



Universiteit
Leiden
The Netherlands

Virtual Neanderthals : a study in agent-based modelling Late Pleistocene hominins in western Europe

Scherjon, F.

Citation

Scherjon, F. (2019, May 28). *Virtual Neanderthals : a study in agent-based modelling Late Pleistocene hominins in western Europe*. Global Academic Press, Vianen. Retrieved from <https://hdl.handle.net/1887/73639>

Version: Not Applicable (or Unknown)

License: [Leiden University Non-exclusive license](#)

Downloaded from: <https://hdl.handle.net/1887/73639>

Note: To cite this publication please use the final published version (if applicable).

Cover Page



Universiteit Leiden



The handle <http://hdl.handle.net/1887/73639> holds various files of this Leiden University dissertation.

Author: Scherjon, F.

Title: Virtual Neanderthals : a study in agent-based modelling Late Pleistocene hominins in western Europe

Issue Date: 2019-05-28

Virtual Neanderthals

**A study in agent-based modelling Late Pleistocene hominins in
western Europe**

Proefschrift

ter verkrijging van
de graad van Doctor aan de Universiteit Leiden,
op gezag van Rector Magnificus prof. mr. C.J.J.M. Stolker,
volgens besluit van het College voor Promoties
te verdedigen op dinsdag 28 mei 2019
klokke 15.00 uur

door

Fulco Scherjon

Geboren te Amsterdam, Nederland
in 1969

Promotor:

Prof. Dr. Wil Roebroeks (Universiteit Leiden)

Co-promotor:

Dr. Katherine MacDonald (Universiteit Leiden)

Promotiecommissie:

Prof. Dr. Corrie C. Bakels (Universiteit Leiden)

Prof. Dr. Paul Bons (Eberhard Karls University Tübingen, Germany)

Dr. Hans Kamermans (Universiteit Leiden)

Prof. Dr. Jan Kolen (Universiteit Leiden)

Dr. Iza Romanowska (Centro Nacional de Supercomputación, Barcelona, Spain)

Prof. Dr. Marie Soressi (Universiteit Leiden)

Dr. Alexander Verpoorte (Universiteit Leiden)

PREFACE

Wil Roebroeks has been kind enough to allocate part of his SPINOZA grant from the Netherlands Organisation for Scientific Research (NWO) to make this research possible. The research described in this thesis was carried out under the supervision of Prof. Dr. Wil Roebroeks, Dr. Kathy MacDonald, Dr. Alexander Verpoorte, and Dr. Hans Kamermans, from the Faculty of Archaeology of Leiden University, The Netherlands. I hereby certify that the research presented in this thesis is my own original work except where specific acknowledgments or references are made. All data and information including full source code necessary for confirming the conclusions presented in the thesis are represented fully within this thesis or in the Supplementary Materials on the accompanying data disk. The title of this thesis is shortened to ‘Virtual Neanderthals’. Virtual as in “being on or simulated on a computer or computer network”, as defined by the Merriam-Webster dictionary on-line: <https://www.merriam-webster.com/dictionary/virtual>, accessed 25 February 2018.

Fulco Scherjon
Leiden

Cover design

The front page is the illustration ‘Cyborg with human skull in his hand’, by Tatiana Shepeleva, used with permission and modified by me. The skull studied by the cyborg is a late *Homo neanderthalensis* skull and mandible from western Europe (La Ferrassie I), skull photo credited to Puwadol Jaturawutthichai. Photo composition designed using a blue sky picture as background (from ZaZa Studio, ‘Blue sky with clouds and sun’). Reverse depicts an early hunter facing a mammoth: ‘Mammoth and primitive man against a starry sky’, illustration by Iurii. All images used for the cover retrieved from <https://www.shutterstock.com>, accessed 10 April 2019.

Copyright

The copyright of the content of this thesis and the associated data carrier remains with the author. All information derived from this thesis and/or the supporting information including software and data files must be acknowledged appropriately. The HomininSpace modelling and simulation software is free software: you can redistribute it and/or modify it under the terms of the GNU General Public License as published by the Free Software Foundation, any version 3.

ISBN/EAN: 978-94-6380-344-1

Publisher: Global Academic Press

Printed by: ProefschriftMaken || www.proefschriftmaken.nl

Cover realization: ProefschriftOntwerp.nl

This work is dedicated to my son, Thor Scherjon, whose innocence in modelling the world and creativity in deconstructing the true meanings of life keep surprising me.

Contents

Extended contents	ix
List of Tables	xiii
List of Figures	xv
List of Equations	xviii
1. Introduction.....	1
Part one: The Lay of the Land.....	9
2. Agent Based Modelling.....	11
3. Case Study: The Late Pleistocene in western Europe.....	25
Part two: Creating the Actors.....	35
4. The Modelled Environment	37
5. The Modelled Hominins	65
6. The Archaeological Data in the Model.....	85
Part Three: Setting the Stage	97
7. Overview, Design concepts and Details (ODD) of HomininSpace.....	99
8. Building the Simulation System.....	117
9. Activating Parts of the Model via Settings.....	143
Part Four: And Action!.....	161
10. Simulation Results	163
11. Analysis	187
12. Discussion	225
13. Conclusions.....	251
References	267
Appendix 1: Abbreviations.....	293
Appendix 2: Supplementary Materials	297
Summary.....	307
Samenvatting	308
Acknowledgements.....	309
Curriculum vitae	311

Extended contents

List of Tables	xiii
List of Figures.....	xv
List of Equations	xviii
1. Introduction.....	1
1.1 Background.....	1
1.2 Study objectives.....	2
1.3 Methods and approaches.....	3
1.4 Thesis structure.....	6
Part one: The Lay of the Land.....	9
2. Agent Based Modelling.....	11
2.1 Introduction.....	11
2.2 Why model?.....	12
2.2.1 <i>In or out: what to include in a model</i>	14
2.2.2 <i>Model credibility</i>	14
2.3 Techniques for modelling dispersal in landscapes.....	16
2.3.1 <i>Agent Based Modelling</i>	17
2.4 HomininSpace – a model of the past world of hunter-gatherers	19
3. Case Study: The Late Pleistocene in western Europe.....	25
3.1 Introduction.....	25
3.2 The environment: climate and topography	26
3.3 The hominins: Neanderthals	31
Part two: Creating the Actors.....	35
4. The Modelled Environment	37
4.1 Introduction.....	37
4.2 Reconstructing topography with fluctuating global sea levels	39
4.3 Distribution of reconstructed temperature and precipitation	44
4.3.1 <i>Reconstruction via interpolation between climate extremes</i>	47
4.4 An energy landscape in two forms	52
4.4.1 <i>Calculating primary productivity</i>	54
4.4.2 <i>Secondary biomass: the continuous energy model</i>	56
4.4.3 <i>Secondary biomass: the reconstructed habitat model</i>	57
4.4.4 <i>The number of edible ungulates: carrying capacity</i>	61
5. The Modelled Hominins	65
5.1 Introduction.....	65
5.2 Demography	67
5.3 What does it take to be a Neanderthal - energy requirements	72
5.3.1 <i>Temperature tolerance</i>	75
5.4 Are Hominins social animals? - hominin groups.....	76
5.4.1 <i>Group demographics - new groups, group extinction, merging of groups</i>	76
5.4.2 <i>Social interaction - home range and foraging range</i>	78
5.4.3 <i>Mobility</i>	80
5.5 Overview: building blocks for the underlying model.....	81

6. The Archaeological Data in the Model.....	85
6.1 Introduction.....	85
6.2 The archaeology of presence and absence.....	86
6.3 What dating information to use?.....	87
6.3.1 <i>Database structure</i>	88
6.4 Checkpoints in Space and Time (CSTs).....	91
Part Three: Setting the Stage	97
7. Overview, Design concepts and Details (ODD) of HomininSpace.....	99
7.1 Introduction.....	99
7.2 Process overview and scheduling.....	99
7.3 Simulation time and stochasticity.....	102
7.4 Model parameters and the ViabilityIndex.....	103
7.5 How to match the archaeology.....	105
7.5.1 <i>Translating simulation results into numbers: MatchedIntervalCoverage</i>	106
7.6 Genetic Algorithms - searching through N-dimensions.....	108
7.7 Traversing the parameter space.....	111
7.7.1 <i>Generating the Standard parameter value set</i>	111
7.7.2 <i>Searching the highest scoring parameter value set with Genetic Algorithms</i>	112
8. Building the Simulation System.....	117
8.1 Introduction.....	117
8.2 Agent-based modelling tools.....	117
8.2.1 <i>Repast Symphony version 2.2</i>	118
8.3 The development environment.....	120
8.3.1 <i>The source code</i>	120
8.3.2 <i>Software development tools</i>	122
8.4 The runtime environment.....	123
8.4.1 <i>Batch execution of simulations</i>	124
8.5 Data files defining a case study.....	126
8.5.1 <i>Simulation grid, topography and climate data</i>	126
8.5.2 <i>Reconstructed global mean temperature and sea level</i>	127
8.5.3 <i>Checkpoints</i>	129
8.6 Input files defining a simulation.....	133
8.6.1 <i>Model parameter values</i>	134
8.6.2 <i>Simulation settings</i>	134
8.7 Simulation output.....	135
8.7.1 <i>Logging and debug information</i>	136
8.7.2 <i>Maps, bar charts and time series</i>	137
8.7.3 <i>Simulation statistics</i>	141
9. Activating Parts of the Model via Settings.....	143
9.1 Introduction.....	143
9.2 Model elements of the reconstructed environment.....	144
9.2.1 <i>Energy versus habitat reconstruction</i>	144
9.2.2 <i>Coastal resources</i>	146
9.3 Model elements of hominin behaviour.....	147
9.3.1 <i>Mobility type: dynamic versus static hominins</i>	147
9.3.2 <i>Imposing a maximum foraging range</i>	149
9.3.3 <i>Allowing the crossing of open water systems</i>	151
9.4 Model elements of population distribution.....	153
9.4.1 <i>Using hominin absence data</i>	153
9.4.2 <i>Using population core areas (hominin factories)</i>	156
9.5 Neutral models - levelling the playing field.....	157

9.5.1	<i>Implementing topographical differences in the landscape</i>	158
9.5.2	<i>Distributing energy equally throughout the grid</i>	159
9.5.3	<i>Randomly walking hominins</i>	159
Part Four: And Action!		161
10. Simulation Results		163
10.1	Overview.....	163
10.1.1	<i>Design of the Experiments (DOE)</i>	165
10.2	Scenario Habitat-A (HabitatDynamic)	166
10.3	Scenario Habitat-B (HabitatDynamicAbsence).....	167
10.4	Scenario Habitat-C (HabitatDynamicMaxrange)	168
10.5	Scenario Habitat-D (HabitatDynamicMaxrangeCoreAbsence).....	169
10.6	Scenario Habitat-E (HabitatDynamicCoastalMaxrangeCore).....	170
10.7	Scenario Habitat-F (HabitatDynamicCoastalMaxrangeCoreAbsence)	171
10.8	Scenario Habitat-G (HabitatStatic).....	172
10.9	Scenario Habitat-H (HabitatStaticCrosswaterCore)	173
10.10	Scenario Habitat-I (HabitatStaticMaxrange)	174
10.11	Scenario Habitat-J (HabitatStaticCoastalMaxrange)	175
10.12	Scenario Energy-A (EnergyDynamic).....	176
10.13	Scenario Energy-B (EnergyDynamicCoastalMaxrange).....	177
10.14	Scenario Energy-C (EnergyDynamicCoastalMaxrangeAbsence)	178
10.15	Scenario Energy-D (EnergyDynamicCoastalMaxrangeCrosswater).....	179
10.16	Scenario Energy-E (EnergyStaticCoastalMaxrange).....	180
10.17	Additional simulations.....	181
10.17.1	<i>Three simulation scenarios with Random walk activated</i>	181
10.17.2	<i>Duplication of scenario Energy-A for verification purposes</i>	184
11. Analysis		187
11.1	Introduction.....	187
11.2	Correlating input to input and output to output	188
11.3	Sensitivity analysis in scenario exploration.....	190
11.3.1	<i>Variability in scenarios</i>	191
11.3.2	<i>Correlations between parameter values and simulation results</i>	194
11.3.3	<i>Relative Variable Importance (RVI) - what makes a Neanderthal tick?</i>	198
11.3.4	<i>Monotonic trends in parameter values</i>	200
11.3.5	<i>Creating impossible Neanderthals and other cheats</i>	201
11.4	Trends in the simulation output	203
11.4.1	<i>The simulation score</i>	203
11.4.2	<i>Characterizing the best models from the Standard set</i>	206
11.4.3	<i>Causes of life and death</i>	207
11.4.4	<i>Influence of data quality on the simulation score</i>	212
11.5	Analysing the modelled environment	213
11.5.1	<i>Topography</i>	214
11.5.2	<i>Energy via habitat reconstruction</i>	218
11.5.3	<i>Energy via direct extrapolation</i>	221
12. Discussion		225
12.1	Introduction.....	225
12.2	System development.....	225
12.2.1	<i>Characterizing Neanderthal presence using radiometrically dated archaeology</i>	227
12.2.2	<i>Genetic Algorithms – do we need them?</i>	229
	<i>Realistic</i>	232
12.2.3	<i>environment reconstruction</i>	232
12.2.4	<i>Probability in HomininSpace</i>	233
12.3	Answering questions with HomininSpace	235

12.3.1	<i>Parameter value evolution in all scenarios</i>	236
12.3.2	<i>Q1 - How does the Energy reconstruction of the environment compare to Habitat reconstruction?</i>	238
12.3.3	<i>Q2 - What is the effect of adding coastal resources to the model?</i>	239
12.3.4	<i>Q3 - How does the addition of ebb and flow dispersal with the available resources influences the match with the archaeology?</i>	241
12.3.5	<i>Q4 - What is an optimal maximum foraging range?</i>	242
12.3.6	<i>Q5 - What happens if we assume that Neanderthals were able to cross large open water systems?</i>	244
12.3.7	<i>Q6 - What influence has adding absence data to the model?</i>	245
12.3.8	<i>Q7 - What is the effect of using population core areas?</i>	246
12.3.9	<i>Q10 - What are the results if the Neanderthals are implemented with random movement?</i>	248
13.	Conclusions	251
13.1	Developing HomininSpace – a tool for modelling hominin mobility	253
13.1.1	<i>Usability of the tool</i>	254
13.1.2	<i>Who were those Neanderthals?</i>	256
13.2	Implications of this study.....	259
13.3	Avenues for further research.....	261
13.3.1	<i>Recommendations when reconstructing past environments</i>	262
13.3.2	<i>Suggestions for simulating hominins</i>	263
13.4	Last words.....	265
	References	267
	Appendix 1: Abbreviations	293
	<i>Abbreviations</i>	293
	<i>Bioclimatic parameters</i>	294
	<i>Biome (Mega) classifications</i>	294
	Appendix 2: Supplementary Materials	297
	<i>Contents of the HomininSpace data disk</i>	297
	<i>Poster: Neandertals on the move. Or not. – ESHE 2015</i>	301
	<i>Poster: How (not) to model Neandertal extinction. –ESHE 2016</i>	302
	<i>Comparing past climate models: CCSM versus MIROC</i>	303
	Summary	307
	Samenvatting	308
	Acknowledgements	309
	Curriculum vitae	311

LIST OF TABLES

Table 1: Common characteristics of agents in Agent Based Modelling.	18
Table 2: Local and global minimum and maximum temperatures from Bintanja and van de Wal (2008), supplementary information. Temperatures are offset in degrees Celsius relative to modern day yearly mean values.	46
Table 3: Color coding of grid cells for temperature and precipitation.	49
Table 4: Example values for primary productivity for given temperatures.	54
Table 5: Different types of climate and their defining boundaries, derived from Binford (2001), Table 4.04, page 70.	59
Table 6: Calculating PB and SB from PP. Values derived from Table 3, page 284 (Kelly 1983, 284, Table 3). Type climate from Table 5 matched against biome type.	60
Table 7: Calculated secondary biomass per grid cell in kilograms per year for different mean yearly temperatures (theoretical values) in different biomes.	61
Table 8: Different mortality rates (in %) and the compounded effects on a starting population of 100 with no replenishment. Bold rows are results after 15 and 20 years.	68
Table 9: Variables on hominin behaviour included in the HomininSpace model.	82
Table 10: Data fields in the archaeological data database.	89
Table 11: Regular Checkpoints in Space and Time with geographical position.	92
Table 12: Checkpoints with x and y grid cell locations and their interval ranges.	93
Table 13: The 16 parameters that can be changed in the HomininSpace model.	104
Table 14: Minimum, maximum, step size, and default values for the Standard parameter set.	112
Table 15: Structure of the climate data file after preprocessing by SAM.	127
Table 16: Structure of input file "Bintanja2008.txt". Timestamp (1), reconstructed temperatures (5) and sea levels (9) are used by HomininSpace.	128
Table 17: Layout of the checkpoint input file. Fields are separated by tabs.	130
Table 18: Default starting locations for groups of the initial population.	131
Table 19: Monitoring checkpoints located at example positions.	132
Table 20: The climate monitoring checkpoints with their locations.	133
Table 21: The header and the first ten parameter value sets (comma separated) from the Standard parameter file.	134
Table 22: Color coding of reconstructed habitats in simulation maps.	138
Table 23: A list of the settings in the system. Each setting is a Boolean value, and must be activated or deactivated by assigning a value of True or False.	143
Table 24: Relative scoring schema when matching real world absence and presence versus modelling results. A '+' indicating a positive contribution of the match to an overall modelling score.	154
Table 25: Summary of the simulated scenarios.	163
Table 26: Overview of the setting values in all scenarios.	165
Table 27: Best three simulation results and parameter values for scenario Habitat-A.	166
Table 28: Best three simulation results and parameter values for scenario Habitat-B.	167
Table 29: Best three simulation results and parameter values for scenario Habitat-C.	168
Table 30: Best three simulation results and parameter values for scenario Habitat-D.	169
Table 31: Best three simulation results and parameter values for scenario Habitat-E.	170
Table 32: Best three simulation results and parameter values for scenario Habitat-F.	171
Table 33: Best three simulation results and parameter values for scenario Habitat-G.	172
Table 34: Best three simulation results and parameter values for scenario Habitat-H.	173
Table 35: Best three simulation results and parameter values for scenario Habitat-I.	174

Table 36: Best three simulation results and parameter values for scenario Habitat-J.....	175
Table 37: Best three simulation results and parameter values for scenario Energy-A.....	176
Table 38: Best three simulation results and parameter values for scenario Energy-B.....	177
Table 39: Best three simulation results and parameter values for scenario Energy-C.....	178
Table 40: Best three simulation results and parameter values for scenario Energy-D.....	179
Table 41: Best three simulation results and parameter values for scenario Energy-E.....	180
Table 42: Best three simulation results and parameter values for scenario Energy-BR, (with randomwalk) for Standard and Evolved parameter value sets.....	182
Table 43: Best three simulation results and parameter values for scenario Energy-CR, with randomwalk.....	183
Table 44: Best three simulation results and parameter values for scenario Energy-ER, with randomwalk.....	184
Table 45: Best three simulation results for scenario Energy-A, batch 2.....	185
Table 46: For all Standard sets the significant Spearman correlation coefficients for parameters versus matchedIntervalCoverage. Green are positive correlations, red negative. Darker colors indicate stronger correlations.....	195
Table 47: The Spearman correlation coefficients of the Evolved sets for parameters versus matchedIntervalCoverage. Green are positive, red are negative correlations.....	198
Table 48: Relative variable importance assuming a linear model for all Standard sets.....	199
Table 49: Relative Variable Importance for the Evolved sets from all scenarios.....	200
Table 50: Correlations between model input parameters and scenario number, for the Evolved datasets. Positive correlations are green colored and darker colors indicate stronger correlations.....	201
Table 51: Number of model parameter value sets per scenario with parameter values manipulated beyond the initial limits. Darker colors identify larger table values.....	203
Table 52: Presenting the best performing models from the Standard set. The first column gives the number of times the simulation number appears in the top-10 scores over all scenarios.	207
Table 53: Maxima for the numbers of created hominins and groups, and maxima for the number of different possible deaths in any simulation. Color coding is per column and darker colors indicate higher scores within the column.....	210
Table 54: Relevant points in time (climate extremes) for screen capturing.....	214
Table 55: The locations of the climate recording checkpoints and their modelled LGM and current day precipitation (P) and temperature (T) values.....	214
Table 56: Contents of the HomininSpace disk.....	297

LIST OF FIGURES

Figure 1: Simulation scores in HomininSpace 1.0. Blue circles indicate some local maxima where the dynamic or ‘ebb and flow’ hominin implementation (in red) score higher than the static or ‘source and sinks’ hominins (in green).	21
Figure 2: Components and data flow in the HomininSpace simulation system.	26
Figure 3: Maximum ice sheet coverages (adapted from van Gijssel 2006, Figure 3.4). The solid red line follows the maximum limits of the Pleistocene glaciations.	29
Figure 4: Topography for western Europe, sea level lowered with 120 meters. Pink areas are now submerged. Adapted from http://topex.ucsd.edu/marine_topo/mar_topo.html , accessed 8 April 2013.	30
Figure 5: The simulation area divided into 14.948 grid cells in the SAM tool.	40
Figure 6: Bathymetry data for the simulation area (the red square), taken from the ETOPO1 dataset.	42
Figure 7: Reconstructed global sea level in meters (Y-axis), from today to 140 ka (from Bintanja and van de Wal (2008)).	43
Figure 8: Red Sea level until 140 ka adapted from the supplementary materials from Grant <i>et al.</i> (2012) converted to equidistant horizontal axis.	43
Figure 9: Overview of reconstructed global mean temperatures (Y-axis) for the last 140ky, drawn according to Bintanja and van de Wal (2008).	45
Figure 10: Interpolation of temperature values between two given data points: LGM and modern day values, with horizontally the reconstructed global mean temperature used as index for the linear interpolation.	48
Figure 11: Mean annual temperature distribution for modern day conditions.	49
Figure 12: Mean annual temperature distribution during the LGM (source CCSM).	50
Figure 13: Annual precipitation distribution for the modern day conditions.	50
Figure 14: Annual precipitation distribution during the LGM (source CCSM).	51
Figure 15: Overview of modern day (left) and LGM temperatures of the warmest month (top) and coldest month (bottom).	51
Figure 16: Relative frequency distribution for the three LGM temperature climate parameters: coldest month (top), yearly mean, and hottest month (bottom).	52
Figure 17: Schema illustrating both pathways to compute carrying capacity.	53
Figure 18: Datasets and derived equations for productivity based on temperature (left) and precipitation values. Figures reproduced from Lieth (1973), Figures 5 and 6.	55
Figure 19: Relationship between herbivore biomass (B) and net primary productivity (NAP) for different types of ecosystem (from McNaughton <i>et al.</i> (1989, Figure 1)).	56
Figure 20: Population calculations for a group with initial size 25: Pre=8, Fertile=11 and Post = 6. Mortality rates are 0.04, 0.02 and 0.08 respectively, the birthrate = 0.33.	71
Figure 21: Population composition after 50 years (left) and after 2000 years (right) with unlimited carrying capacity. Graphs visualize typical exponential growth and are created with "HomininSpace Population Calculator.xlsx", see Supplementary Materials.	72
Figure 22: Foraging ranges and resource acquisition. Larger circles are home ranges with the value of the foraging range of the groups in the centre. A value of ‘2’ means two grid cells in all directions (horizontal, vertical and diagonal) are included when foraging for resources. Black are shared grid cells.	79
Figure 23: Example illustrating the interval construction. Port Racine, two layers with dates, taken from Cliquet <i>et al.</i> (2003).	90
Figure 24: Overview of all checkpoints. Red are regular checkpoints, white monitoring checkpoints, green starting locations, pink climate monitoring points and purple plus signs are core areas.	91
Figure 25: Flowchart presenting the Initialization process in HomininSpace.	100
Figure 26: Flowchart of the Simulation process.	102
Figure 27: Calculating the ViabilityIndex for a group with 25 individuals. Code fragment is taken from the “CreateHSPParameters.R” source file.	105

Figure 28: Counting matching visits. A visit at simulation time tI matches a dated interval for a single archaeological layer (A, C and D). Only in B there is no match.	107
Figure 29: Counting matching visits. A visit at time tI can match two dated intervals that represent two archaeological layers (blue dots for layer X, red for layer Y).....	107
Figure 30: Functional representation of the implemented GA.	114
Figure 31: The Repast Symphony development environment. 1 = main menu; 2 = project directory structure; 3 = source editor; 4 = file structure; 5 = log information window.	119
Figure 32: Source code excerpt from the “HomininSpaceContextBuilder.java” class.	121
Figure 33: The Java source files in the HomininSpace development environment.	122
Figure 34: User interface of HomininSpace after initialization. On the right the Topography layer for the simulation area, on the left the scenario tree.	124
Figure 35: Values for the batch parameters provided in the Batch Parameters tab.....	125
Figure 36: Reconstructed global mean temperature relative to modern day temperatures. Tick 0 is the start of the simulations (131 ka).....	128
Figure 37: Global sea level relative to the modern day sea levels Values in meters <i>below</i> modern day level. Tick 0 is the starting point of the simulations (131 ka) with a global sea level of almost 60 meters below the level of today (0).	129
Figure 38: Google Earth view of the starting locations for the initial population.....	131
Figure 39: Climate recording checkpoint locations (pink crosses numbered 1-6).	133
Figure 40: Flowchart - main simulation routine.....	136
Figure 41: Different map types at the start of a simulation: topography (a), energy levels (b), habitat reconstruction (c) and habitat reconstruction with beaches (d).....	139
Figure 42: Death density map at the end of a simulation. Darker colors indicate more perished hominins.	139
Figure 43: Example output at the end of a simulation: hominin count (totals in dark blue, different cohort sizes underneath) through time.	140
Figure 44: Example output at the end of a simulation: group count through time.	141
Figure 45: Example output from a Climate Monitor object. Taken from “HS Climate Monitor 3 Mediterranean Habitat [x=94, y=7, 0 intervals] 21 2018-03-23 1303.txt”.	142
Figure 46: Habitat reconstruction (left) versus energy level reconstruction.	145
Figure 47: Illustrating the effect of coastal resources on population distribution.	147
Figure 48: Screenshot of simulation 1384 illustrating the patch wise foraging behavior with a varying foraging range (different sizes for the foraging squares).	151
Figure 49: Simulation results for scenario Habitat-A.	166
Figure 50: Simulation results for scenario Habitat-B.....	167
Figure 51: Simulation results for scenario Habitat-C.....	168
Figure 52: Simulation results for scenario Habitat-D.	169
Figure 53: Simulation results for scenario Habitat-E.....	170
Figure 54: Simulation results for scenario Habitat-F.	171
Figure 55: Simulation results for scenario Habitat-G.	172
Figure 56: Simulation results for scenario Habitat-H.	173
Figure 57: Simulation results for scenario Habitat-I.	174
Figure 58: Simulation results for scenario Habitat-J.....	175
Figure 59: Simulation results for scenario Energy-A.....	176
Figure 60: Simulation results for scenario Energy-B.....	177
Figure 61: Simulation results for scenario Energy-C.....	178
Figure 62: Simulation results for scenario Energy-D.....	179
Figure 63: Simulation results for scenario Energy-E.	180
Figure 64: Simulation results for scenario Energy-BR, with random walk.	181
Figure 65: Simulation results for scenario Energy-CR, with random walk.	182
Figure 66: Simulation score for scenario Energy-ER (with random walk).....	183
Figure 67: Simulation results for scenario Energy-A, batch 2.	184
Figure 68: Correlations between the different visit counting output variables for scenario Habitat-A. Top right part of the matrix contains the correlations. Three red stars indicate a significant correlation. Bottom left part are plotted values.	190
Figure 69: Explaining three parameter values used to construct Chernoff faces.	191

Figure 70: Chernoff faces representing model parameter values for all 18 scenarios, illustrating variability within the top-10 best performing models per scenario (line), with the best scoring model numbered 1 (leftmost).	193
Figure 71: Overview of sorted MatchedIntervalCoverage values for different scenarios. Simulations are sorted on score. Scores from the Standard set are colored cyan.	205
Figure 72: Overview of created_hominins and created_groups versus SimulationNumber from scenario Habitat-A. The first 1500 simulations are the Standard set.	208
Figure 73: Relation between the number of created hominins per simulation and the simulation score (scenario Habitat-A).	209
Figure 74: Depicted the numbers of groups that perished due to cold temperatures versus temperature tolerance. In orange evolved hominins, in cyan results from the Standard set (scenario Habitat-E).	211
Figure 75: Average group age for scenario Energy_B.....	211
Figure 76: Output of the simulation variables matchingVisitsWithConfidence (left) and matchingVisits (both from Scenario Energy-B).....	212
Figure 77: Reconstruction of the topography during the simulation period for selected moments in time. Lighter blue indicate higher elevation.....	216
Figure 78: Location of Climate Monitor 6 Channel (left) and the topographical output for the simulation period. Topography type 0 in the graph is water, 2 is beach and 3 is plain. ...	217
Figure 79: Habitat reconstruction for the simulation period.	219
Figure 80: Geographical positions and Habitat types for the checkpoints Climate Monitor 1 Atlantic (bottom left) and Climate Monitor 3 Mediterranean (right). Habitat type 2 is boreal forest, 3 is cool forest, 4 is cool grass, and 6 is warm grass.....	220
Figure 81: Reconstructing habitat types for the Scladina area. Results from HomininSpace (left, with HabitatType 2 = booreal forest, and 3 = cool forest) and López-García <i>et al.</i> (2017).	221
Figure 82: Reconstruction of the energy levels in the landscape for the complete simulation period. Darker colors indicate less energy.	222
Figure 83: Energy levels per year recorded by the Climate Recording Checkpoints for the whole simulation period. Blue line is for Checkpoint 1, Red for 6.	223
Figure 84: Recorded values for reconstructed temperatures per Climate Recording Checkpoint.	224
Figure 85: Recorded values for reconstructed precipitation values per Climate Recording Checkpoint.	224
Figure 86: Correlations between all visit counting output variables for scenario Habitat-A. For instance, the correlation between matchedIntervalCoverage (simulation score) and matchedIntervals (count of all matched intervals) is 0.98, and very significant (three red stars, as have all correlations).	228
Figure 87: Illustrating the bias in the checkpoint dataset: overview of the used intervals in the simulations. X-axis gives Time, with each interval defined by starting point and end point in years ago. Vertical axis is the latitude of the site.	229
Figure 88: Mapping models resulting from mutation (in green) and combination (in red). Horizontal axis the simulation number (from 1500 onwards), the Y-axis presents the simulation score. Data from the Evolved set in scenario Energy-B.....	231
Figure 89: Illustrating the effects of using coastal resources. Left simulation 1384 with coastal resources turned on (scenario Habitat-J). On the right the same simulation with coastal resources disabled (Habitat-I).	240
Figure 90: The attractiveness of coastal resources. Simulation 1365 from Scenario Energy-B but with dynamic hominins.	241
Figure 91: Overview of the average foraging range for part of the simulation period. Largest value around 9.3, minimum value around 7.0, standard deviation around 2. Figure created in HomininSpace, by calculating the average foraging range of all present groups for each time step. Simulation 1384, scenario Habitat-I, the maximum value for the foraging range is 11.	243
Figure 92: Simulation score versus maximum foraging range. For low values of the foraging range good scores are difficult to obtain. Increasing the maximum beyond 9 does not influence the score much. Values are from scenario Habitat-C.....	244

Figure 93: Illustrating the ability to cross larger waterbodies to some of the islands off the coast of France. Produced in Scenario Energy-D with dynamic hominins, simulation 1365.....	245
Figure 94: Overview of the results for the main biological values for CCSM (left) and MIROC climate models with unified colour coding schemes.....	305

LIST OF EQUATIONS

Equation 1: Relation between Temperature and Primary Productivity.....	54
Equation 2: The effect of Precipitation on Primary Productivity.....	55
Equation 3: Relation between Secondary Biomass and Net Primary Production.....	57
Equation 4: Calculation of Effective Temperature using the mean extreme temperatures.....	59
Equation 5: Computing Secondary Biomass from Primary Productivity (a, b from Table 6).....	60
Equation 6: Computing the available Secondary Biomass for hominin consumption.....	62
Equation 7: Calculating the result for Primary Productivity at time step t+1.....	63
Equation 8: Calculating the number of hominins per segment for the next time step.....	70
Equation 9: Combining interval scores for all checkpoints to compute the simulation score.....	108