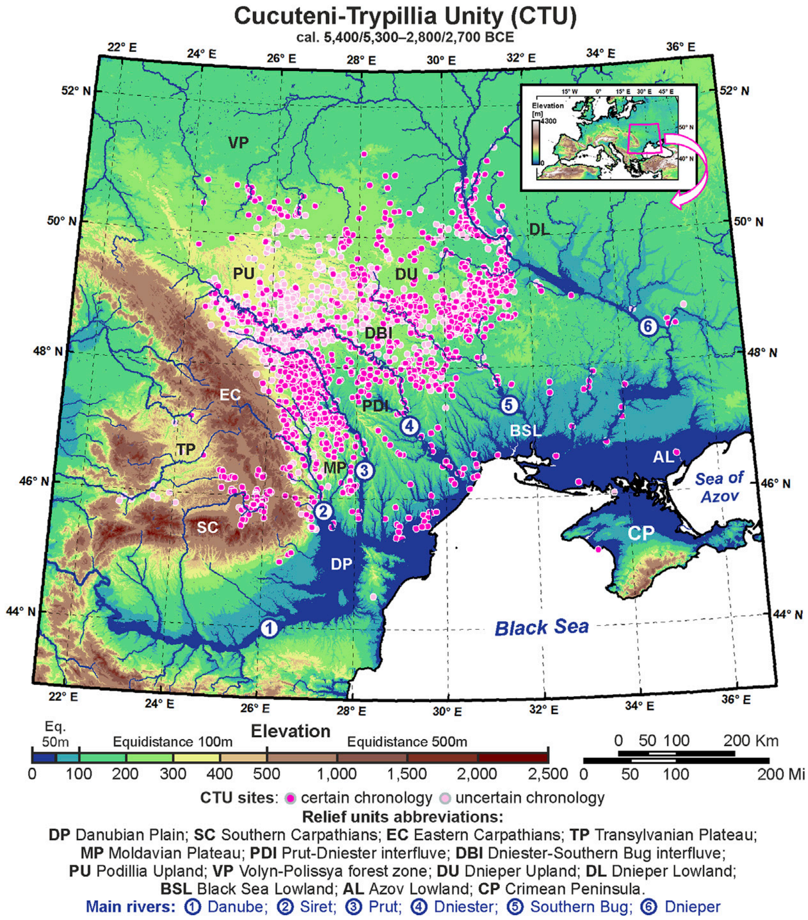

FIGURE 1 | Elevation in Eastern Europe and the distribution of Cucuteni–Trypillia cultural unity (CTU) sites; the relief units and major rivers are highlighted for the study area.

area in the Eastern Carpathian lowland, defined by the Siret and Prut watersheds which are the last Danube tributaries. They came to occupy a territory between the eastern bank of the Dnieper to the east, the Volyn Polissya forest zone of modern Ukraine to the north, and the northwestern coast of the Black Sea to the south. To the west, due to the Eastern Carpathians, which acted as an orographic barrier, the expansion was hampered, and only a small group managed to cross the mountains through the Curvature Carpathians passages and settle in the intra-Carpathian depressions (Transylvanian Plateau). Therefore, the dominant characteristic of the CTU complex was the extension to the eastern forest-steppe zone, defining the transition from continuous spatial dynamics to a relatively sedentary settlement-based agriculture located on more productive soils. Starting with 4,400 BCE, respectively, during the transition from Middle-to-Late Eneolithic, this fact is also highlighted by the demographic development when the significant regional differences in settlement structure and spatial organization between west and east have been attested by archeologists (Harper et al., 2019). Overall, the dominant population movements inside the CTU culture were from west to the northeast and east or from the sub-Carpathians region to the upper and middle basins of Siret, Prut, Dniester, Southern Bug, and Dnieper river basins. In these geographical settings, the major landform units' distribution (e.g., Eastern Carpathian, Black Sea shoreline, and main watercourse) and CTU sites' distribution were used to avoid overrating the eco-cultural niche extents and losing their resolutions used as optimal landmarks for geographical niche delineation. Therefore, the study area we referred to in this work is located in the northeastern region of Old Europe, or more precisely, between 44°N–52°N latitude and 22°E–36°E longitude (**Figure 1**).

Archeological Data Occurrence

In order to identify the links among archaeological settlement placement, human adaptive systems, and the ecological niches exploited by prehistoric populations during the Eneolithic, a geodatabase was created using Esri ArcGIS 10.6 based on field surveys–only in Romania (Mihu-Pintilie and Nicu, 2019), along with relevant archaeological documentation and registries–for the entire study area (Harper et al., 2019). We only used the CTU settlements where independent archaeological documentation was well-grounded in reports, scientific publications (e.g., articles, supplementary material, and data in journal articles),

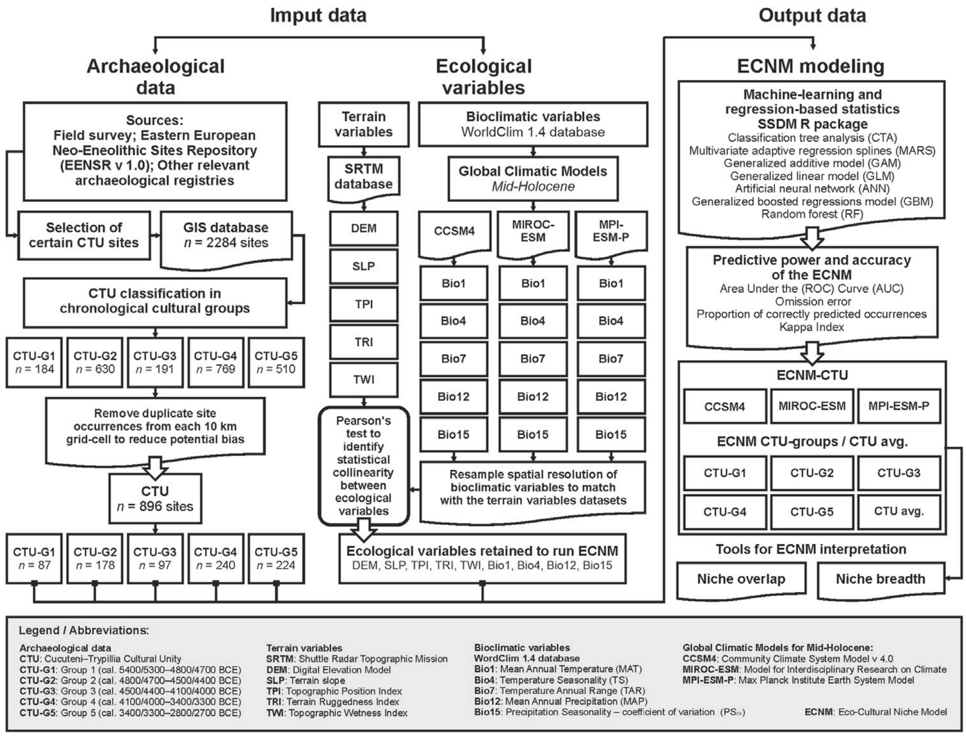

FIGURE 2 | Workflow chart followed in this study to obtain the eco-cultural niche (ECNM) breadth of the Cucuteni–Trypillia cultural unity (CTU) during the Eneolithic in Eastern Europe.

radiocarbon-based chronology, and georeferenced archeological maps (Nikitin et al., 2010; Diachenko and Menotti, 2012; Brigan and Weller, 2013, 2018; Chapman et al., 2014; Chapman et al., 2019; Harper et al., 2019; Mihu-Pintilie and Nicu, 2019). The main source for CTU sites located outside the Romanian territory was the Eastern European Neo-Eneolithic Sites Repository (EENSR) version 1.0 database, published for the first time by Harper et al. (2019), which contains information about more than 8,000 Neo-Eneolithic sites. The EENSR database was constructed based on information recorded in national-level registries such as the Register of Tripoli Culture Monuments (RPTK)–Ukraine, Register of Monuments of the Republic of Moldova (RMRM), and National Archaeological Record of Romania (RAN), along with various other studies (Harper et al., 2019). Therefore, after the EENSR was thoroughly revised to include only archaeological sites with remains recovered from intact stratigraphic contexts and combined with our database (Mihu-Pintilie and Nicu, 2019), only 2,284 sites could be certainly identified as belonging to the specific CTU.

Being one of the most important and best-explored early farming communities in Eastern Europe, the CTU was discovered independently in Eastern Romania (Cucuteni) and Central-Western Ukraine (Trypillia) in the late 19th century. For these reasons, the CTU cultural stages were studied separately by various authors for a long time (Shukurov et al., 2015) and broadly classified into Ariuşd, Cucuteni, and Eastern Tripolye (ETC) and Western Tripolye (WTC) cultures (Harper et al., 2019). However, to overcome this generalized geographical–archaeological classification, the selected CTU sites were chronologically united and classified into five groups, according to Mantu (1998) and Shukurov et al. (2015): CTU-G1 (cal. 5,400/5,300–4,800/4,700 BCE); CTU-G2 (cal. 4,800/4,700–4,500/4,400 BCE); CTU-G3 (cal. 4,500/4,400–4,100/4,000 BCE); CTU-G4 (cal. 4,100/4,000–3,400/3,300 BCE); and CTU-G5 (cal. 3,400/3,300–2,800/2,700 BCE). The last step in archaeological data processing was to remove duplicate site occurrences from each grid cell in order to reduce potential bias and to ensure that the training and testing occurrence datasets in the ECNM were spatially unique (Anderson and Gonzalez, 2011; Boria et al., 2014; Vidal-Cordasco and Nuevo-López, 2021). Furthermore, the occurrence data were reduced to ensure a minimum distance of 10 km between any pair of occurrence points, preventing oversampling of environmental conditions from certain areas and reducing spatial autocorrelation (**Figure 2**). Ultimately, 896 CTU archaeological sites were retained to run the ECNM (**Figure 3**). More details on chronology, cultural stage names in different countries, and CTU groups' abbreviation used in this study are found in **Table 1**.

Ecological Variables

To estimate the eco-cultural niches, we initially used a combination of 10 ecological variables selected based on probable relevance for the CTU site's location in Eastern Europe. Of these, five are terrain variables: the elevation above the sea level (DEM), terrain slope (Burrough et al., 2015), topographic position index (TPI) (De Reu

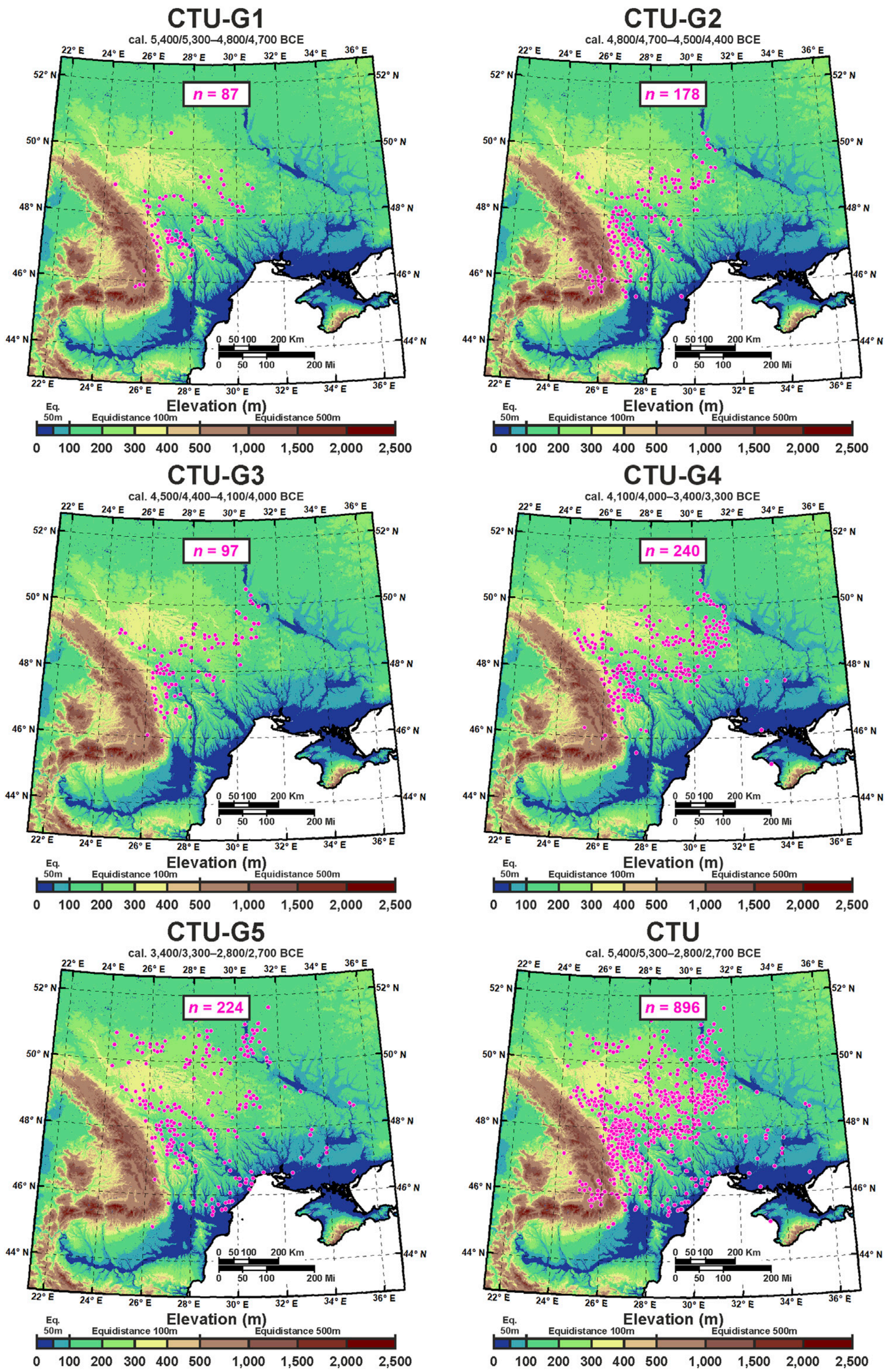

FIGURE 3 | CTU groups' (see **Table 1**) and total CTU sites' distribution were used to run the ECNM; duplicate site occurrences from each grid cell were removed to reduce potential bias.

et al., 2013; Mihu-Pintilie and Nicu, 2019), terrain ruggedness index (TRI) (Riley et al., 1999), and topographic wetness index (TWI) (Moore et al., 1991; Sørensen et al., 2006); and five are WorldClim 1.4, 2022 bioclimatic variables (Hijmans et al., 2005): Bio1/mean annual temperature (MAT), Bio4/temperature seasonality (TS), Bio7/temperature annual range (TAR), Bio12/mean annual

TABLE 1 | Cucuteni–Trypillia Unity (CTU) chronology during the Eneolithic in Eastern Europe (after Mantu, 1998; Shukurov et al., 2015), number of total archaeological sites per cultural stage, and number of sites retained to run the ECNM and CTU groups' abbreviations used in this study.

Period	Cultural stage in Romania and Moldova	Cultural stage in Ukraine	Date ranges (cal. BCE)	Number of total CTU sites	Number of CTU sites retained for ECNM	CTU groups' abbreviations
Late	Gorodişte–Folteşti–Erbiceni	Trypillia CII-γII	3,400/3,300–2,800/2,700	510	224	CTU-G5
	Cucuteni B (1–3)	Trypillia BII + CI	4,100/4,000–3,400/3,300	769	240	CTU-G4
Middle	Cucuteni A-B (1–2)	Trypillia BI/BII	4,500/4,400–4,100/4,000	191	97	CTU-G3
	Cucuteni A (1–4)	Trypillia BI	4,800/4,700–4,500/4,400	630	178	CTU-G2
Early	Precucuteni I, II, III	Trypillia A (1–2)	5,400/5,300–4,800/4,700	184	87	CTU-G1

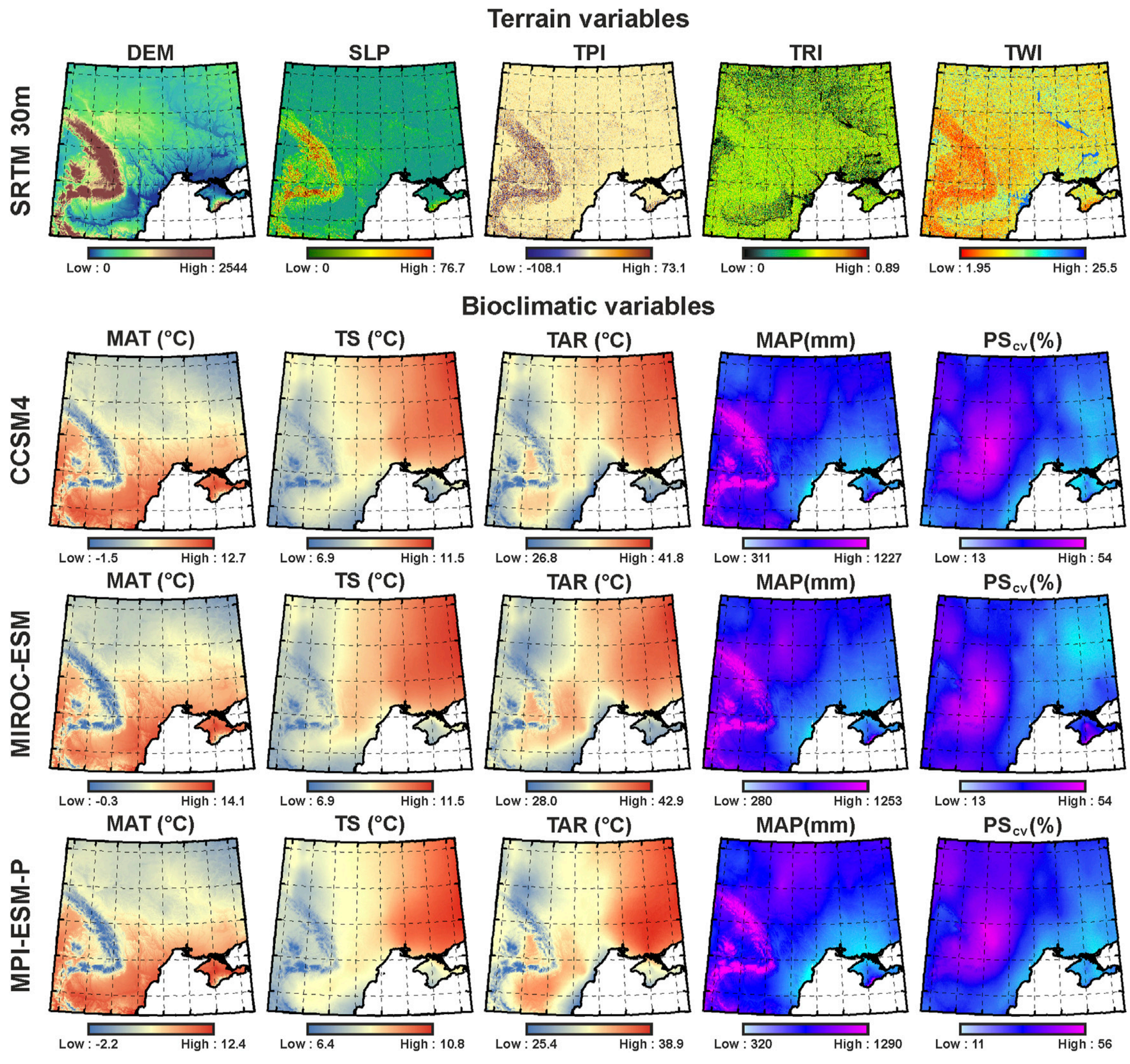

FIGURE 4 | Independent ecological variables selected to run the ECNM: terrain variables generated using DEM-derived raster from SRTM 30 m; mid-Holocene bioclimatic variables selected from three global climatic models (CCSM4, MIROC-ESM, and MPI-ESM-P) provided by the WorldClim 1.4 database.

precipitation (MAP), and Bio15/precipitation seasonality–coefficient of variation (PS_{cv}). Overall, the ecological variables were selected for ECNM for several reasons: first, to include as much as possible the ecological variability in the study area; second, for their applicability for species distribution modeling and their direct affiliation to habitation practice during the Eneolithic; and third, based on

TABLE 2 | Summary statistics of the background raster datasets used for ECNM of the CTU and CTU groups.

Background raster/variable	Mean	SD	Min	Max
CCSM4/MAT (°C)	8.14	1.76	−1.5	12.7
CCSM4/TS (°C)	9.7	0.84	6.91	11.5
CCSM4/TAR (°C)*	36.9	2.2	26.8	41.8
CCSM4/MAP (mm/year)	594.2	91.8	311	1227
CCSM4/PS_{cv} (%)	30.7	8.11	13	54
MIROC-ESM/MAT (°C)	9.71	1.64	−0.3	14.1
MIROC-ESM/TS (°C)	9.69	0.89	6.91	11.5
MIROC-ESM/TAR (°C)*	37.5	2.43	28.1	42.9
MIROC-ESM/MAP (mm/year)	573.5	111.3	280	1253
MIROC-ESM/PS_{cv} (%)	29.7	8.8	13	54
MPI-ESM-P/MAT (°C)	7.82	1.62	−2.2	12.4
MPI-ESM-P/TS (°C)	9.11	7.82	6.41	10.8
MPI-ESM-P/TAR (°C)*	34.8	2.08	25.4	38.9
MPI-ESM-P/MAP (mm/year)	649.5	103.1	320	1290
MPI-ESM-P/PS_{cv} (%)	32.5	9.1	11	56
SRTM/DEM (m asl)	239.1	245.5	0	2544
SRTM/SLP (°)	3.6	5.3	0	76.7
SRTM/TPI	0	2.2	−108.1	73.11
SRTM/TRI	0.43	0.18	0	0.89
SRTM/TWI [*Ln* (*As/tan ß*)]	8.31	2.24	1.95	25.51

**Indicate ecological variables that were not included in the ECNM.*
MAT, mean annual temperature; TS, temperature seasonality; TAR, temperature annual range; MAP, mean annual precipitation; PScv, precipitation seasonality (coefficient of variation); DEM, elevation above the sea level; SLP, terrain slope; TPI, topographic position index; TRI, terrain ruggedness index; TWI, topographic wetness index.

their resolution and ease of availability (Whitford, 2019). Therefore, the terrain variables provide information on the physical setting of the area extent concerning both space and suitability for the construction of sedentary settlements during the Eneolithic, and the bioclimatic variables indicate their impacts on the length of the growing season (e.g., changes in weather, ecology, and amount of daylight) and in influencing the hydrological settings (e.g., drought seasonality and floods).

Regarding the spatial database used for ecological variable modeling, the terrain variables are DEM-derived (30 m) rasters from the Shuttle Radar Topographic Mission (SRTM) terrain data (Farr et al., 2007), and the bioclimatic variables represent interpolations of the current climatic conditions projected on global climatic models (GCMs) corresponding to the mid-Holocene (Hijmans et al., 2005) when the CTU in its different phases flourished (Shukurov et al., 2015). In the case of bioclimatic variables, three different mid-Holocene climatic reconstructions based on three different paleoclimate GCMs were used: Community Climate System Model Version 4 (CCSM4) (Gent et al., 2011), Model for Interdisciplinary Research on Climate (MIROC-ESM) (Watanabe et al., 2011), and Max Planck Institute Earth System Model (MPI-ESM-P) (Gutjahr et al., 2019) (**Figure 4**). Using multiple paleoclimate reconstructions, we were able to account for inter-model variations in the paleoclimate record and not rely only on one model, which increases the overall accuracy of our estimates and improves the interpretation of the results. We obtained the interpolated climatic variables from the WorldClim 1.4, 2022 database (Hijmans et al., 2005; Fick and Hijmans, 2017), widely used in estimating species distribution (Booth et al., 2014). The WorldClim 1.4 database has been previously used to predict the potential geographic ranges and eco-cultural niches of other cultures, showing high accuracy in estimating ecological niches (Banks et al., 2013; Birks et al., 2015; Krauß et al., 2017; Vidal-Cordasco and Nuevo-López, 202; Whitford, 2019). The WorldClim database comprises 19 bioclimatic variables (Booth et al., 2014) characterizing the temperature and precipitation regimes of the studied area from which we have chosen the annually based variables to increase the generality of our predictions and accuracy in interpretation of the results. All the bioclimatic variables were resampled from 30 s or approximately 1 km^2 spatial resolution (Gent et al., 2011; Watanabe et al., 2011; Gutjahr et al., 2019) to 654 m^2 in order to match the spatial resolution of terrain datasets (Farr et al., 2007) for the ECNM procedure (**Table 2**).

Since collinearity can induce errors in estimates, we ran Pearson's correlation coefficient (r^2) to identify collinearity among variables, and all the variables with an r^2 greater than 0.8 were removed from the models (**Table 3**). Nine ecological variables were retained to run the ECNM, from which five are based on the local topography (DEM, SLP, TPI, TRI, and TWI) and four on the climatic datasets (MAT, TS, MAP, and PS_{cv}).

Eco-Cultural Niche Modeling

To model the eco-cultural niches of the five phases of CTU, we used seven machine learning and regression-based statistical methods used in estimating species ecological niches: the classification tree analysis (CTA), multivariate adaptive regression splines (MARS), generalized additive model (GAM), generalized linear model (GLM), artificial neural network (ANN), generalized boosted regressions model (GBM), and random forest (RF) (Prasad, 2018). Using more than one statistical method to estimate the eco-cultural niches and the geographic distributions of CTU groups, we decreased the errors associated with each statistical tool (Sillero and Barbosa, 2019). Stacking resulted in models produced by different modeling methods, minimizing errors, and increasing results and interpretations' accuracy. Ten thousand randomly selected background pseudo-absences were used to produce the models. The models were tested independently using 25% of the occurrence data (not used to train the modeling process). Also, the predictive power and accuracy were assessed using a few metrics, including the area under the ROC curve (AUC), the omission error, the proportion of correctly predicted occurrences, and the Kappa Index (Oliveira et al., 2014) (**Figure 2**). The final model stack was ensemble only for the models that were shown to have a high predictive power by only considering models with an AUC higher than 0.75. We also assessed the percentage contribution of each environmental predictor by using a Pearson correlation coefficient to evaluate the importance of each ecological variable to the ECNMs. The predictions were then exported as probabilities into a GIS, where they were visualized and maps of each prediction were produced in ArcGIS 10.6. All the models were produced and evaluated in the SSDM R package (Schmitt et al., 2017; R Core Team, 2015).

Geographic Ranges and Niches

To study the range shifts in the geographic distribution of different phases of the CTU, we used the relative centroid change to indicate the direction of the range shifts. We

TABLE 3 | Results of Pearson's test for statistical collinearity (variables $r^2 > 0.8$ were removed).

	MAT	TS	TAR	MAP	PS_{cv}	DEM	SLP	TPI	TRI	TWI
MAT	1	–0.1475	–0.039	–0.6038	0.2546	–0.5424	0.0543	0.0162	–0.0186	–0.0199
TS	–0.1475	1	0.8394	–0.3451	–0.6687	–0.5555	–0.1304	0.0422	–0.0367	0.0362
TAR	–0.039	0.8394	1	–0.3205	–0.3291	–0.4156	–0.0927	0.0428	–0.0407	0.0342
MAP	–0.6038	–0.3451	–0.3205	1	0.1843	0.494	0.0159	–0.0481	0.0341	–0.0035
PS_{cv}	0.2546	–0.6687	–0.3291	0.1843	1	0.2825	0.154	0.0301	0.0753	–0.0953
DEM	–0.5424	–0.5555	–0.4156	0.494	0.2825	1	0.1202	0.0144	0.108	–0.0804
SLP	0.0543	–0.1304	–0.0927	0.0159	0.154	0.1202	1	0.1448	0.1259	–0.4205
TPI	0.0162	0.0422	0.0428	–0.0481	0.0301	0.0144	0.1448	1	0.3179	–0.4319
TRI	–0.0186	–0.0367	–0.0407	0.0341	0.0753	0.108	0.1259	0.3179	1	–0.3851
TWI	–0.0199	0.0362	0.0342	–0.0035	–0.0953	–0.0804	–0.4205	–0.4319	–0.3851	1

TABLE 4 | Summary statistics of the reconstructed environmental variables for the CTU groups.

		MAT (°C)	TS (°C)	MAP (mm)	PS_{cv} (%)	DEM (m)	SLP (°)	TPI	TRI	TWI
CTU-G1	Mean	9.07	9.47	588	42.1	200.5	4.05	0.07	0.47	8.12
	SD	0.78	0.33	42.9	8.45	129.1	3.57	2.12	0.14	2.4
	Min	7.13	8.55	465	23	33	0	–9.33	0	4.43
	Max	10.8	10.4	732	53.3	727	19.5	9.89	0.71	17
CTU-G2	Mean	8.97	9.41	595	43.9	254	4.6	0.27	0.47	7.6
	SD	0.92	0.28	41.2	6.58	187.3	4.19	2.6	0.12	2.09
	Min	5.1	8.55	386	21.3	7	0	–32.9	0	4.44
	Max	11.4	10.1	810	53.3	855	31	13.4	0.9	19.3
CTU-G3	Mean	8.82	9.49	609	42.4	194.4	4.26	0.44	0.47	7.76
	SD	0.66	0.24	34.1	7.99	86.7	3.82	2.23	0.13	2.28
	Min	7.43	8.76	532	25.7	33	0	–5.78	0	4.5
	Max	10.1	10.1	686	53	588	24.4	11	0.78	19.3
CTU-G4	Mean	8.77	9.63	599	59.9	182	3.94	0.36	0.47	7.71
	SD	0.78	0.36	44.7	4.47	88.6	3.26	1.95	0.13	2.13
	Min	7.4	8.58	403	40.3	3	0	–7.78	0	4.21
	Max	12	10.7	705	70.5	588	23.9	11	0.78	20.5
CTU-G5	Mean	8.78	9.59	601	35.8	158.3	3.51	0.31	0.46	7.91
	SD	1.01	0.35	67.7	9.19	81.01	3.35	1.94	0.16	2.15
	Min	6.97	8.62	377	17.3	0.00	0	–7.56	0	4.43
	Max	11.5	10.9	710	53.3	486.00	19.5	10.8	0.89	19.3

MAT, mean annual temperature; TS, temperature seasonality; TAR, temperature annual range; MAP, mean annual precipitation; PScv, precipitation seasonality (coefficient of variation); DEM, elevation above the sea level; SLP, terrain slope; TPI, topographic position index; TRI, terrain ruggedness index; TWI, topographic wetness index.

calculated all the niche shifts in ArcGIS 10.6. We also compared the eco-cultural niches of the different phases of the CTU by calculating Schoener's *D* (Schoener, 1968), Warren *I* statistics (van der Vaart, 1998; Warren et al., 2008), and relative rank (Warren and Seifert, 2011) for niche overlap and niche breadth. The rank, *D*, and *I* niche statistics range from 0 to 1, where 0 shows no overlap and 1 shows total overlap. We calculated all the niche breadth and overlap statistics using the ENMToolbox 1.4.4 (Warren et al., 2008) (**Figure 2**).

RESULTS AND DISCUSSION

Environmental Conditions During the Eneolithic

During the Eneolithic, the Cucuteni–Trypillia groups occupied a latitudinal band between 44°N and 52°N latitude in Eastern Europe, with mean annual temperatures (MAT) ranging between 5.1°C and 12°C and mean annual precipitations (MAP) ranging between 377 mm/year and 810 mm/year. The temperature seasonality (TS) or the standard deviation of the mean monthly temperature indicates variability between 9.41°C and 10.9°C. The precipitation seasonality (PS_{cv}) calculated as a coefficient of variation (%) in monthly precipitation totals over the year indicates mean values between 17.3 and 70.5%. The terrain elevation (DEM) varied between 0 m (Black Sea level) and 855 m, and terrain slope (SLP) varied between flat areas and 31°. The topographic position index (TPI), which indicates if the CTU settlement was placed on positive (e.g., hill and ridge) or negative (e.g., valley and depression) landforms, varies between 13.4 and −12.9 (mean 0.29). The terrain ruggedness index (TRI), a hardness indicator of the CTU population's movement through the study area, varies between 0 and 0.9 (mean 0.46). The topographic wetness index (TRI), commonly used to quantify topographic control on hydrological processes (e.g., floodable areas and arid lands), varies between 4.43 and 20.5 (mean 7.82).

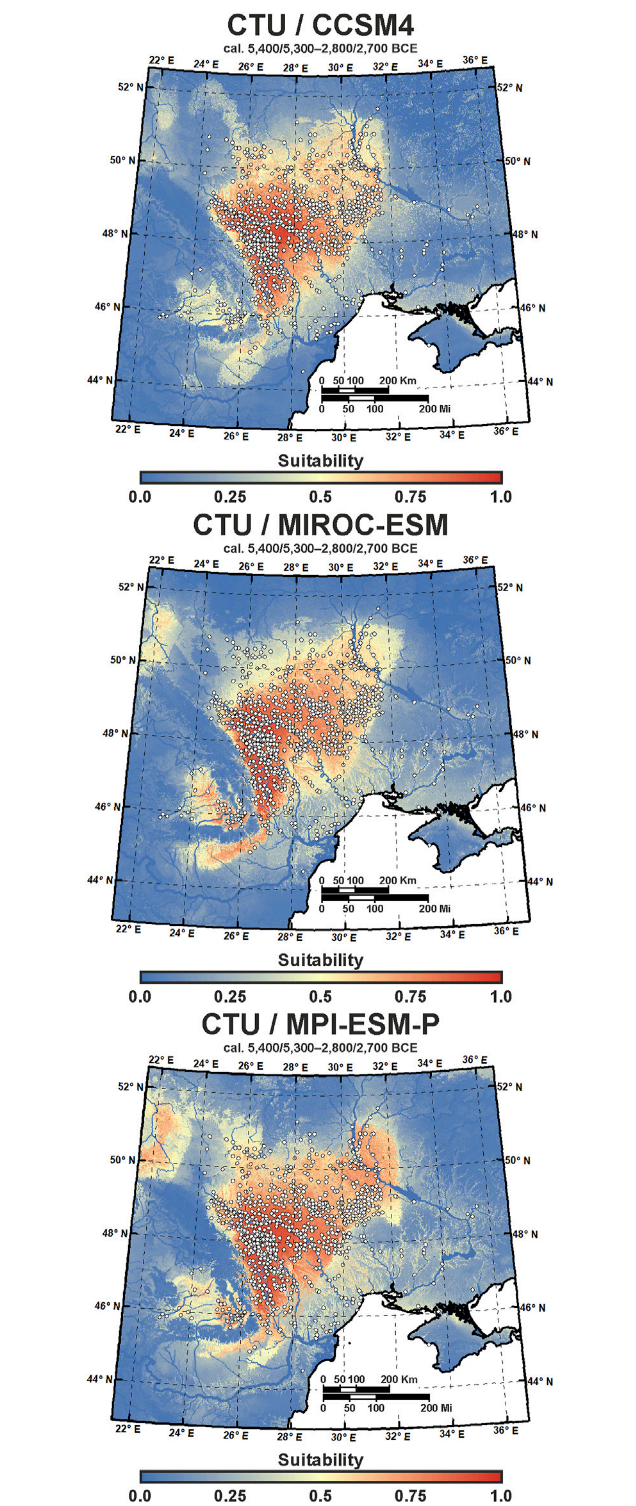

FIGURE 5 | ECNM reconstructions of CTU (cal. 5,400/5,300–2,800/2,700 BCE) using terrain variables and mid-Holocene CCSM4, MIROC-ESM, and MPI-ESM-P bioclimatic variables; colors range from blue (0) to yellow (0.5) and to red (1), or low (0) to high (1) suitability, respectively; the white dots represent CTU sites used for niche reconstruction.

The bioclimatic and terrain datasets were analyzed from one cultural group to another in these environmental conditions depending on the settlement's spatial distribution inside each cultural phase. Therefore, significant differences in terms of annual and seasonal temperature were observed between the Early Eneolithic (CTU-G1) and first phase of Middle Eneolithic (CTU-G2) groups (cal. 5,400/5,300–4,500/4,400 BCE), where mean annual temperatures (MAT) were +0.23°C degrees higher than the second phase of the Middle/Late Eneolithic period (cal. 4,500/4,400–2,800/2,700 BCE) in which the CTU-G3, CTU-G4, and CTU-G5 groups flourished. These thermal characteristics are also observed in the case of temperature seasonality (TS) which increased with +0.13°C by comparing the CTU-G1 and CTU-G2 conditions with the last three CTU phases. However, the general thermal trends were the decrease in annual mean temperature and a slight increase in seasonal temperature variation from the first phase of the CTU culture to the last one. This phenomenon can be explained by the expansion of CTU populations from the west to the northeast, where the occupied steppe region (Black Sea lowland and southern Bug–Dnieper upper basins) showed more significant temperature variations than the Eastern Carpathian lowlands. According to the mean annual precipitation (MAP), the rainiest period was during the Early-to-Middle Eneolithic, when the maximum amount of precipitation ranged between 732 and 810 mm/year. Also, the precipitation seasonality (PS_{cv}) indicates that the beginning of the Late Eneolithic or during the Cucuteni B (1–3)/Trypillia BII + CI phase (CTU-G4) was the time interval with the most significant difference in precipitation amount (59.9% coefficient of variation). Overall, the mean amount of precipitation during the Eneolithic was around 600 mm/year, and the precipitation seasonality in terms of the coefficient of variation was 44.5%.

The climatic conditions are closely related to the terrain variable characteristics, and several differences in CTU habitation practices during the Eneolithic have been observed. Therefore, the mean elevation of CTU sites decreases from the Early/Middle Eneolithic to Late Eneolithic period, respectively, from 200.5 m (CTU-G1) and 254 m (CTU-G2) to 158.3 m (CTU-G5). This trend was determined by the migration from the hilly region in the Eastern Carpathian lowland (Siret, Prut, and upper Dniester basins) to the Southern Bug and Dnieper's lower areas as well to the Black Sea lowlands (**Figure 3**). The largest elevation difference (848 m) between CTU sites occurred during the cal. 4,800/4,700–4,500/4,400 BCE (CTU-G2) due to the Ariușd phase (Cucuteni A), which migrated to the west and occupied the intra-Carpathian depressions. However, the upper limit of CTU sites' altitude did not exceed 600 m than in a few isolated cases referring here to the sub-Carpathian and intra-Carpathian sites. Regarding the terrain slope of CTU settlements, the average values ranging between 3.51° and 4.6° indicate that there are no significant differences from one cultural stage to another and attest that suitable habitat areas have not changed over time. These terrain characteristics also result from the mean values of the topographic position index (TPI), which is positive for all the

TABLE 5 | Model performance of CTU niches reconstructed using bioclimatic variables provided by CCSM4, MIROC-ESM, MPI-ESM-P, and DEM-derived terrain variables.

Model range (cal. BCE)	Model/GCM	AUC	Omission rate	Proportionally correct	Kappa
5,400/5,300–2,800/2,700	CTU/CCSM4	0.782	0.223	0.781	0.542
5,400/5,300–2,800/2,700	CTU/MIROC-ESM	0.785	0.212	0.785	0.553
5,400/5,300–2,800/2,700	CTU/MPI-SM-P	0.787	0.210	0.787	0.553

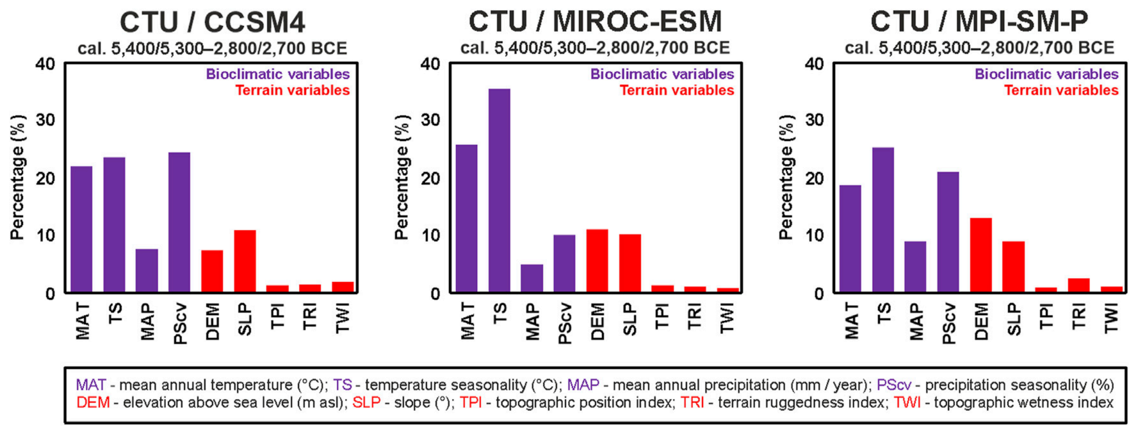

FIGURE 6 | Variable contributions to CTU niches reconstructed using bioclimatic variables derived from CCSM4, MIROC-ESM, and MPI-ESM-P global climatic models (GCM) and DEM-derived terrain variables.

CTU groups (0.07–0.44), from the mean values of the topographic ruggedness index (TRI), which is constant at around 0.47 value, and from the mean values of topographic wetness index (TWI), which slightly ranges between 7.6 and 8.12 (**Table 4**).

Ecological Variables' Performance and Contributions for Eco-Cultural Niche Modeling

The eco-cultural niche models were produced in the SSDM R package, Maxent, and ENMToolbox 1.4.4 using the optimum combination of modeling parameters described earlier (**Figure 2**). First, one model each was produced from the CTU/CCSM4, CTU/MIROC-ESM, and CTU/MPI-ESM-P datasets combined with DEM-derived terrain variables in order to test the performance of global climatic models (GCMs) (Baker and Taylor, 2016) for ECNM (**Figure 5**). The models' performance provided in **Table 5** indicate that there are no significant differences (AUC: 0.78–0.79; omission rate: 0.21–0.22; proportionally correct: 0.78–0.79; and Kappa: 0.54–0.55) between GCMs used to run ECNM for the entire Cucuteni–Trypillia culture. The same conclusion results from the analysis of ecological variable contributions where the bioclimatic variables (MAT, TS, MAP, and PS_{cv}) have relatively similar percentages (±3.59%) in each model obtained by run ECNM procedure: CTU/CCSM4—77.29%; CTU/MIROC-ESM—75.95%; and CTU/MPI-ESM-P—73.7% (**Figure 6**). However, by choosing to account for inter-model variations in the paleoclimate record, the construction quality and interpretation improved (Baker and Taylor, 2016).

To generate the final eco-cultural niche models for each CTU group (CTU-G1—CTU-G5) and for the entire CTU period, the average values of bioclimatic variables obtained from each GCM were used together with all the selected terrain variables (**Figure 7**). The model's performance assessment provided in **Table 6** using four different metrics (AUC, omission rate, proportionally correct, and Kappa index) indicates high predictive power and accuracy for each resulting ECNM: AUC between 0.78 and 0.84, omission rate between 0.16 and 0.22, proportionally correct between 0.78 and 0.83, and Kappa between 0.47 and 0.58. Regarding ecological variable contributions to eco-cultural niche models provided for each CTU group, bioclimatic conditions dominate: CTU-G1—88.34%, CTU-G2—82.5%, CTU-G3—77.02%, CTU-G4—78.04%, and CTU-G5—74.85% (CTU—75.65%). Within the bioclimatic variables, the variation of the precipitation seasonality coefficient (PS_{CV}) has the most significant

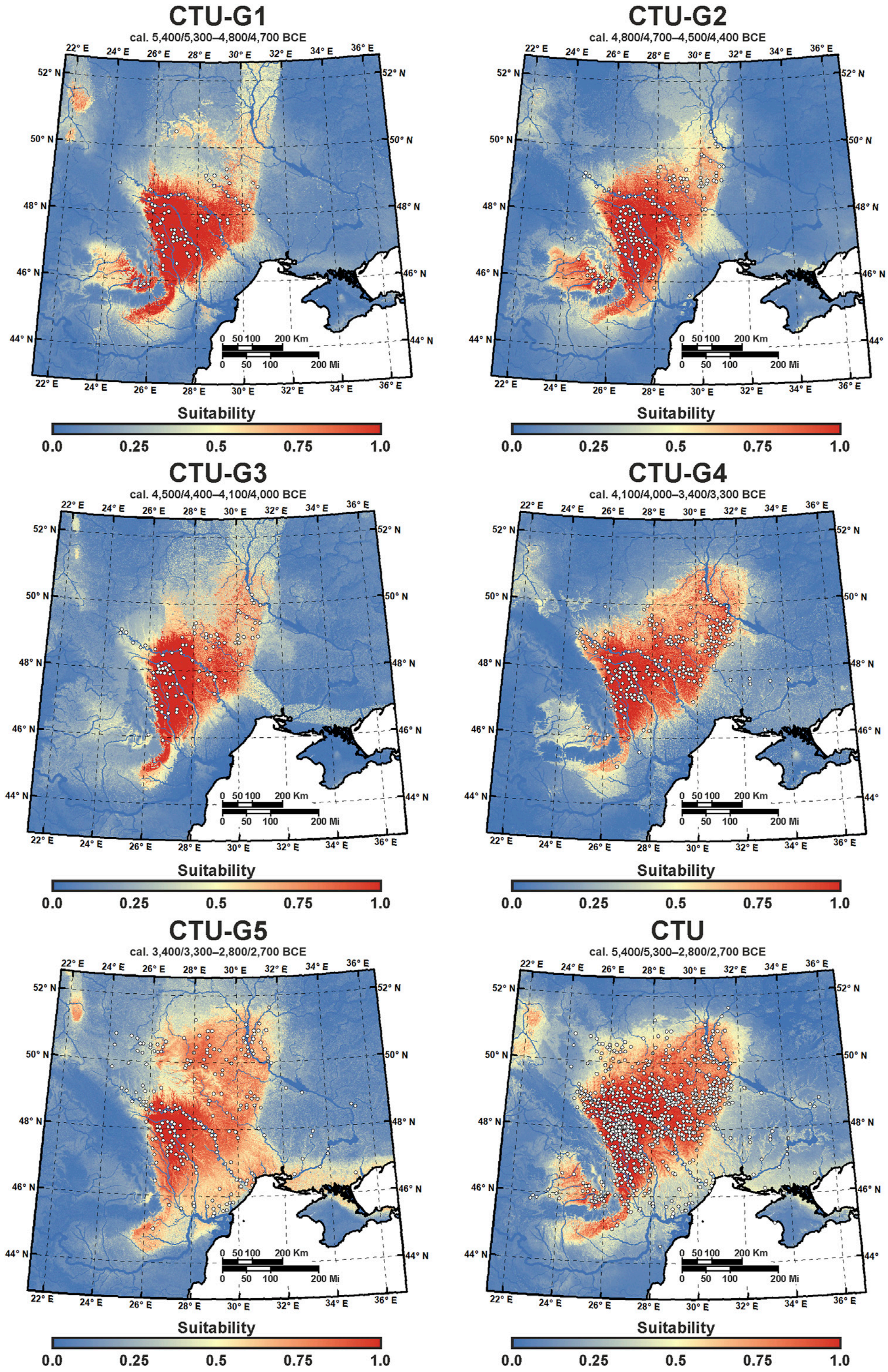

FIGURE 7 | ECNM reconstructions of CTU groups (see **Table 1**) and for the entire CTU culture (cal. 5,400/5,300–2,800/2,700 BCE); colors range from blue (0) to yellow (0.5) and to red (1), or low (0%) to middle (50%) and to high (100%) suitability, respectively; the white dots represent the archaeological sites.

contributions to ECNM in the case of first three cultural phases (36.55–55.3%), the mean annual temperature (MAT 24.5%) in the case of the ECN model of CTU-G4, and the temperature seasonality (TS 41.15%) in the case of the ECN model of the last CTU phase (CTU-G5). The overall analysis of the variable contributions for the entire culture (CTU) niche indicates a

TABLE 6 | Model performance of CTU groups and CTU niches reconstructed using average values of bioclimatic variables provided by CCSM4, MIROC-ESM, and MPI-ESM-P, and DEM-derived terrain variables.

Model range (cal. BCE)	Cultural group	AUC	Omission rate	Proportionally correct	Kappa
5,400/5,300–4,800/4,700	CTU-G1	0.84 (0.032)	0.17 (0.032)	0.83 (0.032)	0.47 (0.056)
4,800/4,700–4,500/4,400	CTU-G2	0.81 (0.018)	0.19 (0.023)	0.81 (0.018)	0.50 (0.078)
4,500/4,400–4,100/4,000	CTU-G3	0.84 (0.035)	0.16 (0.04)	0.83 (0.033)	0.47 (0.058)
4,100/4,000–3,400/3,300	CTU-G4	0.83 (0.027)	0.18 (0.027)	0.83 (0.027)	0.58 (0.04)
3,400/3,300–2,800/2,700	CTU-G5	0.78 (0.012)	0.22 (0.015)	0.78 (0.012)	0.48 (0.033)
5,400/5,300–2,800/2,700	CTU	0.78 (0.003)	0.22 (0.007)	0.78 (0.003)	0.55 (0.007)

The values in parenthesis are the standard deviation.

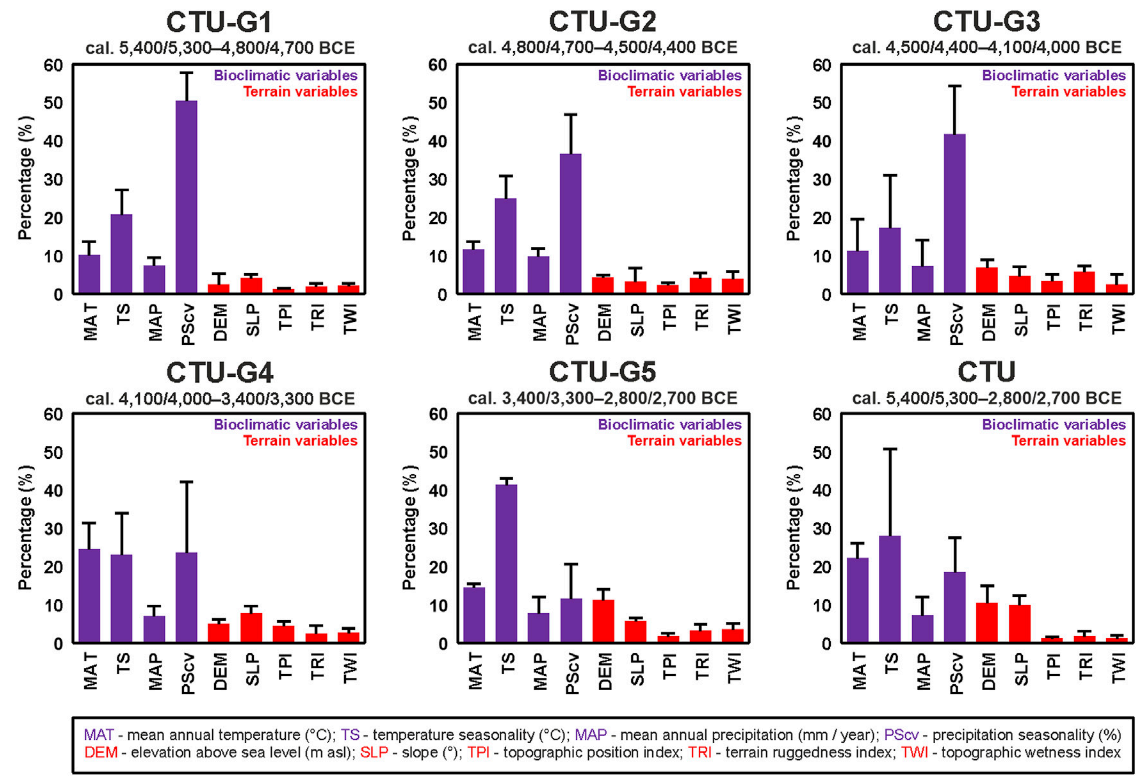

FIGURE 8 | Variable contributions to CTU and CTU groups' niches reconstructed using GCM-derived bioclimatic variables (see **Figure 5**) and DEM-derived terrain variables.

relative balance among MAT (22.07%), TS (28.02%), and PS_{CV} (18.43%) and a significant increase in elevation (DEM—10.41%) and terrain slope (SLP—9.95%) contributions to ECNM compared to each CTU group models (**Figure 8**). Accordingly, the answer to the first question stated at the end of the Introduction section of this study is affirmative: yes, the heterogeneous ecological characteristics in Eastern Europe play a significant role in the evolutionary process of each successive phase of the CTU, but the bioclimatic variables were more important for habitation suitability than terrain variables during the Eneolithic.

Eco-Cultural Niche Modeling Breadth and Overlaps Between Cucuteni–Trypillia Cultural Unity Groups

As we showed before, the AUC values indicate the significant predictive ability (**Table 6**) of the CTU groups' ECNM (**Figure 7**).

TABLE 7 | Niche breadth statistics (after Levins, 1968; Whitford, 2019).

Model range (cal. BCE)	Cultural group	B1 (inverse concentration)	B2 (uncertainty)
5,400/5,300–4,800/4,700	CTU-G1	0.971	0.403
4,800/4,700–4,500/4,400	CTU-G2	0.97	0.411
4,500/4,400–4,100/4,000	CTU-G3	0.972	0.446
4,100/4,000–3,400/3,300	CTU-G4	0.969	0.415
3,400/3,300–2,800/2,700	CTU-G5	0.979	0.549
5,400/5,300–2,800/2,700	CTU	0.98	0.55

TABLE 8 | Schoener's D, *I* statistic, and relative rank niche overlap statistics (0 = no overlap; 1 = perfect overlap) for consecutive CTU groups.

Cultural group	Schoener's D	*I* statistic	Rank
CTU-G1/CTU-G2	0.798 (0.011)	0.962 (0.005)	0.820 (0.020)
CTU-G2/CTU-G3	0.746 (0.008)	0.939 (0.004)	0.734 (0.045)
CTU-G3/CTU-G4	0.754 (0.036)	0.941 (0.012)	0.740 (0.039)
CTU-G4/CTU-G5	0.728 (0.034)	0.932 (0.014)	0.724 (0.027)

The values in parenthesis are the standard deviation.

TABLE 9 | Schoener's D, *I* statistic, and relative rank niche overlap statistics (0 = no overlap; 1 = perfect overlap) between the CTU model and each cultural group.

Cultural group	Schoener's D	*I* statistic	Rank
CTU/CTU-G1	0.728 (0.034)	0.939 (0.014)	0.707 (0.037)
CTU/CTU-G2	0.726 (0.014)	0.935 (0.009)	0.697 (0.019)
CTU/CTU-G3	0.738 (0.063)	0.933 (0.024)	0.644 (0.069)
CTU/CTU-G4	0.788 (0.041)	0.960 (0.012)	0.820 (0.011)
CTU/CTU-G5	0.794 (0.012)	0.958 (0.007)	0.779 (0.024)

The values in parenthesis are the standard deviation.

Although Late Eneolithic groups (CTU-G4 and CTU-G5) have more extended areas with high ecological suitability than Early-to-Middle Eneolithic groups (CTU-G1, CTU-G2, and CTU-G3), the ECNM's predictions yield similar geographic patterns for the entire Cucuteni–Trypillia culture. In other words, the highest niche probability areas for CTU groups are observed in the same regions: 1) along the Eastern Carpathian lowland (Moldavian Plateau–Podillia Upland), particularly in the upper Siret, Prut, and Dniester basins; 2) in the Middle Prut–Dniester–Southern Bug interfluves up to the Volyn Polissya forest zone; and 3) in the Dnieper Upland (Middle Dnieper basin) (see **Figure 1**). Similarly, the outside of these areas, respectively, Black Sea lowland, Danubian Plain, Transylvanian Plateau, and Volyn Polissya forest zone, show a lower niche probability for all the CTU groups, except for the Transylvanian Plateau, where the niche probabilities are higher for Early Eneolithic groups (CTU-G1 and CTU-G2) than for Middle-to-Late Eneolithic groups (CTU-G3, CTU-G4, and CTU-G5). These outcomes indicate that CTU groups generally preferred lowland areas and wide river valleys instead of higher areas for their niche selection, with slightly ecological niche breadth between them (±0.01 inverse concentration; ± 0.15 uncertainty) (**Table 7**).

Statistical analysis of the niche overlap between the successive Cucuteni–Trypillia groups during the Eneolithic reveals that the population did not occupy exclusive ECNM (**Table 8**). Although CTU-G1 and CTU-G2 groups (cal. 5,400/5,300–4,500/4,400 BCE) have a geographic distribution that includes a broader range of terrain conditions (e.g., elevation and terrain slope) compared with CTU-G3, CTU-G4, and CTU-G5 groups (cal. 4,500/4,400–2,800/2,700 BCE), there is a significant overlap in their ECNMs: Schoener's *D* between 0.728 and 0.798; *I* statistic between 0.932 and 0.962; and rank between 0.644 and 0.82. More than that, by analysis of the niche overlaps between the ECNM of the entire Cucuteni–Trypillia culture with the ECN models of each CTU group, the results also indicate significant overlapping: Schoener's *D* between 0.726 and 0.794; *I* statistic between 0.933 and 0.96; and rank between 0.724 and 0.82 (**Table 9**). Accordingly, the answer to the second question is stated at the end of the Introduction section in connection with the fact that the particular trails of the successive CTU groups can be correlated with the modification of habitation practices and that the subsequent occupation of other territories is partially affirmative due to the characteristics of the niche. Therefore, the ECNMs' breadth and overlap results indicate a close connection between habitation practices and human migrations to the other territories but as a consequence of cultural evolution (e.g., population growth) and not as the one related to environmental conditions. We supported this statement because the CTU groups did not have exclusive eco-cultural niches, and the main difference between them was found just in their ECNM breadths and not in their overlap.

Chronological Considerations and Limitation to Eco-Cultural Niche Modeling

The ECNM methodology, which was adopted by archeologists and from the bio-computational architecture to explore the interactions between cultural and natural systems (Banks, 2017), offers a high potential to understand how and when the environmental conditions and ecological dynamics influenced adaptation and movement of prehistoric populations through the inhabited territories (Banks et al., 2008; Banks et al., 2009; d'Errico and Banks, 2013; Vidal-Cordasco and Nuevo-López, 2021; Whitford, 2019). The outcomes obtained in this work reveal that the eco-cultural niche of all the CTU groups significantly overlapped. However, the first three cultural phases from Early-to-Middle Eneolithic (CTU-G1, CTU-G2, and CTU-G3) had slightly more restricted ecological niches than prehistoric populations of the last two CTU groups from

Late Eneolithic (CTU-G4 and CTU-G5). Consequently, the population which belonged to the Precucuteni I, II, and III/ Trypillia A (1–2), Cucuteni A (1–4)/Trypillia BI, and Cucuteni A–B (1–2)/Trypillia BI/BII cultural stages had higher probabilities of occupying cooler and drier environments like the sub-Carpathians or inner landscapes of the Eastern Carpathians. Conversely, the population which belonged to the Cucuteni B (1–3)/Trypillia BII + CI and Erbiceni/Trypillia CII-γII groups had ecological niches that were more restricted to Eastern Carpathian areas. However, there is a higher probability of occupying the eastern steppe territories between the Middle Dnieper basin and Black Sea lowlands (**Figure 7**). These results have significant implications for understanding the geographical range and distribution of the last great Chalcolithic society of Old Europe (Chapman et al., 2019).

Overall, according to the large number of CTU sites discovered in Eastern Europe, it might be suggested that the populations belonging to different Eneolithic groups could have adapted to different ecological settings. However, the results obtained in this study suggest that CTU groups did not occupy exclusive ecological niches and that the difference in their geographic distribution is rather a consequence of their ecological niche breadths. Accordingly, although the most suitable areas overlap with all the CTU groups, respectively, Siret, Prut, and Dniester watersheds, the broader ecological niche breadth of the last two CTU groups probably made it easier for them to occupy large territories, including Southern Bug and Dniester watersheds. Therefore, the increase in population during the Late Eneolithic period probably allowed the expansion of the ecological niches and reduced their vulnerability to changes in the ecosystems. On the other hand, the larger niche breadth of the CTU-G5 group may be essential to understanding the transition of the Cucuteni–Trypillia culture to the Early Bronze Age (EBA).

The ECNM methodology used in this approach has some limitations that should be explored in future studies. We treated Cucuteni–Trypillia phases as a uniform culture in Eastern Europe, but there were some differences, especially among the Ariușd, Cucuteni, Eastern Tripolye (ETC) groups, and Western Tripolye (WTC) groups. Therefore, it would be helpful for future works to expand this research by focusing on more specific geographic regions for these two cultural stages and comparing the resulting niches. Also, it should be considered that despite ECNM constituting a well-established approach, all the reconstructed niches are partial because they must focus only on a limited number of ecological variables. It would be desirable that future works based on ECNM methodology compare reconstructed niches presented here with the distribution models of some vegetation or animal species consumed by Eneolithic groups.

CONCLUSION

In this study, we applied for the first time the ECNM methodology to explore the socio-ecological dynamics inside the Cucuteni–Trypillia culture (CTU), which flourished in Eastern Europe during the Eneolithic (cal. 5,400/5,300–2,800/2,700 BCE). The interpretation of the eco-cultural niche breadth and overlaps of the successive phases has provided valuable insight into the relationship between the culture (site distributions) and ecology (bioclimatic and terrain variables) and its impacts on the cultural development process. Therefore, the ECNM significantly overlapped, and the expansion trend of the last two CTU groups (Late Eneolithic—cal. 4,100/4,000–2,800/2,700 BCE) into the northeastern steppe regions or even to the Black Sea lowland was not due to ecological niche differences but rather a result of other cultural factors (e.g., population growth, subsistence agriculture, and mixed with other cultures). However, the first three CTU groups (Early and Middle Eneolithic—cal. 5,400/ 5,300–4,100/4,000 BCE) had more restricted ecological niches than the last two groups (Last Eneolithic). In other words, the broader ecological niches of the last CTU groups probably allowed them to occupy large steppe territories and exclude the inner areas of Eastern Carpathians, whereas the narrower eco-cultural niche breadth of the first CTU groups made the prehistoric population more vulnerable to the climatic changes (e.g., temperature seasonality variation) that affect the northeastern steppe ecosystems. These results have significant implications for understanding the geographical range and distribution of the last great Chalcolithic society of Old Europe and contribute to the characterization of ecological niches they have exploited during the cultural evolutionary process.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material; further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

All the authors have equal contributions in conceptualization, methodology and formal analysis, data validation, investigation, data curation, writing, original draft preparation, and reviewing and editing of the manuscript.

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GLOSSARY

GIS Geographic Information System
ECNM eco-cultural niche modeling
ENM ecological niche modeling
NCT niche construction theory
BCE before common era
CTU Cucuteni–Trypillia cultural unity
CTU-G1 Group 1: Precucuteni I, II, III/Trypillia A (Early Eneolithic)
CTU-G2 Group 2: Cucuteni A (1–4)/Trypillia BI (Middle Eneolithic)
CTU-G3 Group 3: Cucuteni A-B (1–2)/Trypillia BI/BII (Middle Eneolithic)
CTU-G4 Group 4: Cucuteni B (1–3)/Trypillia BII + CI (Late Eneolithic)
CTU-G5 Group 5: Trypillia CII-γII (Late Eneolithic)
EENSR Eastern European Neo-Eneolithic Sites Repository
RPTK Register of Tripoli Culture Monuments–Ukraine
RMRM Register of Monuments of the Republic of Moldova
RAN National Archaeological Record of Romania
ETC Ariuşd, Cucuteni, and Eastern Tripolye cultures
WTC Western Tripolye culture
DEM digital elevation model
SLP terrain slope
TPI topographic position index
TRI terrain ruggedness index
TWI topographic wetness index
MAT mean annual temperature
TS temperature seasonality
TAR temperature annual range
MAP mean annual precipitation
PScv precipitation seasonality–coefficient of variation
GCM global climatic models
CCSM4 Community Climate System Model version 4
MIROC-ESM Model for Interdisciplinary Research on Climate
MPI-ESM-P Max Planck Institute Earth system model