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## Evaluation of Out of Africa hypotheses by means of agent-based modeling

Ericson Hölzchen <sup>a, b, \*</sup>, Christine Hertler <sup>a, b</sup>, Ingo Timm <sup>c</sup>, Fabian Lorig <sup>c</sup>

<sup>a</sup> Senckenberg Research Institute, ROCEEH, Senckenberganlage 25, 60325 Frankfurt am Main, Germany

<sup>b</sup> ROCEEH, Heidelberg Academy of Sciences, Karlstraße 4, 69117 Heidelberg, Germany

<sup>c</sup> University of Trier, Business Informatics I, 54286 Trier, Germany

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### ABSTRACT

According to the Out of Africa theory early hominins originated in Africa subsequently dispersing into Eurasia. At least two dispersal events are documented, during which Pleistocene hominins left the African continent. Out of Africa 1 refers to the early hominin dispersal prior to *Homo sapiens* (e.g. *Homo erectus/ergaster*) while Out of Africa 2 deals with the dispersal of *H. sapiens*. Many hypotheses try to explain why early hominins dispersed beyond the African continent. Suggested causes include factors such as climate, geography, vegetation, demography, competition, ecology and cognition. However, no attempt has been made yet to model the hypotheses' mechanisms explicitly in order to compare them on a quantitative scale. We therefore explore the potential of agent-based modeling. An agent-based model consists of the acting entities, the so-called agents, an environment and rules of interaction among them. We analyzed the most common Out of Africa hypotheses and systematically formalized them by aid of an agent-based modeling framework. Our results show that the most common Out of Africa hypotheses can be attributed to at least four different scenarios. We refer to the scenarios as environmental, demographic, resource driven, ecology and cognition based scenarios. Our study provides a framework that helps designing agent-based models with respect to the dispersal of early hominins out of the African continent.

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### 1. Introduction

According to the Out of Africa theory, early humans originated in Africa (Templeton, 2002). This theory is supported by fossil, archaeological and genetic evidence (Groucutt et al., 2015). In view of a worldwide distribution of humans at present, they must have dispersed beyond the African continent for at least a single time. Out of Africa dispersals can be distinguished at several separate occasions and they are associated with different *Homo* species (Groves, 2013). *Homo erectus* dispersed out of the African continent and reached as far as Indonesia in the Early Pleistocene (Bettis et al., 2009). *Homo sapiens* dispersed out of Africa at least 60,000 years ago (Armitage et al., 2011). Even earlier *H. sapiens*

dispersals out of Africa that did not lead to a permanent expansion of the distribution area around 100–130 thousand years ago are documented (Grün et al., 2005). Recent evidence from China suggests the presence of *H. sapiens* from 80 to 120 thousand years ago (Liu et al., 2015). Pleistocene dispersals where hominins dispersed out of the African continent are summarized as “Out of Africa” events. Here, we distinguish between the early pre-*H. sapiens* (*H. erectus/ergaster*) dispersals as “Out of Africa 1” and the dispersal of *H. sapiens* as “Out of Africa 2”. The mechanisms that led to Out of Africa dispersals are unknown. There are several hypotheses trying to explain the dispersals out of the African continent. They include environmental changes (Dennell, 2003; Agustí et al., 2009; Belmaker, 2009; Van der Made and Mateos, 2010; Leroy et al., 2011; Van der Made, 2011; Abbate and Sagri, 2012; Eriksson et al., 2012; Stewart and Stringer, 2012), sea level changes (Armitage et al., 2011; Lambek et al., 2011; Abbate and Sagri, 2012), demographic pressure (Dennell, 2003; Abbate and Sagri, 2012), faunal turnover events (Arribas and Palmqvist, 1999; Palombo, 2013), tectonics (King and Bailey, 2006; Bailey

\* Corresponding author. Senckenberg Research Institute, ROCEEH, Senckenberganlage 25, 60325 Frankfurt am Main, Germany.

E-mail addresses: [ericson.hoelzchen@senckenberg.de](mailto:ericson.hoelzchen@senckenberg.de) (E. Hölzchen), [christine.hertler@senckenberg.de](mailto:christine.hertler@senckenberg.de) (C. Hertler), [ingo.timm@uni-trier.de](mailto:ingo.timm@uni-trier.de) (I. Timm), [lorigf@uni-trier.de](mailto:lorigf@uni-trier.de) (F. Lorig).

and King, 2011; Reynolds et al., 2011; Winder et al., 2015), resources (Turner, 1992; Dennell, 2003; Shea, 2003; Leroy et al., 2011; Rodríguez-Gómez et al., 2013; Parton et al., 2015), technology (Carbonell et al., 2010; Agustí and Lordkipanidze, 2011) and cognition (Mellars, 2006; Klein, 2008; Tattersall, 2009; Grove et al., 2015) as well as ecology (Antón et al., 2002; Dennell, 2003; Tattersall, 2009). The relevant factors promoting the hominin dispersals out of Africa are under debate (Palombo, 2013), and the causes remain poorly understood (Rolland, 2010). For better insights, models for the formulation and testing of explicit hypotheses are required. The model which is applied most frequently in studies of hominin dispersal patterns is a reaction-diffusion model. A reaction-diffusion model is a mathematical model where the speed of range expansion of a population is predicted (Fort et al., 2004). 'Reaction' refers to population growth and 'diffusion' to dispersal. Reaction-diffusion models are also called 'wave of advance', 'Fisher-Skellam' or 'Fisher-KPP' models (Fisher, 1937; Skellam (1951); King and McCabe, 2003; Steele, 2009). In wave of advance models migratory activity is modeled as a spreading wave. Population growth and expansion are considered simultaneously. The model assumes that dispersal can be understood as a diffusion process (Ammerman and Cavalli-Sforza, 1971). This results in a wave front which spreads radially from a point of origin at a constant rate. The wave of advance model was first described by Fisher (1937). Ammerman and Cavalli-Sforza (1971, 1973) introduced the model to archeology. The main elements of a reaction-diffusion model for hominin migration are dispersal and population growth. The population growth is considered as a growth with limitation and therefore is usually modeled as a logistic growth curve (Ammerman and Cavalli-Sforza, 1984). Dispersal is considered as long distance movement of a larger group of people and is assumed to have a constant rate and to be spatio-temporally continuous (Ammerman and Cavalli-Sforza, 1984). Numerous studies applied a reaction-diffusion model to examine hominin dispersal, for example the global expansion of modern humans (Young and Bettinger, 1995), Paleolithic dispersal (Steele et al., 1998), the Neolithic transition (Fort and Méndez, 1999), to the Late Glacial human recolonization of Europe (Fort et al., 2004), the dispersal along waterways during the Neolithic (Davison et al., 2006), heterogeneous landscapes with multiple populations (Ackland et al., 2007) and the spread of farming in the Indian subcontinent (Patterson et al., 2010). The advantage of reaction-diffusion models is that they are able to compactly represent a phenomenon and allows direct calculation if the equation is solvable (Wilensky and Rand, 2015). However, a major disadvantage of such models consists of over-simplification (Wilensky and Rand, 2015). Reaction-diffusion models cannot adequately deal with high numbers of individuals with distinct features. Therefore, dispersal routes can only be approximated by wave directions and not by the tracking of individuals and their descendants. Furthermore, reaction-diffusion models are inherently continuous and thus inaccurate to describe discrete systems (Barnes and Chu, 2010). The introduction of cellular automata in paleontology was a first approach to overcome the limitations of reaction-diffusion models. Eventually, they developed into agent-based models. The cellular automaton was first proposed by Von Neumann (Von Neumann and Burks, 1966). The application of cellular automata (CA) developed very slowly (Chen et al., 2002) until Wolfram (1984) contributed to the theoretical construction of CA. The best known cellular automaton is Conway's game "life". A cellular automaton consists of a lattice/array that consist of cells (=automata/sites). Each cell has a position on the lattice and a

state. The state is changed by a transition function (=cell-transition rule/local evolution rule). This function is dependent on the cell itself and on its direct neighbors. A cellular automaton is a dynamic system with discrete time steps. Various applications of CA are listed in Balzter et al. (1998): modeling chemical reactions with spatial diffusion, development of spiral galaxies, phase transitions, crystal growth, biological and ecological systems. CA are widely applied in ecosystem modeling (Jørgensen et al., 2009). They were used for modeling the hominid dispersal out of Africa (Mithen and Reed, 2002; Nikitas and Nikita, 2005; Hughes et al., 2007). Cellular automata are similar to agent-based models except for the fact that in cellular automata there is no explicit distinction between agents and the environment. Wilensky and Rand (2015) describe them as agent-based models with stationary agents. Agents and environment are summarized in one cell. The explicit distinction between agents and environment has various advantages: multiple agents with different features can be represented on one patch while in cellular automata this can only hardly be accomplished. Moreover, changing the features in a cellular automaton is more difficult because one has to consider not to change the environment. In agent-based modeling, agents and environment can be modified independently. Agent-based modeling is a widely used method in modeling and simulating artificial societies (Davidsson, 2002). An agent-based model consists of agents, an environment and rules of interaction between the entities. Agent-based modeling is well suited to study emergent phenomena that are based on simple rules (Timm et al., 2006). Moreover, agent-based modeling is the appropriate tool to simulate heterogeneous entities, stochastic effects and interactions (Barnes and Chu, 2010). The models presented in Mithen (1987, 1990) are perhaps the most recent agent-based models which were not called agent-based models (Lake, 2015). In these models, the agent learns about the environment and uses this knowledge in decision-making (Lake, 2015). Lake (2000) presented an agent-based model to simulate Mesolithic foraging. The program is called MAGICAL (Multi-Agent Geographically Informed Computer Analysis). MAGICAL allows exploring what individuals might have been thinking in order to produce an observed behavior. In this model, the agents may behave differently according to age, gender and social standing. Consequently, three elements of human cognition are modeled. These are individual learning, cultural learning and decision making. New to this model is that these elements are applied to spatially referenced data. The agent's properties include energy level, current rate of return on foraging, various kinds of search and the exchange of information. Individuals rationally calculate the benefit of a movement to a location of the landscape. The agent's energetic state decreases when moving and increases when resources are captured. The agent's spatial knowledge is modeled explicitly. Group behavior emerges from individual behavior, and agents can conduct their own mental simulations. The feature of genotype mechanism allows the users to build their own simulation models. They can decide what properties and actions the agents shall have. One simulation example is the use of MAGICAL to examine whether the Mesolithic flint artifacts on the Southern Hebridean Island could be explained by small groups landing on the coast and foraging for Hazelnut. Agent-based modeling was then further improved as a tool for exploring hominin dispersal (Dallmeyer et al., 2010; Griffith et al., 2010; Barton and Riel-Salvatore, 2012; Callegari et al., 2013; Romanowska, 2013; Wren et al., 2014).

We systematically formalize Out of Africa hypotheses by representing them in an agent-based modeling framework. We

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