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Invited Paper

Spatial resilience and population replacement in Europe during MIS 3: a comparative study of Neanderthals and *H. sapiens*

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ABSTRACT

Homo sapiens dispersed out of Africa several times during the Late Pleistocene. The most recent dispersal event, which began around 60,000 years ago, resulted in the permanent establishment of Sapiens populations in Europe, followed by the disappearance of Neanderthals from the archaeological record. Various hypotheses suggest that the process of population replacement in Europe was influenced by climate change, habitat dynamics, demographic processes, and/or competitive exclusion. To test these hypotheses, we use habitat suitability modeling and GIS tools to predict the optimal distribution of Neanderthal and Aurignacian populations in Europe during stadial and interstadial events of Marine Isotope Stage 3 (MIS 3) and reconstruct their regional networks. The models show that while relatively more suitable habitat was available for *Homo sapiens* under interstadial conditions, both groups were affected by climate change resulting in shifts in the location of optimal regions and concomitant changes in the social networks that connected them.

Our analysis indicates that optimally suitable habitat persisted across the potential ranges of both species despite climate change. Climate stress alone is not indicated as a cause of Neanderthal's extinction, therefore. Several "core" regions are identified that could have sustained a pattern of demographic resilience, allowing populations to rebound and re-expand during climate upturns, notably in southwestern Europe and, in the case of Neanderthals, in southern Iberia. The optimal regions and the networks they form indicate a potential for interaction between Neanderthals and Sapiens across Europe. While their ranges overlap, however, there are subtle differences in habitat preference that mitigate the potential impact of interactions, suggesting that competition for resources may not have been the primary cause of Neanderthal extinction. The results also suggest regional differences in the combination of stressors that could have influenced Neanderthal extinction, with Sapiens potentially playing a more active role in Western Europe, where regional overlaps impinge on the "core" regions. In Southeastern Europe, where regional connection within the Neanderthal network were relatively tenuous, Neanderthal groups may have been more vulnerable to random events and demographic pressures, including genetic assimilation.

A more complex interplay of climate change, population dynamics and demographic factors is suggested to have contributed to the eventual disappearance of the Neanderthals. Ultimately, the study suggests that the process of population replacement in Europe is the result of the complex and regionally differentiated interplay of climate, geography, demography and interspecific interactions rather than a homogeneous, climate-driven process.

1. Introduction

The hominin lineage diversified during the Middle Pleistocene, resulting in the emergence of modern humans in Africa (*Homo sapiens*) and two archaic human groups in Eurasia: the Neanderthals (*H. neandertalensis*) and the Denisovans. During the Late Pleistocene, archaic human populations were replaced by *H. sapiens* on a global scale. Various hypotheses have been proposed to explain this loss of diversity,

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which is correlated with a series of modern human dispersals out of Africa the most recent of which, at the beginning of Marine Isotope Stage 3 (MIS 3), around 60,000 years ago (60 ka) (Stringer and Crété, 2022), lead to the permanent presence of *H. sapiens* (henceforth Sapiens) populations in Europe by ~45 ka. Testing these hypotheses requires an understanding of the dynamics of human dispersal, the spatial distribution of suitable habitat and the respective roles of habitat selection and climate change in shaping them.

Habitat suitability modelling (also known as species distribution or niche modelling) is an ecological technique for predicting the potential distribution of a given taxon from a set of occurrences. It is used in archaeological research to predict the archaeological potential of survey regions, describe the potential distribution of past human populations as a function of palaeoenvironmental variables, and identify those variables that may have shaped the human niche. In this research, we build upon two previous studies that created SDMs (habitat suitability models) to investigate the impact of strongly contrasting climate conditions on the distribution of Neanderthal (Albouy et al., 2024) and Aurignacian populations (Paquin et al., 2024) in Europe during MIS 3. In what follows we develop a novel workflow that uses geospatial tools and habitat suitability (HS) models to compare the impact of climate change on different hominin groups and make predictions about their potential distribution on the landscape and the structure of their social networks with implications for larger debates concerning patterns of dispersal, population replacement.

1.1. Human diversity in Eurasia

The diversification of the human lineage during the Middle Pleistocene is strongly patterned, geographically and chronologically, which suggests that adaptive processes were operating at a similar pace on a geographically segmented metapopulation. Neanderthals emerged in the fossil record of Europe sometime between 300,000 and 400,000 years ago (300-400 ka)(Rosas et al., 2022) and disappeared ~41 ka (Higham et al., 2014; Devièse et al., 2021). Their geographic range, centered in Western Europe, once extended as far as the Levant and Eastern Siberia (Pomeroy, 2023). Denisovans are relatively poorly documented in the archaeological record and skeletal remains have only been recovered from two locations in Asia so far (Chen et al., 2019; Derevianko et al., 2020). Genetic data suggests that they diverged from Neanderthals roughly 400 ka (Liu et al., 2021)and ranged from Siberia to Southeast Asia (Sawafuji et al., 2024), partially overlapping with Neanderthals to the West, where the two populations interbred (Slon et al., 2018).

H. sapiens first appears in the fossil record of North Africa around 315 ka, having apparently evolved from a pan-African metapopulation (Hublin et al., 2017; Scerri et al., 2018). Evidence from the Levant (Hershkovitz et al., 2018) and Southeast Europe (Harvati et al., 2019) indicates that Sapiens groups began dispersing out of Africa prior to 200 ka, but these early dispersals were likely intermittent and limited in scope. Archaeological and genetic data indicate that a more sustained, and ultimately more successful wave of dispersal out of Africa was initiated around 60 ka (Stringer and Crété, 2022), a suggestion supported by chronological evidence for the appearance of early/initial Upper Palaeolithic assemblages at various locations in Europe, e.g. (Slimak et al., 2022; Sánchez-Yustos et al., 2024). This dispersal culminated with the spread of Aurignacian technology around 41 ka, ushering in the Middle to Upper Palaeolithic transition (Hublin et al., 2020).

1.2. Population replacement and the Middle to Upper Palaeolithic transition

Historically, the Middle to Upper Palaeolithic transition in Europe, identifiable in the archaeological record as a marked shift in technology, was thought to correlate with the replacement of the Neanderthals and the initial arrival of *H. sapiens* groups (Mellars, 1992). Although recent evidence indicates that the situation was more complex and drawn out in time, competitive exclusion is still invoked as a potential driver of population replacement, e.g., (Melchionna et al., 2018; Timmermann, 2020). There have been numerous attempts to identify the technological, cognitive and/or social variables that might have conferred an adaptive advantage on Sapiens. New data and close scrutiny of the archaeological record has revealed that Neanderthals were equally capable of developing novel technological and organisational solutions however (Conard et al., 2015), including the adoption of composite tools (Mateo-Lomba et al., 2024), symbolic behaviour (Zilhão et al., 2010; Majkić et al., 2017; Hoffmann et al., 2018) and logistical mobility (Spinapolice, 2012, Moncel et al., 2019).

Alternative explanations for the replacement of Neanderthal populations by Sapiens include demographic processes (Kolodny and Feldman, 2017, Degioanni et al., 2019), climate stress (Sepulchre et al., 2007)and finally, spatially differentiated combinations of stressors (Haws et al., 2020; Vahdati et al., 2022). For example, it has been suggested that Late Pleistocene climate cycles may have repeatedly challenged Neanderthal populations (Bradtmöller et al., 2012; Klein et al., 2023), leading to a series of population contractions followed by demographic rebound when conditions improved. This pattern of long-term demographic resilience was hypothetically disrupted by the influx of Sapiens populations, whose dispersals into Western Eurasia are thought to coincide with climate upturns, e.g., (Müller et al., 2011; Timmermann, 2020). In this scenario, instead of rebounding from climate-driven decline Neanderthal populations could have been absorbed into an expanding Sapiens gene pool (Stringer and Crété, 2022).

In a related but different scenario, genetic (Lalueza-Fox et al., 2011; Prufer et al., 2014; Skov et al., 2020) and morphological evidence (Trinkaus, 2018, Ríos et al., 2019; Urciuoli et al., 2025) suggest that population turnover and the repeated cycles of expansion and contraction of Neanderthal populations left them with low genetic variability. Some populations may have been isolated for tens of thousands of years (Slimak et al., 2024). Coupled with smaller effective population and social group sizes (Lalueza-Fox et al., 2011; Bocquet-Appel and Degioanni, 2013, Castellano et al., 2014; Mafessoni and Prüfer, 2017) than Sapiens, this lack of genetic diversity within and between populations may have left Neanderthals more vulnerable to extinction by the time Sapiens successfully established in Eurasia (e.g. (French, 2016, Vaesen et al., 2019),).

Competing hypotheses about human dispersal and population replacement in Europe can be addressed using species distribution models (SDMs). The spatiotemporal distribution of suitable habitat exerts an influence on population structure, e.g., promoting the formation of larger groups or longer residence times or conversely, triggering mobility and encouraging exploration to identify more suitable regions. The spatial analysis of HS models, therefore, allows us to build hypotheses concerning when and where Neanderthals and Sapiens may have overlapped and potentially interacted in time and space, with implications for several of the hypotheses cited above. Quantitative analyses of HS models also allows us to assess whether Sapiens populations were more spatially resilient than Neanderthals, which could be construed as conferring a competitive advantage thus contributing to ongoing debates about the loss of human diversity during the Late Pleistocene.

1.3. Species distribution models

The use of modelling techniques to reconstruct the spatial distribution of humans in the past is not new. Archaeologists use GIS tools to develop models of site location, for example, that are widely discussed and reviewed in the literature, e.g., (Kvamme, 2006; McCoy and Ladefoged, 2009; Verhagen and Whitley, 2012). These models are typically designed using environmental and taphonomic variables for the purpose

of predicting the archaeological potential of a given location. More recently, there has been a marked increase in the use of Species Distribution Models (SDMs) as a tool for investigating larger-scale processes such as hominin dispersals, human/environmental interactions and the impact of climate change (Timmermann et al., 2024).

SDMs use locational information and environmental variables to define what is variously described as the "niche", "ecocultural niche", "climate niche", "climate envelope" or "suitable habitat" of an organism and map its distribution in space. The extent to which the models reflect an organism's niche is subject to debate given the limited number of variables available and frequent lack of information about species interactions (Elith and Leathwick, 2009). In what follows we use the terms "habitat" and "range" because we recognise that, like most archaeological SDMs, our models don't address the full spectrum of multidimensional variables and relations implied by use of the term "ecological niche" (e.g. (Pianka, 1983; Soberon and Peterson, 2005; Soberón, 2007)). Nevertheless, Elith & Leathwick (2009) rightfully argue that models are ultimately used to map out favourable habitats for a given species under the assumption that the explanatory variables are sufficient to predict habitat suitability. Since we have framed our hypotheses in terms that are explicitly spatial and temporal, the spatial output of these models is the focus of this work.

Ecological niche models (e.g., Soberon and Peterson, 2005) can also be used to measure the overlap of species in the space defined by environmental variables, this information is less relevant to our hypotheses. First, investigating overlap in the environmental spaces assumes that SDMs provide an accurate and exhaustive estimate of the niche of the species, which is unlikely given the potentially large disconnect between the fundamental niche and the resultant species distributions, especially when the later are shaped by demographic processes (Pagel et al., 2020). Because these models are trained on observed spatial data, they more accurately provide an estimate of the spatial occupancy of the species, itself loosely related to the realized niche. Second, areas of the space defined by environmental variables in which species have strong overlap only really matter if this overlap (i) is found to be materialized in space due to the spatial distribution of predictors and (ii) occurs in areas where the predicted habitat suitability is high enough that the local patch is likely to have been favourable to at least one species. Since the testing of our hypotheses only requires access to the predicted habitat suitability in a spatial context, therefore, we do not model overlap in the environmental space.

A growing number of SDMs, variously described as "climate envelope", "niche", "ecocultural niche" or "habitat suitability" models, describe the distribution of Neanderthal (Banks et al., 2008, d'Errico et al., 2008; Gilpin et al., 2016; Benito et al., 2017; Melchionna et al., 2018; Timmermann, 2020, Yousefi et al., 2020; Banks et al., 2021; Yaworsky et al., 2024; Degioanni et al., 2025)) and Aurignacian populations ((Banks et al., 2013; Kondo et al., 2018; Shao et al., 2021; Shao et al., 2024)) in Europe; some of the models are explicitly designed to compare the two taxa (Klein et al., 2023)). Differences between the models reflect differences in algorithm selection (e.g., GLM, GARP, MAXENT, RF), the climate model selected for use, the spatial and chronological resolution of the models, and the selection of predictive variables and archaeological observations used as input to the models.

Candidate predictors typically include average and minimum annual temperature and precipitation values, and topographic variables such as slope and elevation. The main difference between our approach and most of the models cited above is our use of an iterative modelling process to identify the minimum set of relevant variables from an expanded library of candidate variables while optimising the predictive power of the models. Candidate variables include indices of climate variability because earlier work has demonstrated that these can be relevant factors in human habitat selection (Burke et al., 2017; Albouy et al., 2024; Paquin et al., 2024). Finally, the same modelling workflow was used to model habitat suitability for Sapiens and Neanderthal, which makes direct comparisons between the models possible.

2. Materials and methods

2.1. Timeframe and preliminary models

The timeframe of interest, from ~60 to 33.7 ka, corresponds to the period during which Sapiens populations established a permanent presence in Europe (Posth et al., 2016) and Neanderthal populations disappear from the archaeological record (Wood et al., 2013). Ten stadial/interstadial cycles occurred during this timeframe, from Greenland interstadial 17 (GI 17) to Greenland stadial 7 (GS 7), highlighting the climate instability that characterises MIS3 (Peral et al., 2024) .

The four, previously published habitat suitability (HS) models used in this analysis (Fig. 1) describe the distribution of suitable habitat for Sapiens (Paquin et al., 2024) and Neanderthal (Albouy et al., 2024) groups under interstadial (GI) and stadial (GS) conditions of MIS 3. Models were obtained from: Albouy, B., 2025 (https://doi.org/10.5683/SP3/NPWF28, Borealis, V1) and Paquin, S., 2025 (https://doi.org/10.5683/SP3/VXBMSW, Borealis, V1). The models use archaeological data, pseudo-absences and a suite of geographical variables, climate variables and climate variability indices in addition to high-resolution climatology. The screening process for species occurrences (archaeological sites) was based on chronological and paleoenvironmental data (for full details see: Paquin et al., 2023; Albouy et al., 2023). The Neanderthal dataset (dated GI 17 to GS 9) is associated with the Mousterian technocomplex and the Sapiens dataset (GI-12 to GS-7) only includes Aurignacian sites. Chatelperonian, Proto-Aurignacian and Initial Upper Palaeolithic sites are deliberately excluded since they are not unambiguously attributed to species (Gravina et al., 2018; Gravina et al., 2022; Zilhão et al., 2024).

The models were produced using Random Forest (RF), a non-parametric algorithm for regression and variable selection based on decision trees (Breiman, 2001) that is well-suited for use with non-linear relationships, large numbers of predictors and small numbers of presences (Genuer et al., 2010; Grömping, 2009). Used with cross-validation, it is a technique that overcomes overfitting in comparison with other methods (e.g. (Fox et al., 2017),) that is not sensitive to model tuning (Freeman et al., 2016). Standard data preparation and modelling procedures were followed as described briefly below and more fully elsewhere (Paquin et al., 2023, 2024; Albouy et al., 2023, 2024; Burke et al., 2017).

Masks were applied to the spatial domain to avoid generating false pseudoabsences and confounding the SDMs. Ice sheets were masked out using the maximum distribution of LGM ice (consistent with the forcings used in the climate model) and modern coastlines were used to mask coastal regions.

An Atmosphere-Ocean General Circulation Model, IPSL-CM5A-LR (Dufresne et al., 2013), run using the PMIP3 protocol (Kageyama et al., 2013), was used to simulate stadial and interstadial conditions during MIS 3 at a spatial resolution of ~1.9° latitude and 3.75° longitude. 50-year time series of monthly values were extracted from the simulations and statistically downscaled to 15 km × 15 km resolution using a Generalized Additive Model (Vrac et al., 2007; Vrac, 2024). The downscaled climatology was used to calculate average, minimum and maximum values for precipitation and temperature at monthly, seasonal and annual scales, and climate variability indices. Topographic variables (elevation, slope) were derived from the SRTM 90 m digital elevation model (Farr et al., 2007) and added to the list of candidate predictors. This produced a stack of rasters from which values were extracted (using arcGIS© software by ESRI) using archaeological sites as presences and a library of pseudo-absences randomly generated from a 1 × 1 km grid feature.

The resulting set of variables was used as input in an iterative modelling workflow using the RF function from the "caret" package in R (Team, 2024). Highly correlated variables (>0.8) (Dormann et al., 2013) were eliminated beforehand using the *find correlation* function of the "caret" R package, producing a definitive list of candidate variables. The

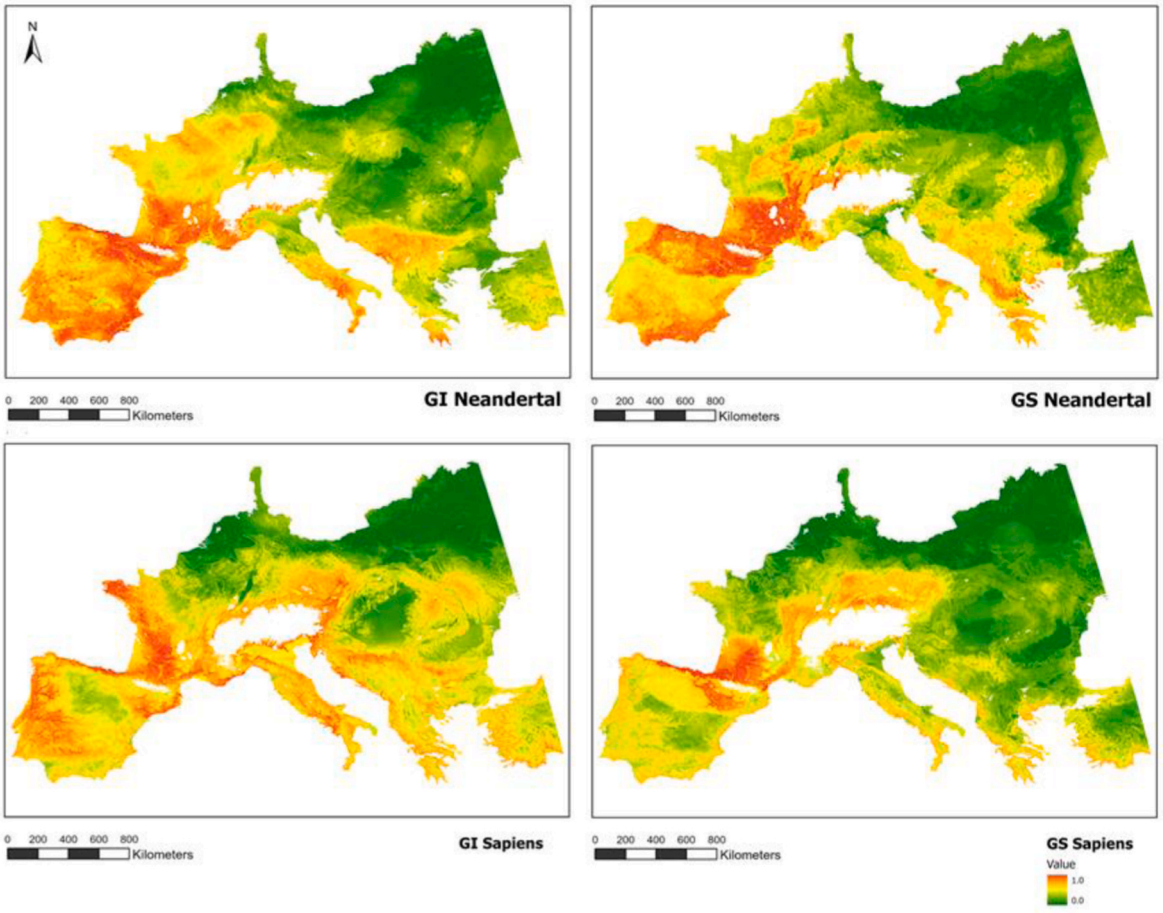

Fig. 1. Habitat suitability models used in this analysis, including: Neanderthal models and Sapiens models under contrasting climate conditions (GS: stadial/GI: interstadial).

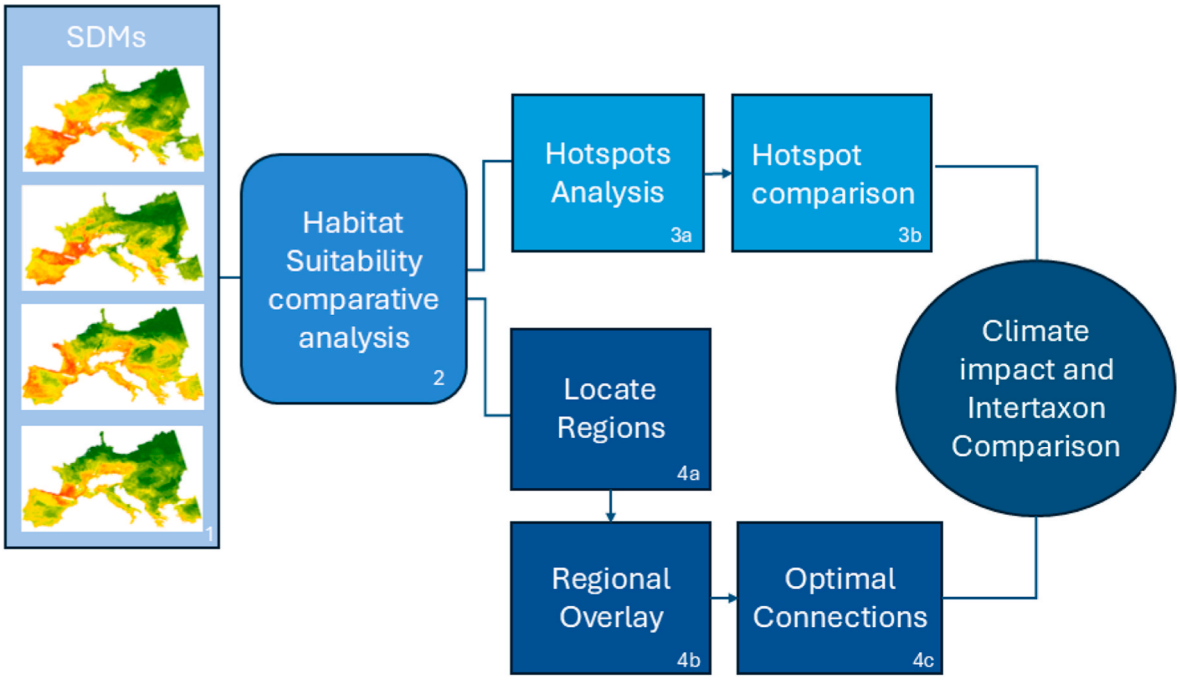

Fig. 2. The workflow developed for this research to compare multiple HS models.

RF function was then run iteratively, with 10-fold cross validation, producing a series of models with decreasing numbers of variables, each

of which represents the average of 100 runs. The Variable Importance index (VI) was used to eliminate the 20% least important variables at each step following Genuer et al. (2010). Model Accuracy and the OOB rate (defined as one minus the out of bag accuracy) were used jointly to select the best performing model.

2.2. Modelling groups and territories

Archaeologists use ethnographic and archaeological data to model the spatial distribution of past human populations. The ethnographic literature documents the multi-tiered structure of hunter-gatherer populations (see below), the fluid nature of social groups and the important role played by individual mobility, with consequences for the design of archaeological models (Burke, 2021). The complex interplay of historical, social and adaptive processes operating at different spatial and temporal scales influences the size and spatial distribution of hunter-gatherer groups. Broad generalisations useful both for interpreting the archaeological record and studying the spatial behaviour of past human groups are possible, however.

A recurring pattern in the ethnographic record is the size of the social group at local, regional and supra-regional scales of organisation across cultures, the so-called "magic numbers" (see (Gamble, 2000; French, 2021): and references cited therein). At the local scale, groups tend to be formed of 25 individuals. Many, if not most, archaeological sites probably reflect the activities of these groups. Individuals moving between local groups form intersecting social networks (Myers, 1986; Guenther, 1996, Bird et al., 2019), i.e., regional bands, numbering ~500 individuals. Regional bands are visible in the archaeological record when they form coresident groups, or "aggregation sites" (Conkey, 1980; Gravel-Miguel and Wren, 2018) and when shared forms of material culture expression are identified. The next, and highest level of social integration, the "supra-regional" band or linguistic group, does not necessarily emerge and is difficult to sustain (Myers, 1986; Guenther, 1996). In this research we are primarily interested in the regional scale, i.e., the "regional band".

2.3. Spatial analyses

This research uses geospatial techniques to compare four HS models (Fig. 2). HS models are used in conservation ecology to identify key regions within the potential range of a species and corridors of movement between them that ensure the long-term survival of a species (Powers and Jetz, 2019; Suzzi-Simmons and Devarajan 2023). ESRI has developed several geoprocessing tools in ArcPRO for this purpose, including the Locate Regions tool (https://pro.arcgis.com/en/pro-app/latest/tool-reference/spatial-analyst/how-locate-regions-works.htm) and the Optimal Regions Connections tool (https://pro.arcgis.com/en/pro-app/latest/tool-reference/spatial-analyst/connect-regions-with-the-optimal-network.htm) whose use is more fully described below.

First, the four HS models were reclassified into 10% bins and exploratory statistics generated (Fig. 2: box 2) and resampled to the native resolution of the climatology, i.e., 15 x 15 km. This step provides an overview of the potential of the spatial domain to provide suitable habitat for Sapiens and Neanderthal groups under contrasting climate conditions. A Hot Spot analysis was then undertaken in arcPRO 3.4 ©ESRI using the Hot Spots tool (Spatial Statistics) which uses the Getis-Ord Gi* statistic to identify significant clusters of contiguous cells with high (hot) and low (cold) HS values (Fig. 2: box 3a). The Hot Spot Comparison tool was then used to compare the distribution of Hot Spots and calculate global similarity values under contrasting climate conditions (GI/GS) and between taxa (Neanderthal/Sapiens) (Fig. 2: box 3b). The Conceptualization of Spatial relationships parameter for this tool was set to inverse distance, the distance method to Euclidian distance and the distance band was set to 200 km.

Next, we focussed on locating regions within the spatial domain large enough to sustain a regional band (Fig. 2: box 4a-c). The Locate Regions tool (Spatial Analyst) was used to identify regions of interest based on habitat suitability (HS). The tool grows a specified number of regions selected on the basis of their average HS value. Parameters set by the user include the minimum and maximum area, the shape and the number of regions required.

To estimate the required parameters for the Locate Regions tool we adopted a heuristic model developed by Whallon (2006), based on Weniger's work on the spatial organisation of Magdalenian hunter-gatherers in Central Europe (Weniger, 1987). Thus, the estimated area occupied by a local group (the "minimal band") is 2500 km^2 which scales up to an area of 47500 km^2 for a regional band, aka the "maximal" band (Whallon, 2006: Fig. 4). These estimates are comparable with the size of the territories occupied by ethnographically known groups of hunter-gatherers in the Northern hemisphere (Binford, 2001; Kelly, 2013) once the appropriate filters are applied to account for differences in environmental context and modes of subsistence. They are also comparable to archaeological estimates for metapopulation size for both Sapiens and Neanderthals during the timeframe of interest, e.g., (Bocquet-Appel et al., 2005; Bocquet-Appel and Degioanni, 2013, Degioanni et al., 2019; Schmidt and Zimmermann, 2019). Finally, although Whallon's model was developed using material culture transfer data dating to the Postglacial, it is compatible with local and "exotic" lithic transfer distances reported in the archaeological literature for MIS 3, e.g., Feblot-Augustin (1999), Schmidt and Zimmermann (2019).

The minimum and maximum area parameter was set to 17,500 km^2 and 47,500 km^2 respectively, corresponding to Tier 1 and Tier 2 regional band territories as suggested in Whallon's heuristic model. We chose not to parameterise the minimum or maximum distance between regions in the absence of *a priori* information about group spacing, however. The region shape parameter is circular by default but we set the Shape/Utility trade-off to 25% to allow HS values to influence the shape, producing regions that more closely reflect local topography.

The number of regions parameter required additional testing, because archaeological estimates of the size of Palaeolithic populations vary by several orders of magnitude, e.g., Bocquet-Appel and Degioanni (2013). In the absence of realistic estimates of population size, which would have enabled us to set the number of regions the tool could produce, we tested 4 regional scenarios (5, 10, 15 and 20 regions) for each combination of species and climate event. Next, we identified the number of regions with average utility scores clearly demarcated from background HS values using two thresholds: a) average HS scores >1

Table 1
Number of regions within each scenario with average HS values more than one standard distribution above the mean (>1 s.d.) or within the third quartile (Q3).

N REGIONS	>1 s.d.	Q3
SAPIENS GI		
20 reg	9	15
15 reg	8	11
10 reg	8	10
5 reg	5	5
SAPIENS GS		
20 reg	8	10
15 reg	8	9*
10 reg	8	9*
5 reg	5	5
NEANDERTHAL GI		
20 reg	8	9
15 reg	8	9
10 reg	8	9
5 reg	5	5
NEANDERTHAL GS		
20 reg	7	9
15 reg	7	9
10 reg	7	9
5 reg	5	5
*10th region is within 0.003 of Q3		

standard deviation above the mean; and b) HS scores > Q3 (the third quartile) in each scenario (Table 1). The scenario with the highest proportion of regions within these thresholds, for all combinations, is N = 10 regions and the number of regions parameter was set accordingly.

Once the Locate Region tool was run, the Overlay Analysis toolset (Analysis toolbox) was used to assess the degree to which the predicted regions overlap for each combination of climate conditions (GI/GS) and species (Neanderthal/Sapiens). Regional overlaps between GS and GI events measures the spatial persistence of a species' range (their spatial resilience). Overlaps between Neanderthal and Sapiens regions measures the potential for interaction during each climate event.

Finally, the Optimal Regions Connections tool (Spatial Analyst) was used to connect the regions and identify the optimum connection between each region and its neighbours for the various test conditions. The (inverse) HS models were used as cost surfaces for this analysis, the maximum extent of ice sheets during the Last Glacial was used as a barrier and current coastlines used as a mask. HS in this instance serves as a proxy for ease of travel, assuming that movement occurred over relatively long periods of time during which resources would have been required. The mapped connections represent the optimal communication network between the hypothetical habitats (regions), i.e., the ideal social network assuming the environment was being optimally exploited.

3. Results

3.1. Statistical comparisons

Fig. 3 compares the availability of suitable habitat for Sapiens and Neanderthal groups as a proportion of the total spatial domain during GI and GS events. The intertaxonomic comparison (Fig. 3: left panel) highlights important differences during interstadials (GI events), when the proportion of relatively suitable habitat favours Sapiens. The cumulative frequencies of HS values for the four models under consideration (Fig. 3: right panel) confirm: a) that the proportion of the total spatial domain that is relatively suitable for Neanderthals remains stable during GS/GI events albeit with a slight amelioration during interstadials; and b) that the same can't be said for Sapiens groups who would have been at a slight disadvantage relative to Neanderthals during stadial events (HSGS) but enjoyed a relative advantage during interstadials (HSGI).

A chi-square test of the cumulative frequencies of HS scores for the four test conditions confirms the existence of intertaxonomic differences in response to climate change (GI/GS) and a greater contrast between Neanderthals and Sapiens responses during interstadials.

3.2. Hot Spots analysis

Clusters ("Hot Spots") of highly unfavourable habitat occur primarily in Northern Europe (on the periphery of the ice sheets) for both groups during GS and GI events; Fig. the distribution of highly favourable Hot Spots is skewed in favour of SW Europe (Fig. 4). During the transition from GI to GS events the distribution of favourable Hot Spots is more spatially focussed on SW Europe (including Franco-Cantabria, the Ebro valley and the southern Rhone valley, and southern Iberia for Neanderthal groups).

The spatial persistence of favourable Hot Spots during contrasting climate events suggests a potential for long-term residential stability. Persistent Hot Spots can be designated as core zones, i.e., regions where relatively stable populations could have persisted over time, serving as sources for the repopulation of smaller, less persistent habitats as climate conditions changed (e.g., Wren and Burke, 2019).

The Hot Spot Analysis Comparison tool measures the overall similarity between Hot Spot results layers (Fig. 5). The distribution of favourable Hot Spots for Sapiens and Neanderthals is more similar during the spatially focussed stadials (Fig. 5: left panel) than during interstadials (Fig. 5: right panel).

Shifts in the significance level of Hot Spot results between Neanderthals compared with Sapiens (Fig. 6) are influenced by the shift in location of suitable Sapiens habitat during GI events to include the Atlantic coast (Normandy) and Portugal, in addition to small gains in the southern and southeastern Alps and Italy. Differences during GS events are influenced by a shift in Sapiens habitat away from the Atlantic coast towards peri-Alpine regions and small gains in the Balkan Peninsula (Fig. 4; right-hand panels).

These observations are broadly confirmed by the distribution of optimal regions (section 3.3, below) by taxon and by climate event.

3.3. Optimal regions analysis

We created four scenarios for each of the four possible combinations of climate interval and taxon using the Locate Regions tool (Spatial Analyst) in ArcPro. After testing 5, 10, 15 and 20 regions using the HS surface (SI Fig.s 1-4) parameters were set to 10 regions (see "Methods"). The 10-region scenarios are illustrated below (Fig. 7) with the results of the Optimal Region Connections tool. The core areas identified using the Hot Spots tool (Section 3.2, above) are consistent with the results of the Locate Regions tool, which seeks to maximise mean HS values during the region selection process.

The regions produced by the Locate Regions tool for all of the 10-region scenarios include areas previously identified as persistent Hot

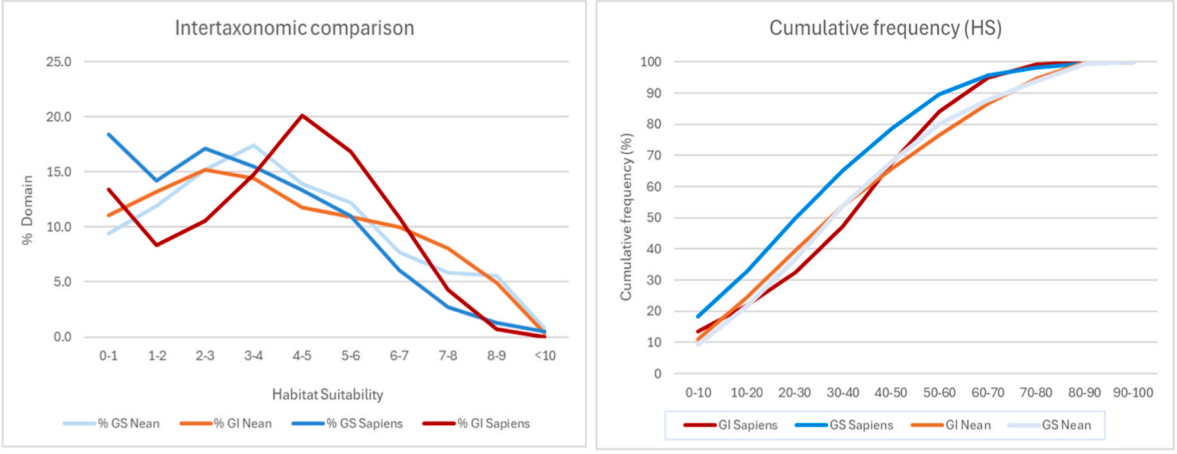

Fig. 3. Left panel: percentage of the total domain as a function of binned HS scores for Neanderthal (GS Nean/GI_Nean) and Sapiens (GS Sapiens/GI Sapiens). Right panel: cumulative frequencies of HS scores during stadial and interstadial events for Neanderthal (Nean_GS/GI) and Sapiens (HSGS/HSGI).

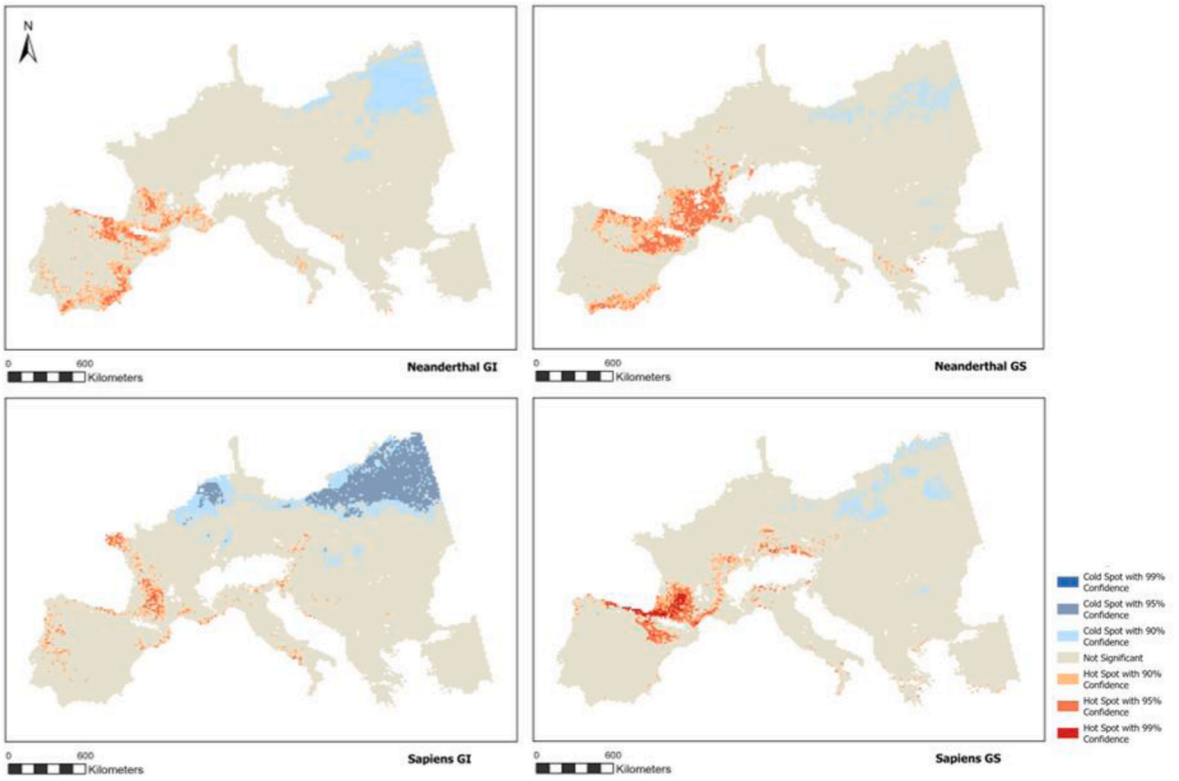

Fig. 4. Hot Spot analysis of the HS models for the four possible combinations of climate cycle (GS/GI) and taxon (Neanderthal/Sapiens).

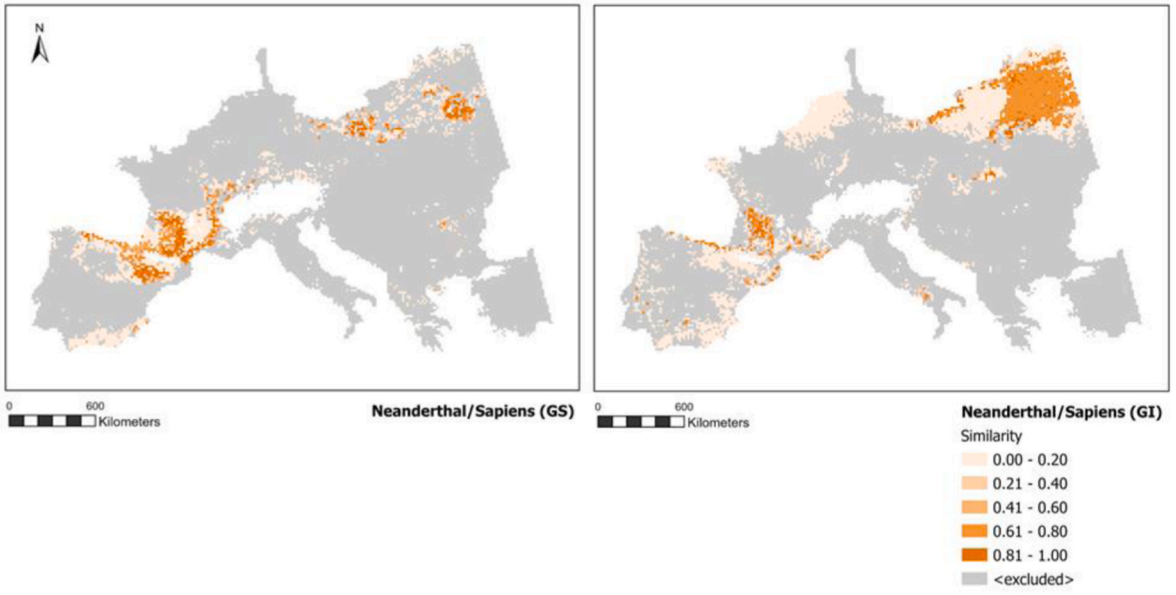

Fig. 5. Hot Spots analysis: similarity between Hot Spot results for Neanderthals and Sapiens under stadial (GS) and interstadial (GI) conditions.

Spots, e.g., Franco-Cantabria and the Ebro valley, in addition to new areas such as the southern Italian Peninsula (Fig. 7). The Neanderthal regional pattern is remarkably consistent during GI and GS events: optimal regions persist in Western Europe (Normandy), Central Europe and in southern Italy as well as the Balkan Peninsula (Fig. 7: upper panels). The most notable shift in the distribution of Neanderthal regions occurs during the transition to GS conditions in the center of the Iberian Peninsula (Fig. 7: top right panel). Otherwise, there is no indication that climate-driven changes severely affected the availability or distribution of suitable habitat.

For Sapiens, optimal regions persist in Franco-Cantabria, coastal Iberia (excluding the south) and the southern Rhone valley, and include the Italian Peninsula (Liguria, Lazio and Campania), the southern flank of the Alps and Western Turkey during GI and GS events (Fig. 7: bottom panels). During GI events however, optimal regions extend northwest to Brittany, along the Côte d'Azur from the mouth of the Rhone to Liguria, and include the eastern flank of the Alps, the Danube valley and the Balkans (Fig. 7: bottom right panel). During GS events, the regional

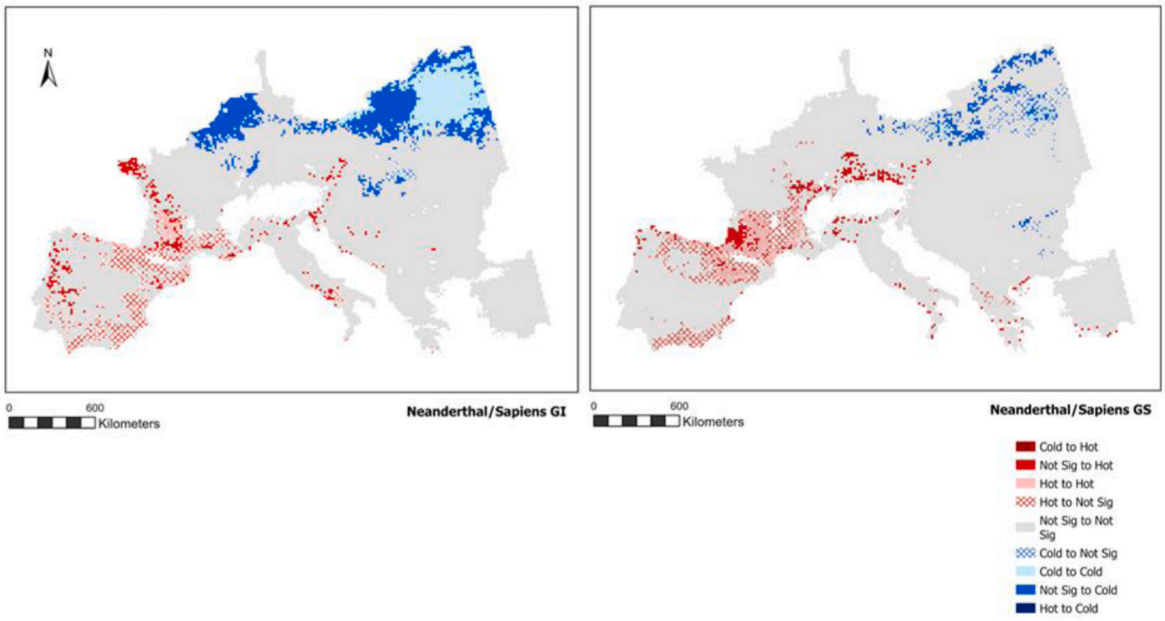

Fig. 6. Hot Spots analysis: pairwise comparisons of the significance of Hot Spot results for Neanderthal versus Sapiens under stadial (GS) and interstadial (GI) conditions.

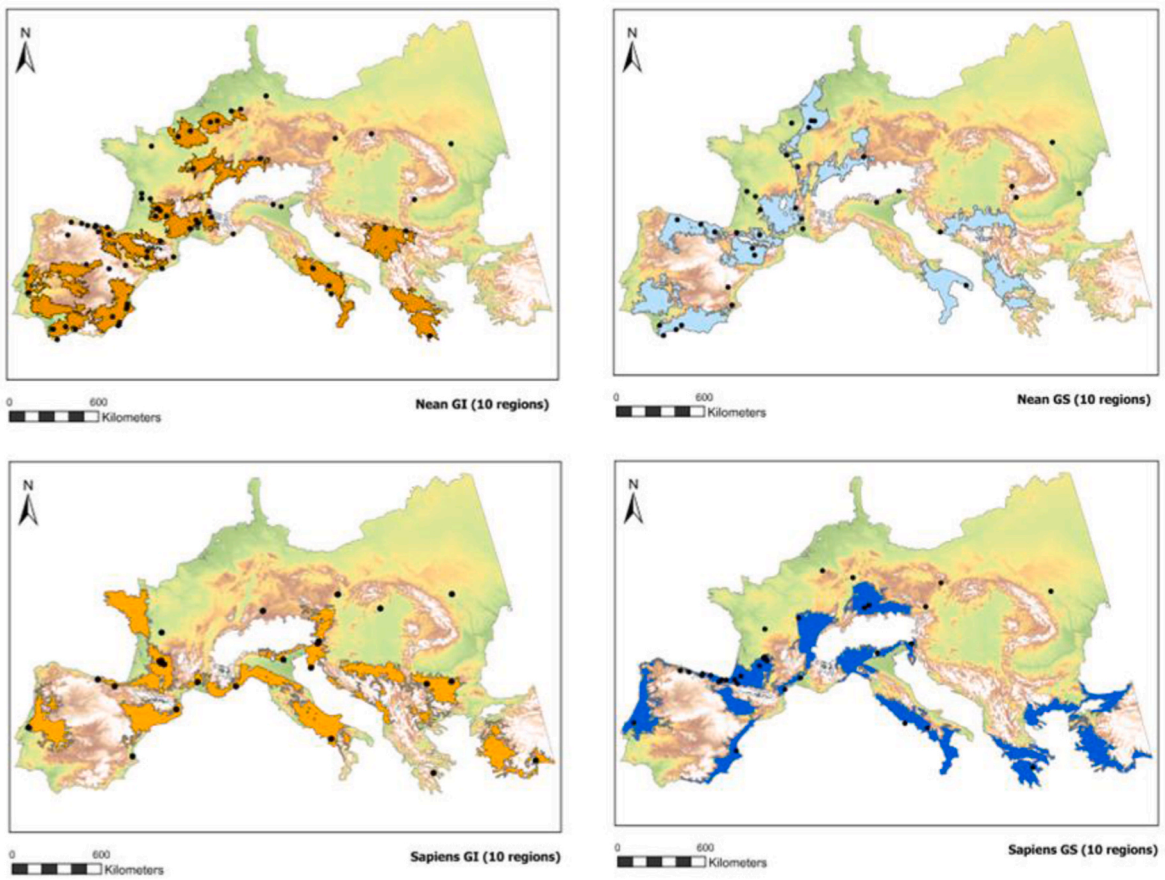

Fig. 7. Locate regions: 10-region scenarios for Neanderthal (top panels) and Sapiens (bottom panels) during GI (left panels) and GS (right panels) intervals. Sites used in the HS models, assigned to the appropriate climate interval, are illustrated (black dots).

focus shifts to include Central Europe. In the East, the distribution of optimal regions shifts southwards to include Greece and the northern Aegean (Fig. 8: bottom right panel).

The Optimal Regions Connection tool uses Euclidian distance and habitat suitability scores to produce a network of connections linking regions (Fig. 8). Connections are designed to maximise habitat

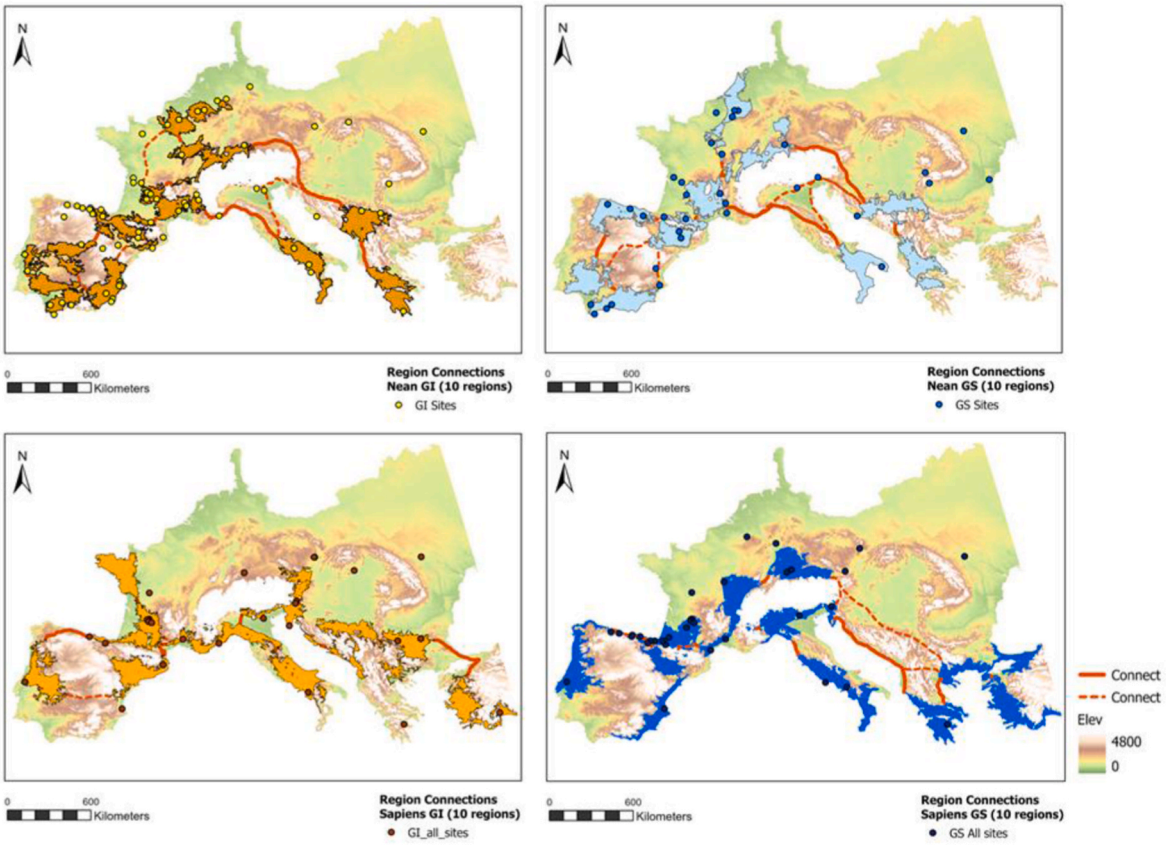

Fig. 8. Connectivity between regions under the 4 test scenarios. Optimal connections are illustrated with solid red lines and neighbouring connections are dashed. The distribution of sites used in the HS models is also indicated. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

suitability and minimise the distance travelled, assuming movement across the landscape would have been guided by the availability of resources. Neanderthal regions in southern Italy and the Balkans are only loosely connected to regions in Western Europe regions which form a tighter network of connections, during both GI and GS events (Fig. 8: top panels). In contrast, the network of Sapiens regions is relatively better connected, with the exception of the Balkan Peninsula during GS events (Fig. 8: bottom panels). During both GS and GI events the network of connections between Sapiens regions maintains a southern, coastal focus.

During both GS and GI events most of the sites used to construct the HS models either map onto optimal regions or the network of connections between them (Fig. 7, SI-1-4) with the notable exception of sites in Eastern Europe (see discussion).

3.4. Regional overlays analysis

There is relatively more overlap between regions occupied during GI and GS events across the Neanderthal habitat range *versus* the Sapiens range (Fig. 9, bottom panels) Once again, this confirms that the distribution of suitable habitat for Sapiens groups between GI and GS events is relatively more contrasted.

If Neanderthal and Sapiens groups made optimal use of available habitat their ranges would have overlapped in northern Spain and central/southern Italy during both GI and GS events (Fig. 9: top panels). This affects the Franco-Cantabrian core region identified above (Section 3.2) but the second Neanderthal core region in southern Iberia is only minimally affected. Additional overlaps between Sapiens and Neanderthal regions potentially occurred in Portugal during GI events (Fig. 9: top left panel), and in southeastern Spain (Andalucia), Central Europe, southern Italy and the Balkans during GS events (Fig. 9: top right panel).

Subtle differences in habitat preference between Neanderthals and Sapiens means that despite a shared regional focus on SW Europe - especially during GS events (see section 3.2) – the proportion of either species' range that overlaps never exceeds 5% (Table 3).

The existence of overlays raises the possibility of social interactions between Sapiens and Neanderthal groups during both climate events, however.

4. Discussion

4.1. Synopsis

Several interesting patterns emerge from these results. The distribution of suitable habitat reveals interspecific differences in response to contrasting climate conditions. The relative proportion of Neanderthal habitat distributed across the spectrum of habitat suitability (HS) scores is stable during the transition from GI to GS events, but contrasted in the case of Sapiens groups, indicating that GI conditions were more favourable (Fig. 3). The spatial distribution of highly suitable Hot Spots (core regions) is relatively persistent over time for Neanderthals and more contrasted for Sapiens (Fig.s 4–6) confirming the previous result. Similar patterns emerge when comparing the broader spatial distribution of optimal regions for both groups over time (Fig. 7). The networks produced by connecting optimal regions also suggest differences in the connectivity of Neanderthal and Sapiens populations during MIS 3. Compared with Sapiens, the Neanderthal network is less well connected at the European scale, with a potential East/West divide (Fig. 8). The Sapiens network is comparatively better connected and primarily focussed on southern, coastal routes (Fig. 8). Neanderthal and Sapiens

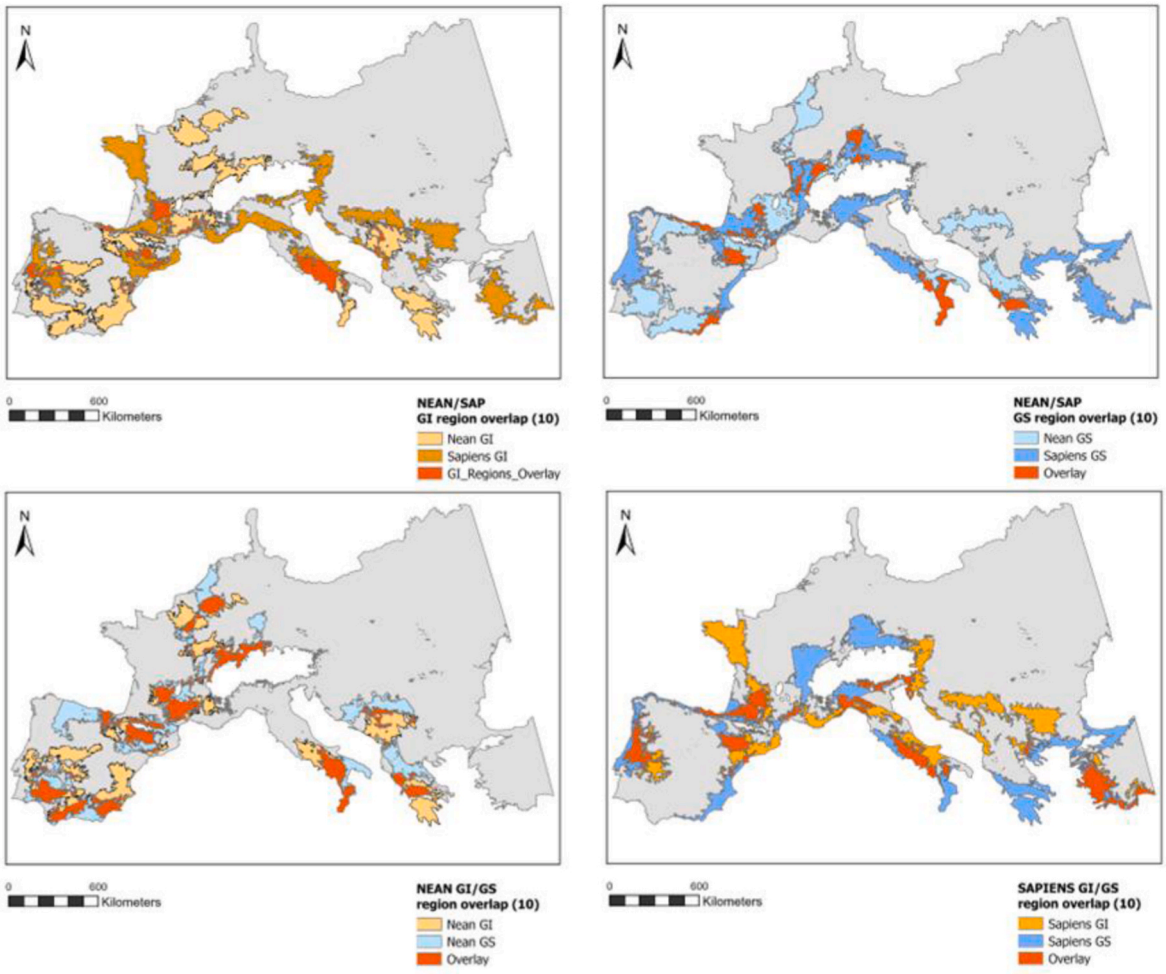

Fig. 9. Overlapping regions under 4 scenarios. Top panels: comparison between the distribution of optimal regions for Neanderthals and Sapiens during GI (left) and GS (right) conditions. Bottom panels: comparison between the distribution of optimal regions during GI and GS for Neanderthals (left) and Sapiens (right).

Table 2
Intra- and inter-specific differences in HS values for stadial/interstadial events (GS/GI).

COMPARISONS	Chi-sq
NEANDERTHAL GS/GI	55172
SAPIENS GS/GI	319635
NEANDERTHAL/SAPIENS GS	224676
NEANDERTHAL/SAPIENS GI	349895
$p < 2.2e\text{-}16$	(df = 9)

Table 3
Quantifying the overlay between optimal regions. OVERLAY (km^2); the total area of overlay between a) two taxa for each climate event (top two rows); and b) two climate events for each taxon (bottom 2 rows). PERCENT OVERLAY: the overlay between two taxa for GI and GS (a) expressed as the proportion of the total available area (10 regions) for a given taxon, for each climate event.

COMPARISONS	OVERLAY (km2)	SAPIENS/ NEANDERTHAL	PERCENT OVERLAY
SAPIENS/ NEANDERTHAL GI	105070	SAPIENS GI	5.08
SAPIENS/ NEANDERTHAL GS	129926	SAPIENS GS	4.11
SAPIENS GI/GS	201333	NEANDERTHAL GI	2.54
NEANDERTHAL GI/ GS	243710	NEANDERTHAL GS	2.07

regions never overlap by more than 5% of the habitat available to either group, regardless of climate phase, weakening the case for competitive exclusion as an explanation for the eventual extinction of the Neanderthals. But the potential for interaction clearly exists, specifically in Franco-Cantabria and Italy, with clear implications for several of the hypotheses that have been proposed to explain population replacement in Europe.

4.2. HS models

Comparison of the variables retained in the HS models suggests differences in the environmental preferences of Neanderthals and Sapiens (SI-Table 1). RF takes variable interactions and non-linear relationships between variables into account, making it difficult to interpret the results in terms of individual variables; broadly speaking, the models show that both groups responded to climate variability during stadial and interstadial events. This is logical since climate variability is an element of ecological risk to which hunter-gatherers will have been sensitive as they planned their movements (Burke et al., 2017). Temperature maxima and minima are not significant predictors in any of the models, indicating tolerance for a wide range of temperatures. Precipitation rates are important determinants of habitat suitability, especially during spring and fall, likely reflecting their impact on plant productivity. Slope is a predictor in all models, possibly due to the impact of slope angle on moisture levels and thus plant growth, and/or the availability of fixed (rock shelters) and mobile resources (prey) along river valleys. Full discussion of the models is presented in (Paquin et al.,

2024; Albouy et al., 2024).

Subtle differences in their response to environmental conditions could explain differences in the quality of available habitat during GS and GI events (see section 3.1, above). Sapiens groups were apparently at a relative disadvantage during GS events but were at an advantage during GI events (Fig. 3, Table 2). This is consistent with proposals that Sapiens populations dispersed more readily during interstadials (Müller et al., 2011; Timmermann, 2020).

4.3. Hot Spots and persistent "core" regions

Regional-scale analyses that differentiate between clusters of suitable habitat able to support regional groups and small or isolated islets of suitable habitat, such as Hot Spots analyses, provide unique information when dealing with high-resolution mapping (Moorter et al., 2023). Conceptually, suitable Hot Spots can be used as proxies for the location of potential core regions. The number and size of these regions and their spatial persistence over time have important implications in terms of population structure, social cohesion and mobility. Smaller core regions would have sustained relatively small populations that would have been more vulnerable to climate downturns and/or stochastic events (Vaesen et al., 2019), while larger core regions are potential sources of population expansion when conditions improve (Dennell et al., 2011; Wren and Burke, 2019, Klein et al., 2023).

The distribution of suitable Hot Spots (Fig.s 4, SI-5 to 8) is more spatially focussed during stadial events, when a prominent, favourable Hot Spot is centered on Franco-Cantabria and the Ebro valley. This core region would have acted as a climate refugium for Neanderthal and Sapiens groups during climate downturns and as a source for population recovery and re-expansion during upturns. In addition, a second core region located in southern Iberia is indicated for Neanderthal groups (Fig. 4: lower left panel).

The distribution of Hot Spots is more spatially extensive during interstadial events (Fig. 4), but the clusters are smaller - a trend that is more pronounced for Sapiens. Contrasting similarity values between GS/GI Hot Spots for Neanderthals and Sapiens (Fig.s 5 and 6) confirm this trend. The presence of more extensive and persistent Neanderthal core regions supports the proposal that their population underwent climate-driven cycles of contraction and re-expansion, demonstrating a long-term pattern of demographic resilience (Klein et al., 2023). The contrasting response to climate change displayed in the Sapiens models, on the other hand, could reflect a pattern of expansion and contraction due to climate stress or the fact that as an invasive species, the Sapiens population was not in a state of demographic or spatial equilibrium.

4.4. Regional networks and demography

We parameterised the Locate Regions tool to identify the 10 best patches of suitable habitat large enough to sustain regional bands numbering between 175 and 570 individuals (see Methods section, above). If Aurignacians occupied all the regions meeting one or both of our selection criteria (Table 1), i.e., discarding regions whose average HS score falls below the mean for the spatial domain, we can estimate the size of the population. The results indicate a range from 3800 to 4560 (2 criteria) to 4750-5700 (1 criterion) individuals. Similarly, maximum population size for Neanderthals ranges from 3325 to 3990 to 4750-5700 individuals. These numbers are coherent with previous population estimates based on archaeological data. For example, the Aurignacian population based on 2 criteria is similar to the estimate proposed by Schmidt and Zimmermann (2019) and at the lower end of more recent estimates (Shao et al., 2024); our Neanderthal estimates fall within the broad range proposed by Bocquet-Appel and colleagues and others (Bocquet-Appel and Degioanni, 2013). We are confident, therefore, that our scenarios are plausible and consistent with the archaeological record.

Establishing the size, shape and location of habitable regions and the shape of the network connecting them is important because these are structural features emerging from the landscape that contribute to governing patterns of social interaction. Smaller regions may be sources of variability, contributing to the rate of cultural innovation and complexity in a population, but only as a function of their connectedness to other regions, e.g. (Derex and Boyd, 2016, Derex et al., 2018). One of the patterns that emerges from our analysis is the relatively tenuous connection between Western and Eastern portions of the Neanderthal network (for both GS and GI events) which is consistent with the proposal, based on genetic evidence, that their metapopulation was subdivided and thus potentially vulnerable to stochastic events (French, 2016, Vaesen et al., 2019; Slimak et al., 2024).

In a mature occupation phase, movement between regions for the purpose of exchanging information, making social contacts and engaging in trade and/or as a means of providing temporary relief from local resource failure will have taken place, e.g., (Whallon, 2006, Whallon et al., 2011). The optimal connections tool provides us with tools for suggesting hypothetical networks of communication between regions that reflect this potential (Fig. 8). It also provides a basis for examining the mobility of the system, e.g., patterns of dispersal, and even the mobility of individuals.

Sapiens groups are assumed to have dispersed into Europe from the Levant (Hublin, 2014, Bosch et al., 2015). Proposed dispersal routes include a southern, coastal route and an inland route along the Danube valley, e.g. (Mellars, 2006). Since the initial size of the Aurignacian population, and thus the number of occupied regions, would have been relatively small it is interesting to note that in the Hot Spots analysis (Fig. 4) Western European regions are highlighted and in the regional analysis they have consistently higher average HS scores in every scenario. Recent archaeological evidence also points to a much earlier arrival of Aurignacian groups in Southwestern Europe than previously thought (Cortés-Sánchez et al., 2019; Haws et al., 2020; Berlioz et al., 2025) all of which argues for a rapid westward dispersal of Sapiens populations. If, as has been suggested elsewhere, Aurignacian dispersals were facilitated by interglacial conditions our data suggest that they are likely to have propagated via a southern, coastal route - mapping onto the regional network reconstructed for GIs (Fig. 8: lower left panel).

We assume that initial movement between regions was exploratory, rather than directed, i.e., until optimal regions were encountered people will have moved through the landscape somewhat randomly (although we expect that their movements were influenced by HS, especially when the distances involved required multi-day travel, as people will have acquired resources *en route* until such time as they encountered relatively more suitable regions than the ones they had already visited. In other words, we expect that without perfect knowledge of their environment humans will leave an archaeological signature that doesn't always map onto optimal regions. This could explain why some archaeological sites in our analysis are outliers, for example (see: Fig. 7).

The presence of outliers is worthy of further discussion. The regional analysis presented above identifies ideal networks and highly mobile Neanderthals and Sapiens groups were likely present elsewhere on the landscape. The response-time of regional groups may lag behind climate-driven changes to their habitat (HS) for various reasons, including the necessity of weighing the relative importance of maintaining social networks against declining economic returns and the cost of exploratory movement. This means that individual sites may occur in "satisfactory" but not optimal locations. Furthermore, the scale of our analysis is too coarse to capture residence patterns at sub-millennial or seasonal scales. Outliers occur in Eastern Europe in all our test scenarios, mostly located in the Carpathians (Fig. 8). The Carpathians have moderately good HS scores in the initial models (Fig. 2) but they border the North European Plain, which has very low scores. This pattern bears further analysis but suggests that although the Carpathian region was undoubtedly occupied, it was peripheral to the regional networks described in this research.

The SDMs and resulting regional analysis indicate that Neanderthals

and Sapiens made somewhat different use of the landscape, although there are overlaps (Fig. 9) that suggest a potential for interaction across both species' ranges. The affected areas are proportionally small, however (Table 3). The potential for interaction would have been strategically significant in the core Southwestern region where source populations hypothetically formed the basis of demographic resilience. The extirpation of Neanderthal populations from this core region would have placed their population at risk, although the existence of a persistent Neanderthal core region in southern Iberia could have mitigated risk, at least for a time.

The degree to which niche overlap is tolerated depends on the intensity of competition and the degree to which a faunal community is saturated in species (Pianka, 1983). Without assessing the degree of saturation, which would not be feasible at the spatial scale at which this analysis was conducted (for steps in this direction, however, see (Vidal-Cordasco et al., 2023)) it isn't possible to determine to what extent interactions between Neanderthals and Sapiens were competitive. Low intensity competition would explain the archaeological and genetic evidence that Neanderthals and Sapiens populations were able to co-exist and interbreed. Evidence of overlap in the strategically important core region located in Franco-Cantabria and northeastern Spain may have had more impact, however, given its potential role as a source of long-term demographic resilience (see above).

4.5. Demographic implications

Our regional analysis consisted of building optimal networks of up to 10 regions for both Neanderthals and Sapiens, remaining agnostic as to their relative rates of growth or decline. The demographic profiles of fossil species are difficult to infer, but evidence from age at death estimates and genetic analyses suggest effective population sizes were consistently lower among Neanderthals (Trinkaus, 1995; Caspari and Lee, 2004; Bocquet-Appel and Degioanni, 2013, Prufer et al., 2014). Demographic differences between Sapiens and Neanderthals have several implications. While some argue that Neanderthals and modern humans had similar capacities for cultural flexibility and innovation (e.g. (Sykes, 2020)) the cultural adaptability of Neanderthals may have been limited by virtue of their smaller, more dispersed populations compared with modern humans (Bocquet-Appel and Degioanni, 2013); our network reconstructions also suggest their population was less well-connected. Differing patterns of hybrid fertility and integration into Neanderthal and modern human social groups might also have played a role. While early modern humans show substantial components of Neanderthal introgression (Hajdinjak et al., 2018; Iasi et al., 2024), this was followed by a fairly rapid expunging of many Neanderthal elements from the genome (Juric et al., 2016; Iasi et al., 2024; Sümer et al., 2025). The combination of male hybrid sterility and unidirectional absorption of hybrid individuals into modern human populations could have placed late Neanderthal populations in a precarious position and at risk of extinction or absorption in the face of migrating modern human populations with larger population sizes, more extensive social networks, and biased introgression (e.g. (Stringer and Crété, 2022),).

The predicted overlaps between Neanderthal and Sapiens regions (Fig. 9) suggest the potential for interaction across both species' ranges although the affected areas are proportionally small (Table 3). Recent work suggests a single (Sümer et al., 2025) or at most few (Iasi et al., 2024) interbreeding events over a period of perhaps just 6000 years (Op. Cit.), although multiple inbreeding events are proposed elsewhere (Fu et al., 2014; Fu et al., 2015; Hajdinjak et al., 2018; Hajdinjak et al., 2021). A single interbreeding phase, perhaps in Southwest Asia (Sankararaman et al., 2012), is argued to account for the ubiquitous inclusion of Neanderthal derived genes across modern human populations outside Africa (Green et al. 2010). However, some of the first Sapiens populations in Eurasia (e.g. Zlatý kůň, Ranis, Oase 1, Ust'-Ishim) show recent Neanderthal interbreeding in their genome, although they did not contribute to more recent European populations (Hajdinjak et al., 2021; Sümer et al., 2025), which raises the possibility of more widespread admixture than previously assumed. These events may not have left a mark on more recent Sapiens genomes, given the extinctions of some early Sapiens lineages, or may not have been identified to date, given how few genomes have been sequenced so far, especially in Western Europe.

4.6. Limitations of the study

There are limitations to this research, which uses SDMs and tools borrowed from conservation biology to study population replacement in Europe during MIS 3, including.

1) The palaeoclimate models used to produce the initial HS models are equilibrium models. Given how short stadial/interstadial cycles were during MIS 3 it is likely that the environment was in a state of non-equilibrium much of the time. Furthermore, Sapiens and Neanderthal populations were probably not in equilibrium either, since the former were expanding their range across Europe whilst the latter were in decline. This means that our SDMs and the regional analyses contain an element of uncertainty that cannot be quantified at present. Even when a species is not at equilibrium, however, pseudo-absence-based SDMs are thought to provide fairly accurate estimates of a species' range (Barbet-Massin et al., 2012) which means that they are fit for our purposes.
2) The HS models did not include primary productivity (NPP) as a candidate variable, which means we cannot estimate carrying capacity (K) and thus, potential population size. The number of sites for each timeframe could be used to produce demographic estimates, but this approach is inherently risky (Tallavaara and Jørgensen, 2021). We countered this problem by testing several scenarios to identify the number of highly suitable regions available to sustain the population. Recent work has shown that it is possible to model biomass productivity (Vidal-Cordasco et al., 2023) and this would be a step towards adding demographic parameters to the analysis.
3) The decision to restrict the geographic domain of the analysis to the contemporary European landmass means coastal regions are not fully represented in the models, particularly where the continental shelf is shallow. Optimal network connections between the Balkan Peninsula and the Italian Peninsula are probably mis-represented in our study, for example, since the continental shelf under the Adriatic would have been emergent during MIS 3. Similarly, connections across the paleochannel to what is now Great Britain are not included in the models.

Despite these limitations this research offers useful avenues for reflection concerning the potential of the European landscape to support Neanderthal and Sapiens groups under different climate scenarios and allows us to shed light on the process of population replacement in Europe during MIS 3.

5. Conclusion

The results of this research indicate that Neanderthal habitat was not significantly degraded by climate change (a result supported by (Degioanni et al., 2025)) but that the distribution of suitable habitat shifted in response to climate stress induced by GS/GI cycles. The degree of spatial overlap between GS/GI regions and the similarities observed in the networks they generate suggest the potential for spatial resilience. The strategic importance of core regions in southwestern Europe (specifically Franco-Cantabria and northeastern Spain) and in southern Iberia could have contributed to demographic resilience. Climate stress alone, therefore, is unlikely to explain the extinction of Neanderthals. On the other hand, the reconstructed optimal networks for both GS and GI events indicate that Neanderthals living in Western and Southeastern Europe were only tenuously connected as the distances separating them

were quite large.

Generally speaking, the HS models used in this research suggest that interstadial conditions were relatively more favourable for Sapiens groups than stadial conditions. The regional analysis, on the other hand, suggests that the landscape offered similar potential for sustaining up to 10 regional bands during these contrasting climate events. Exploiting this potential would have required spatial shifts in the regional network, however. During GS events, optimal ranges in Western Europe shift away from the Atlantic coast of France towards Central Europe (including the Swabian Alps) while in Southeastern Europe, optimal regions located in the Balkans shift southwards. The hypothetical networks that result have a distinctly southern and coastal focus during GIs, connecting with the northern perialpine range via the Balkan coast (and more tenuously, the Danube valley) during GS. Of the two proposed dispersal routes, the Mediterranean coastline is consistently favourable.

There is growing awareness that the process of population replacement need not have been uniform across Europe (Haws et al., 2020) and that different combinations of stressors may have been involved (Vahdati et al., 2022). It is possible, for example, that Sapiens played a more active role in the extinction and/or genetic assimilation of Neanderthals in Western Europe, where their core regions overlap, whereas in Southeastern Europe (e.g., the Balkans and southern Italy), where Neanderthal regional networks were stretched to the limit, genetic and/or demographic vulnerabilities may best explain their disappearance.

Finally, a large number of SDMs has been published recently to investigate patterns of human dispersal and address the complex issue of population replacement in Europe during MIS 3 (Banks et al., 2008; Banks et al., 2013; Benito et al., 2017; Kondo et al., 2018; Melchionna et al., 2018; Timmermann, 2020, Yousefi et al., 2020; Banks et al., 2021; Shao et al., 2021; Timmermann et al., 2022; Vidal-Cordasco et al., 2022; Klein et al., 2023; Ruan et al., 2023; Vidal-Cordasco et al., 2023; Albouy et al., 2024; Guran et al., 2024; Paquin et al., 2024; Shao et al., 2024; Yaworsky et al., 2024; Degioanni et al., 2025). Comparisons between these models reveal broad similarities, but also notable differences in the spatial distribution of suitable habitat at regional and local scales. These differences result from decisions made during model design, including: the use of different climate models to simulate climatological variables, the resolution of the climate variables, the downscaling methods used, the number and type of predictive variable used, the choice of modelling algorithm and of course, the archaeological data used as input. As a result, while it is possible to compare the broad patterns that emerge from these models, the models themselves are not directly comparable. Statistical tools such as the ones used in this research counter some of the problems of model inter-comparability by isolating significant patterns in the spatial distribution of suitability indices and using them to predict their impact on the distribution of human populations.

Author contributions

Burke: Conceptualization, Supervision, Formal analysis, Funding acquisition, Writing – original draft. Pomeroy: Writing – review & editing. Poisot: Writing – review & editing. Albouy: Investigation. Paquin: Investigation.

Declaration of generative AI in scientific writing

The authors declare that AI tools were not used at any point during the preparation of this work.

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Declaration of competing interest

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

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2026.109850.

Data availability

The archaeological databases (Albouy et al., 2023; Paquin et al., 2023) and habitat suitability models analysed in this paper are available here:

Albouy, Benjamin, 2025, "Habitat suitability models for Neanderthals in Europe during MIS 3″, https://doi.org/10.5683/SP3/NPWF28, Borealis, V1.

Albouy et al. (2024), "Supplementary materials for Albouy et al. (2023)", https://doi.org/10.5683/SP3/REV2IW, Borealis, V1, UNF:6: t426kiVpCsPf3Ir4jIDw5Q = = [fileUNF]

Paquin, Simon, 2025, "Habitat Suitability model for Aurignacian populations in Europe during MIS 3.", https://doi.org/10.5683/SP3/VXBMSW, Borealis, V1.

Paquin et al. (2024), "Supplementary Materials for Paquin et al. (2023)", https://doi.org/10.5683/SP3/RLHVBL, Borealis, V1, UNF:6: gG + tpNFJHgbxtGcReXo1Hg = = [fileUNF]

The underlying climate models are available here:

Kageyama, Masa, 2024, "IPSL-CM5A-LR GCM climate simulation for Marine Isotope Stage 3 over Europe", https://doi.org/10.5683/SP3/DXGXTM, Borealis, V1.

Vrac, 2024, "IPSL-CM5A-LR GCM downscaled climate simulation for Marine Isotope Stage 3 over Europe.", https://doi.org/10.5683/SP3/JBZQKS, Borealis, V1.

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